

**ICHNOTAXONOMY AND PALEOENVIRONMENTAL ANALYSIS OF TRACE
FOSSILS IN THE LATE DEVONIAN CATSKILL FORMATION, NORTH-CENTRAL
PENNSYLVANIA, USA**

**A thesis submitted to the Department of Geology
of the University of Kansas
in partial fulfillment of the requirements for the degree
Master of Science in Geology**

Wade Tyler Jones

B.S. *cum laude*, with honors, St. Lawrence University, 2008

Advisory committee:

Stephen T. Hasiotis, Chair

Paul A. Selden

Anthony W. Walton

Date defended _____

**The thesis committee for Wade T. Jones certifies
that this is the approved version of the following thesis:**

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ABSTRACT

The purpose of this thesis is to interpret the ichnotaxonomy, paleoenvironmental distribution, and paleoecological ramifications of trace fossils from the Frasnian–Famennian Catskill Formation (CF), north-central Pennsylvania, USA. The CF contains a suite of approximately 14 traces, 11 of which represent animal behavior, and 3 of which represent preservational styles and morphologies of plant roots. CF traces occur in paleosols and strata exhibiting no evidence of pedogenesis. Paleosol traces represent terraphilic to hydrophilic soil biota. Traces in strata with no evidence of pedogenesis represent aquatic organism behavior. Backfilled burrows—*Beaconites antarcticus* and *B. barretti*—represent dwelling and feeding by soil-dwelling arthropods. Rhizoliths represent shallow to deep rooting by plants with terraphilic–hydrophilic affinities. Backfilled burrows and rhizoliths form a characteristic ichnofabric that is superimposed on all pedogenically modified deposits. Lungfish estivation burrows—*Hypero euthys teichonomos*—are commonly superimposed on and subsequently overprinted by the dominant ichnofabric. *Diplichnites gouldi* is present in weakly developed paleosols and represents locomotion of an arthropod of unknown taxonomic affinity. *In situ* stump casts occur in paleosols of differing maturity and likely represent the life position of an arborescent plant. *Camborygma eumekonomos* and *C. litonomos* represent dwelling burrows of terraphilic to hydrophilic arthropods and are also overprinted by the dominant ichnopedofabric. Bivalve resting (*Lockeia siliquaria*), locomotion (*Lockeia ornata*), and escape traces, as well as fish swimming traces (*Undichna multiloba*), and *Sagittichnus lincki*—the resting trace of an unknown organism—represent aquatic organism behavior. The presence of terraphilic to hydrophilic and hydrophilic traces in CF paleosols indicates that Late Devonian soil organisms exhibited nearly as much behavioral complexity as Mesozoic–recent soil organisms. The abundance and degree

of trace crosscutting increases in increasingly mature paleosols, indicating that CF paleosol ichnoassemblages, despite being controlled by paleohydrology, also represent ecological succession. Continental organisms are known exhibited behaviors that beneficially modify their environment (ecosystem engineering) by modulating resource flow paths (allogenic engineering) or modifying their bodies in ways that create new habitats for themselves (autogenic engineering). The idea that middle Paleozoic continental organisms were ecosystem engineers has not been examined. Our data suggest that the inception of allogenic ecosystem engineering in continental environments had occurred by the Late Devonian.

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“Those who believe in telekinetics, raise my hand.”

Kurt Vonnegut

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION.....	1
CHAPTER 2: ICHNOTAXONOMY AND PALEOENVIRONMENTAL ANALYSIS OF TRACE FOSSILS IN THE UPPER DEVONIAN CATSKILL FORMATION, NORTH- CENTRAL PENNSYLVANIA, USA.....	15
CHAPTER 3: PALEOENVIRONMENTAL DISTRIBUTION OF TRACE FOSSILS IN THE FRASNIAN–FAMENNIAN CATSKILL FORMATION, NORTH-CENTRAL PENNSYLVANIA, USA: AN ASSESSMENT OF A LATE DEVONIAN SOIL ECOSYSTEM AND INITIATION OF ECOSYSTEM ENGINEERING BY MIDDLE PALEOZOIC SOIL BIOTAS.....	106
CHAPTER 4: LUNGFISH BURROWS OF THE UPPER DEVONIAN CATSKILL FORMATION, NORTH-CENTRAL PENNSYLVANIA, USA: MORPHOLOGICAL DISTINCTION AND EVOLUTIONARY IMPLICATIONS.....	182
CHAPTER 5: CONCLUSION.....	228

LIST OF TABLES AND FIGURES

FIGURES:

FIGURE 1—Map of Clinton and Lycoming Counties, Pennsylvania, with localities examined during this study.....	21
FIGURE 2— Measured section at Powys Curve showing stratigraphic position of traces.....	22
FIGURE 3— Measured section at Trout Run showing stratigraphic position of traces.....	25
FIGURE 4— Measured section at Red Hill showing stratigraphic position of traces.....	26
FIGURE 5—Diagram of the root rank ordering and angle measurement scheme modified from Fitter (1987); rank order of a root=the number of branches emanating from the root.....	27
FIGURE 6— <i>Beaconites antarcticus</i> ; Scale=5 mm. A. Closeup of <i>Beaconites antarcticus</i> in slabbed section. B. Line drawing of 4A showing backfill packets. C. Close-up of subhorizontal <i>Beaconites antarcticus</i> . D. Close-up of subvertical <i>Beaconites antarcticus</i> in cross section. E. Close-up of <i>Beaconites antarcticus</i> crosscutting a rhizoliths. F. Line drawing of 4D showing burrow lining. G. Rhizolith crosscutting <i>Beaconites antarcticus</i> . H. <i>Beaconites antarcticus</i> in thin section. I. Line drawing of 4H showing backfill packets and lining. J. Multiple <i>Beaconites antarcticus</i> and rhizoliths on a very fine sandstone slab.....	28
FIGURE 7— Maximum vs. minimum diameter of <i>Beaconites antarcticus</i>	32
FIGURE 8— <i>Beaconites barretti</i> ; scale=10 mm. A. Subhorizontal <i>Beaconites barretti</i> with well-defined arcuate menisci, Powys Curve. B. Several <i>Beaconites barretti</i> and multiple rhizoliths on a slab of very fine sandstone, Powys Curve. C. Line drawing of 9A showing burrow outline and menisci. D. Subvertical <i>Beaconites barretti</i> in a vertic claystone, Powys Curve. E. Horizontal <i>Beaconites barretti</i> in a very fine sandstone, Trout Run. F. Interpretive drawing of 8E.....	37

FIGURE 9— Minimum vs. maximum diameter of <i>Beaconites barretti</i>	38
FIGURE 10— <i>Camborygma eumekonomos</i> and <i>C. litonomos</i> ; scale= 10 mm. A. <i>C. litonomos</i> in outcrop, Red Hill. B. Cross section of <i>C. litonomos</i> ; L= lining; F= fill. C. Closeup of <i>litonomos</i> in outcrop; Ba= <i>Beaconites antarcticus</i> . D. Surficial morphology of <i>C. litonomos</i> . E. Closeup of <i>C. eumekonomos</i> . F. Interpretive line drawing of E. G. <i>C. eumekonomos</i> in outcrop, Red Hill.....	44
FIGURE 11— <i>Diplichnites gouldi</i> ; scale=10 mm. A. <i>Diplichnites gouldi</i> type 1. B. Large <i>Diplichnites gouldi</i> type 2. C. <i>Diplichnites gouldi</i> type 2 track. D. Line drawing of <i>Diplichnites gouldi</i> type 2 track. E. <i>Diplichnites gouldi</i> type 1 track. F. Line drawing of <i>Diplichnites gouldi</i> type 1 track. G. Small <i>Diplichnites gouldi</i> type 2.....	48
FIGURE 12— <i>Hypero euthys teichonomos</i> ; scale=10 mm. A. <i>H. teichonomos</i> in a slab of very fine sandstone, Trout Run. B. Large, nearly complete <i>H. teichonomos</i> , Steam Valley. C. Terminus of <i>H. teichonomos</i> , Trout Run. D. Nearly complete <i>H. teichonomos</i> , Powys Curve. E. <i>H. teichonomos</i> with well-defined lining and fill. F. Line drawing of E. G. Shaft pieces of <i>H. teichonomos</i> , Powys Curve.....	51
FIGURE 13— Bivalve burrows; scale=20 mm. A. Multiple <i>Lockeia siliquaria</i> on the sole of a fine sandstone bed, Steam Valley. B. Multiple <i>Lockeia ornata</i> and <i>Pleurocurvus arenaorte</i> on the sole of a very fine sandstone bed, crosscutting a fabric of flute casts, Trout Run. C. Line drawing of D. D. <i>Pleurocurvus arenaorte</i> , Trout Run. E. <i>Lockeia ornata</i> on the sole of a very fine sandstone bed, Trout Run. F. <i>Pleurocurvus arenaorte</i> from the sole of the very fine sandstone bed, Trout Run. G. Cross section of <i>Lockeia ornata</i> , Trout Run. H. <i>Pleurocurvus arenaorte</i> on the sole of a bed, Trout Run.....	59

FIGURE 14— <i>Sagittichnus lincki</i> ; scale=5 mm. A. Multiple <i>Sagittichnus lincki</i> on the sole of a very fine sandstone block, Powys Curve. B. Close-up of <i>Sagittichnus lincki</i> —same block as 14A. C. Close-up of <i>Sagittichnus lincki</i> —same block as 14A.....	62
FIGURE 15— <i>Undichna multiloba</i> ; scale=10 mm. A. The Holotype with discontinuous <i>Undichna multiloba</i> and <i>Sagittichnus lincki</i> . B. The Paratype with discontinuous <i>Undichna multiloba</i> . C. Line drawing of 12A. D. The Holotype with continuous <i>Undichna multiloba</i>	66
FIGURE 16— Interpretive drawing of <i>Undichna isp.</i> production.....	67
FIGURE 17—Rhizoliths; scale=5 mm. A. Clay-filled, hematite-rich rhizoliths penetrating a very fine sandstone bed, Powys Curve. B. Closeup of a clay-filled, hematite-rich rhizoliths, Trout Run. C. Rhizohalo, Steam Valley. D. Carbonate rhizocretions in thin section, Trout Run. E. Line drawing of B showing branching pattern of rootlets. F. Clay-filled, hematite-rich rhizoliths, Powys Curve. G. Cross section of small rhizohaloes in thin section, Powys Curve. H. Cross section of carbonate-cored, clay-filled hematite-rich rhizoliths, Powys Curve; M=micrite, C=hematite-rich clay, S=sparry calcite.....	77
FIGURE 18— <i>In situ</i> stump casts. A. <i>In situ</i> stump cast with taproot, Red Hill. B. Interpretive line drawing of A. C. <i>In situ</i> stump cast without taproot, Red Hill.....	80
FIGURE 19—Map of Clinton and Lycoming Counties, Pennsylvania with localities examined during this study.....	113
FIGURE 20—Diagram of the root rank ordering and angle measurement scheme modified from Fitter (1987); rank order of a root=the number of branches emanating from the root.....	114
FIGURE 21—Finely laminated mudstone-sandstone interbeds; Ba= <i>Beaconites antarcticus</i> ; Rh=rhizolith; scale=10 mm. A) Finely laminated siltstone crosscut by <i>Beaconites antarcticus</i> , Powys Curve, PA. B) Finely laminated siltstone crosscut by <i>Beaconites antarcticus</i> , and clay-	

filled hematite-rich rhizoliths, Powys Curve, PA. C) Finely laminated mudstone, Powys Curve, PA. D) Oscillation Ripples in Finely laminated mudstone, Powys Curve, PA.....116

FIGURE 22—Weakly laminated—platy mudstone-sandstone interbeds; Ba=*Beaconites antarcticus*; Rh = rhizolith; scale bar =10 mm. A) *Camborygma eumekonomos* in platy mudstone, Red Hill. C) Platy mudstone with a prominent pseudoanticline, crosscut by *Camborygma litonomos*., Red Hill. D) Platy mudstone crosscut by *Beaconites barretti*, Powys Curve. E) Platy mudstone crosscut by a lungfish estivation burrow, Red Hill.....120

FIGURE 23—Trough cross-stratified, scour-based sandstones. A) Trout Run. B) Steam Valley. C) Trout Run. D) Powys Curve.....123

FIGURE 24—Thoroughly homogenized vertic claystones; Ba=*Beaconites antarcticus*, Pa=Pseudoanticline; Pc=Pedogenic carbonate; RH=rhizohalo, CR=carbonate rhizocretions, Cl=clayskin, AB= angular blocky ped, Clr- clayfilled rhizoliths. carbonate; scale bar=10 mm. A) Rhizohalo in a vertic claystone with well developed angular blocky peds, Steam Valley. B) Vertic claystone with angular blocky peds crosscut by *Beaconites antarcticus*, Red Hill. C) Pseudoanticlines in a Vertisol, Red Hill. D) Slabbed section of a vertic claystone paleosol; RH=rhizohalo, CR=carbonate rhizocretions, BF=backfilled burrow, Cl= clayskin, AB= angular blocky ped, Clr- clayfilled rhizoliths. E) *Camborygma litonomos* and backfilled burrows crosscutting a vertic claystone, Red Hill. F) Horizonation in a vertic claystone paleosol, Steam Valley. G) Horizonation in a vertic claystone paleosol, Red Hill.....126

FIGURE 25—*Beaconites antarcticus* and *Beaconites barretti* Ba=*Beaconites antarcticus*; Bb=*Beaconites barretti*; Rh=rhizolith; scale=10 mm. A) Polished slab of siltstone crosscut by *Beaconites* and rhizoliths. B) Interpretive line drawing of A. C) Polished slab of very fine sandstone crosscut by multiple *Beaconites antarcticus* and rhizoliths. D) Interpretive line

drawing of C. E) Multiple <i>Beaconites barretti</i> and rhizoliths on a slab of very fine-grained sandstone, Trout Run. F) Multiple <i>Beaconites antarcticus</i> crosscutting a block of very fine sandstone, Powys Curve.....	129
FIGURE 26—CF bivalve burrows; scale=1 cm. A) <i>Lockeia ornata</i> , Trout Run. B) Bivalve equilibrichnium, Trout Run. C) <i>Lockeia siliquaria</i> , Steam Valley.....	130
FIGURE 27—CF <i>Diplichnites gouldi</i> ; scale bar=10 mm. A) Large Type 2 <i>Diplichnites gouldi</i> , Trout Run. B) Type 1 <i>Diplichnites gouldi</i> , Steam Valley.....	136
FIGURE 28—Lungfish estivation burrows; Ba= <i>Beaconites antarcticus</i> ; Rh=rhizolith; scale=10 mm. A) Nearly complete shaft with a robust wall lining, Trout Run. B) Terminus <i>in situ</i> , Trout Run. C) Small shaft with robust wall lining in cross-section, Trout Run. D) Terminus crosscut by <i>Beaconites antarcticus</i> and clay-filled hematite-rich rhizoliths, Powys Curve. E) Portion of shaft in cross-section, crosscut by rhizoliths, Powys Curve.....	139
FIGURE 29— <i>Sagittichnus lincki</i> and <i>Undichna multiloba</i> ; S= <i>Sagittichnus</i> ; U= <i>Undichna</i> ; scale=1 cm. A) <i>Sagittichnus lincki</i> and continuous <i>Undichna multiloba</i> , Powys Curve, PA. B) <i>Sagittichnus lincki</i> and discontinuous <i>Undichna multiloba</i>	142
FIGURE 30—Rhizoliths; scale=10 mm. A) Clay-filled hematite-rich rhizoliths in finely laminated siltstone, Red Hill. B) Thin section of a clay-filled hematite-rich rhizolith cored with quartzose silt and pedogenic carbonate, Powys Curve. C) Rhizohalo in vertic claystone paleosol, Powys Curve. D) Rhizohaloes in vertic claystone, Red Hill, PA. E) Carbonate rhizocretions in platy claystone, Powys Curve.....	149
FIGURE 31—Block diagrams of paleosol ichnocoenoses with facies occurrences and interpreted environments.....	152
FIGURE 32—Block diagram of aquatic ichnocoenoses with facies occurrences and interpreted	

environments.....	159
FIGURE 33—Diagram illustrating inferred ecosystem engineering activities of CF soil biota.....	167
TEXT-FIG. 34—Generalized stratigraphy of our field area.....	187
TEXT-FIG. 35—Location of study outcrops.....	189
TEXT-FIG. 36—Measured sections at Trout Run and Red Hill, Pennsylvania showing the occurrence of the Catskill Formation burrows and associated traces.....	190
TEXT-FIG. 37—Explanatory drawing of burrow dimensions, and morphological features.....	192
TEXT-FIG. 38—Catskill Formation burrow architectural and surficial morphologies; scale= 10 mm; A) The holotype, KUVVP152145; T= terminus; S= shaft; B) The terminal end of the Holotype in cross-section; C) A portion of shaft with multiple wall-linings in cross-section, KUVVP152157; F= fill; L= lining; D) A burrow terminus in cross-section, KUVVP152154; Rh= rhizolith; Ba= <i>Beaconites antarcticus</i> ; E) A portion of burrow shaft cross-cut by pedogenic carbonate nodules, KUVVP152187; PC= pedogenic carbonate; F) A portion of burrow shaft in cross-section with an indistinct wall lining, KUVVP152183; G) Same burrow as F showing well- preserved surficial morphology; H) A close-up of G; arrows indicate surficial striations; I) A portion of burrow shaft with well-preserved surficial morphology; arrows indicate surficial striations, KUVVP152179.....	197
TEXT-FIG. 39—CATSKILL FM. Large diameter burrow architectural and surficial morphologies; scale=10 mm; A) A large portion of burrow shaft with a distinct wall-lining, Trout Run; B) Interpretive drawing of B; C) The holotype in outcrop before collection, Powys Curve; T= terminus; S= shaft; D) A portion of burrow shaft in cross-section with a line-tracing of the lining-fill boundary, KUVVP152194; L= lining; F= fill; E) A burrow terminus,	

KUVP152178; F) A complete burrow in outcrop, Steam Valley; T= terminus; S= shaft; G) A portion of burrow shaft with multiple distinct wall-linings in transverse section, KUVP152157;	
H) A portion of burrow shaft cross-cut by <i>Beaconites antarcticus</i> and rhizoliths, KUVP152166;	
Ba= <i>Beaconites antarcticus</i> ; Rh= rhizolith; I) A portion of burrow shaft in cross-section crosscut by <i>Beaconites antarcticus</i> and rhizoliths, KUVP152184; Ba= <i>Beaconites antarcticus</i> ; Rh= rhizolith; J) A portion of burrow shaft cross-cut by <i>Beaconites antarcticus</i> and rhizoliths, KUVP152194; Ba= <i>Beaconites antarcticus</i> ; Rh = rhizolith.....	199
TEXT-FIG. 40— Scatterplot of long and long and short diameter of the Catskill Formation burrows.....	201
TEXT-FIG. 41— <i>Gnathorhiza</i> burrows from the Lower Permian Blue Springs Shale Member; scale=10 mm—A) Complete burrow; S=shaft; T=terminus; B) Terminus in cross section; C) Segment of shaft in cross section; F= fill; L=lining.....	213
TEXT-FIG. 42—Lungfish burrows architectural morphologies; scale bar= 10 mm; A–C redrawn from Hasiotis et al. (1993); D redrawn from Romer and Olson (1954).....	214
TEXT-FIG. 43—Modern lungfish burrow architectural morphologies, redrawn from Kerr (1898).....	215
TEXT-FIG. 44—Scale bar= 10 mm; A) Crayfish burrow architectural morphologies from the Upper Triassic Chinle Formation; after Hasiotis et al. (1993); B) Holotype of <i>Macanopsis pagueyi</i> , redrawn from Macsotay, 1967; C) <i>Psilonichnus</i> architectural morphologies, redrawn from Frey et al. (1984); D) Architectural morphology of lysorophid burrows, redrawn from Hembree et al. (2004).....	219

TABLES:

TABLE 1—Locations from which lungfish skeletal material has been recovered; * indicates localities where we found <i>Hyperoethys teichonomos</i>	52
TABLE 2—Associations of lithofacies, sedimentary structures, pedogenic features, and trace fossils.....	118
TABLE 3—Previous studies of lungfish estivation burrows.....	208

CHAPTER 1. INTRODUCTION

This thesis aims to assess the ichnotaxonomy, paleoenvironmental distribution, and evolutionary implications of trace fossils from the Frasnian–Famennian Catskill Formation (CF) of north-central Pennsylvania, USA. Contained herein are 3 chapters that: 1) ichnotaxonomically assess the trace fossil assemblage of the CF; 2) assess the paleoenvironmental distribution of CF trace fossils; 3) interpret the tracemakers and behaviors represented by CF trace fossils; and 4) provide a detailed description, interpretation, and ichnotaxonomic framework for CF lungfish estivation burrows, which have long been in need of reevaluation.

The purpose of chapter 2 is to ichnotaxonomically assess the trace fossils of the Frasnian–Famennian CF, as well as to document their paleoenvironmental occurrences in CF deposits and alluvial paleosols. We describe an assemblage of 14 traces, 11 of which represent disparate behaviors of animals that inhabited the CF alluvial plain, and 3 of which represent preservational styles and architectural morphologies of plant roots. The CF trace fossil assemblage indicates that the organisms inhabiting the CF alluvial plain exhibited a high degree of trophic and environmentally dependent behavioral specialization, which has not been previously recognized in Devonian continental trace fossil assemblages.

Nearly all CF ichnotaxonomic work is greater than 20 years old, and no complete ichnotaxonomic assessment of CF alluvial traces has been conducted. Gordon (1988) assessed the ichnotaxonomy and paleoenvironmental occurrence of trace fossils from the Middle to Late Devonian Catskill Magnafacies (CM) of New York. Berg (1972), Thoms and Berg (1985), Bridge et al. (1986), and Driese et al. (1997) made assessments of CF and CM bivalve burrows,

rhizoliths, and *in situ* progymnosperm stump casts, respectively. CF traces have not been evaluated in the context of the modern understanding of continental ichnology, however (e.g., Bown and Kraus, 1983; Smith, 1993; Smith and Mason, 1998; Hasiotis, 1998, 2002, 2003, 2004, 2007, Hembree and Hasiotis, 2007, 2008; Hasiotis, 2008; Smith et al., 2008).

Analysis of CF traces indicates that the distribution of Devonian continental organisms was controlled by paleohydrology, and that continental organisms contributed greatly to the pedogenic process, as has been observed in Mesozoic to recent continental ecosystems (e.g., Hasiotis, 2002, 2007; Hasiotis et al., 2007).

Siluro-Devonian continental trace fossils have historically been considered to be shallowly penetrative, of low diversity, and representative of simple, unspecialized behaviors (e.g., Buatois et al., 1998). Trace and body fossil evidence suggests that invertebrates and plants colonized land during the Late Ordovician (Retallack and Feakes, 1987; Johnson et al. 1994; Retallack, 2001; Shear and Selden, 2001), however contentious this evidence may be (e.g., Davies et al., 2010). By the Late Devonian, continental organisms had been evolving separate from marine organisms for as much as 100 million years, and a minimum of ~70 million years (Selden and Edwards, 1989; Shear and Kukulová-Peck, 1990). We hypothesize that CF traces should exhibit a high degree of specialization, reflecting evolution of continental organisms since that time. Our findings are consistent with that hypothesis.

The purpose of chapter 3 is to assess the facies distribution, paleoecology, and paleopedologic associations of alluvial trace fossils in the Late Devonian Catskill Formation (CF), north-central Pennsylvania, USA. Previous studies of Devonian continental ichnoassemblages (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004) have assessed the ichnotaxonomy and facies distribution of Devonian continental

ichnoassemblages, as well as the behaviors that they represent. These studies, however, did not examine Devonian continental traces in the context of our most recent understanding of the controls on continental trace fossil distribution, especially with respect to the contributions that soil-dwelling organisms make to the pedogenic process.

CF alluvial deposits contain a moderately diverse suite of traces, representing behaviors characteristic of continental organisms. Backfilled burrows, rhizoliths, and lungfish estivation burrows occur in nearly all pedogenically modified CF alluvial deposits. We interpret these traces to represent the behavior of soil-dwelling organisms. CF arthropod trackways (*Diplichnites gouldi*) represent locomotion of arthropods on undeveloped to poorly developed CF paleosols. Bivalve traces, fish swimming traces, and cubichnia produced by an unknown tracemaker (*Sagittichnus lincki*) represent the behavior of aquatic organisms that lived in CF fluvial channels.

Continental trace fossil distribution is controlled by factors distinct from those that control the distribution of marine traces (Smith, 1993; Smith and Mason, 1998; Hasiotis, 2002, 2007; Hembree and Hasiotis, 2007; Hasiotis, 2008; Hembree and Hasiotis, 2008; Smith et al., 2008). The most important of these is the level of the water table, which is largely responsible for vertical tiering of burrowing, soil-dwelling organisms (Hasiotis, 2002, 2007). Hasiotis (2002, 2007) categorized soil organisms by their relationship of burrowing depth to the depth of the water table. Soil organism distribution is also controlled by soil oxygenation and nutrient availability, which can be solely a function of the environment, or substantially modified by densely distributed soil-dwelling organisms (Villani et al., 1999).

Hydrophilic organisms burrow below the water table to fulfill physiological moisture needs (Hasiotis 2002, 2007). For similar reasons, hygrophilic organisms remain in the lower

vadose zone, where soil is consistently moist, and terraphilic organisms remain in the vadose zone. The CF trace fossil assemblage suggests that Late Devonian continental organisms exhibited behaviors characteristic of all three behavioral categories of Hasiotis (2002, 2007). This indicates that middle Paleozoic soil organism behavior was nearly as sophisticated as that of Mesozoic to recent soil organisms.

Soil organism behavior has also been categorized based on organisms' residence times in soil. Residence time of soil organisms varies depending on the life cycle and life habits of juvenile and adult forms of an organism (Wallwork, 1970; Hasiotis, 2002, 2007). The CF ichnoassemblage documents the behavior of temporary, transient, and periodic soil organisms, *sensu* Wallwork (1970), and Hasiotis (2002, 2007).

Bioturbation by soil biotas is recognized as a major contributor to pedogenesis in Mesozoic–recent continental environments via modifications of soils that affect their physical, chemical and biotic properties (Reichle, 1977; Lavelle et al., 1992; Chauvel et al., 1999; Konaté et al., 1999; Dauber et al., 2001; Hasiotis, 2003; Johnson et al., 2005; Jouquet et al., 2006; Lavelle et al., 2006). Soil organisms modify soil properties so significantly that they strongly influence spatial and temporal heterogeneity of biomass and species distribution (Lavelle et al., 1992; De Deyn et al., 2003; Jouquet et al., 2006; Lavelle et al., 2006).

Organisms that substantially beneficially modify their physical environment have been termed ecosystem engineers by Jones et al. (1994). Jones et al. (1994) established two categories for ecosystem engineers: 1) allogenic engineers, which modify the physicochemical environment by modulating one or more resource flow paths (e.g., beavers blocking stream flow to create large, semi-permanent wetlands); and 2) autogenic engineers, which modify the environment by

modifying their own bodies (e.g., trees blocking sunlight, which creates shady patches that benefit their own root system in addition to creating habitat for understory vegetation).

Evidence of ecosystem engineering in Mesozoic–recent continental (predominantly soil) environments, by social insects and other arthropods is common (Hasiotis, 2002, 2003, 2007; Jouquet et al., 2006; Jones et al., 2006). Fossil evidence of ecosystem engineering is predominantly evidence of allogenic engineering by modification of soil pore space, and improvement of soil drainage via creation of macropores and macrochannels by plants and soil-dwelling invertebrates and vertebrates (Hasiotis 2002, 2003, 2007; Hasiotis et al., 2007). The idea that Devonian continental organisms may have been ecosystem engineers has not been examined, however. We also assessed CF trace fossils as potential evidence of ecosystem engineering by Devonian soil biota. Trace fossil evidence from the CF suggests that soil ecosystem engineering by plants and animals was both prevalent, and influential on community structure and biomass distribution by the Late Devonian.

The purpose of chapter 4 is to compare large-diameter, subvertical–vertical burrows of the CF with other large-diameter vertical and subvertical burrows in order to: 1) interpret the tracemaker; 2) interpret the behavior represented by the burrows; and 3) establish their ichnotaxonomy. CF large-diameter, vertical to subvertical burrows exhibit architectural and surficial morphology that suggests that they represent lungfish (Dipnoi) estivation—a state of dormancy in response to seasonal drought. Catskill Formation large-diameter burrows, however, are not known to contain lungfish skeletal material, as is true of many fossil lungfish estivation burrows reported in the literature (e.g., Romer and Olson, 1954; Carlson, 1968; Olson and Bolles, 1975; Dalquest and Carpenter, 1977; Hasiotis, 2002).

Here we provide architectural and surficial morphological evidence that the CF large-

diameter burrows are most likely lungfish estivation burrows. We compare CF large-diameter burrows to estivation burrows of the Permian lungfish *Gnathorhiza*, many of which contain lungfish skeletal material, as well as to late Paleozoic burrows interpreted as lungfish burrows and to estivation burrows of the modern lungfishes *Protopterus* and *Lepidosiren*. We also compare CF large-diameter burrows to decapod burrows (*Camborygma* isp., and *Psilonichnus* isp.), and *Macanopsis* isp., all of which exhibit morphological similarity to CF large-diameter burrows.

The morphological uniqueness of CF lungfish burrows and other lungfish estivation burrows from ichnotaxa interpreted to represent other behaviors and tracemakers indicates that they merit the erection of a new ichnogenus and one or more new ichnospecies (e.g., Hasiotis et al., 2002). The presence of lungfish estivation burrows in the Frasnian–Famennian CF is significant, because this trace fossil evidence extends the evolutionary timing of vertebrate estivation by more than 57 million years. The previous earliest well-documented lungfish estivation burrows are early Pennsylvanian in age (Carroll, 1965).

Lungfish skeletal material in the form of tooth plates and cranial bone is known to occur rarely in the CF, including at the sites investigated during this study (Daeschler and Mullison, 2004; Friedman and Daeschler, 2006). Catskill Formation large-diameter burrows have, in fact, long been recognized as probable lungfish estivation burrows (Woodrow and Fletcher, 1969; Hasiotis et al., 1999). The lack of preservation of skeletal material in these burrows, however, has led researchers to doubt whether or not they are truly lungfish estivation burrows (e.g., Daeschler and Mullison, 2004; Friedman and Daeschler, 2006).

Catskill Formation claystone paleosols exhibit well developed pedogenic carbonate horizons, pedogenic slickensides, and pseudoanticlines (Woodrow et al., 1973; Driese et al.,

1993). These indicate that the CF alluvial plain experienced pronounced wet-dry seasonality. The presence of wet-dry seasonality in the CF is consistent with the need for lungfish to aestivate, and is further consistent with the climatic conditions under which modern lungfish aestivate (Kerr, 1898; Carter and Beadle, 1930; Johnels and Svernnson, 1954; Bouillon, 1961; Greenwood, 1987; Hembree, 2010).

The results of this thesis indicate that the trace fossils of the CF represent highly specialized behaviors of hygrophilic to terraphilic and hydrophilic soil-dwelling animals, as well as aquatic animals that inhabited CF fluvial channels. Three distinct rhizolith morphotypes are further recognized, representing rooting by plants with terraphilic to hydrophilic affinities. Our results further indicate that CF trace fossils represent temporary, transient, and periodic soil organisms. The presence of hygrophilic to terraphilic, hydrophilic, temporary, transient, and periodic soil biota in the CF indicates that Devonian continental organisms exhibited nearly as much behavioral specialization as Mesozoic to recent continental organisms (Bown and Kraus, 1983; Smith, 1993; Smith and Mason, 1998; Hasiotis, 1998, 2002, 2003, 2004, 2007, Hembree and Hasiotis, 2007, 2008; Hasiotis, 2008; Smith et al., 2008).

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CHAPTER 2. ICHNOTAXONOMY AND PALEOENVIRONMENTAL ANALYSIS OF TRACE FOSSILS IN THE UPPER DEVONIAN CATSKILL FORMATION, NORTH- CENTRAL PENNSYLVANIA, USA

WADE T. JONES*, STEPHEN T. HASIOTIS

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ABSTRACT.—We assess the ichnotaxonomy and paleoenvironmental occurrence of trace fossils of the Frasnian–Famennian Catskill Formation (CF) in north-central Pennsylvania, USA. We identified 14 distinct trace fossil morphotypes: eleven record unique animal behaviors and three represent different morphotypes and preservation of plant roots. Trace occurrences and associations in incipient (Protosols) and moderate to well-developed (Vertisols and Argillisols) paleosols represent colonization of alluvial floodplains by plants and animals. The dominant ichnopedofabric is composed of 3–60 mm diameter backfilled burrows—*Beaconites antarcticus* and *Beaconites barretti*—and 1–50 mm diameter rhizoliths. Backfilled burrows represent dwelling and feeding by soil-dwelling arthropods of unknown taxonomic affinity. Rhizoliths represent shallow to deep rooting by plants in actively forming soils. Lungfish estivation burrows—*Hypero euthys teichonomos*—represent transient soil biota and commonly are superimposed on the *Beaconites*-dominated ichnofabric. Lungfish estivation burrows were subsequently overprinted by the *Beaconites*-dominated ichnopedofabric. *Diplichnites gouldi* is present in weakly developed paleosols and represents locomotion of an arthropod of unknown taxonomic affinity. *In situ* stump casts occur in paleosols of differing maturity and likely represent the life position of the arborescent progymnosperm *Archaeopteris*. *Camborygma*

eumekonomos and *C. litonomos* represent dwelling burrows of hydrophylic organisms, possibly soil-dwelling arthropods. These burrows are also overprinted by the dominant ichnopedofabric. Bivalve resting (*Lockeia siliquaria*), locomotion (*Lockeia ornata*) and escape traces, as well as fish swimming traces (*Undichna multiloba*), and *Sagittichnus lincki*—the resting trace of an unknown organism—represent behavior of aquatic organisms. The disparity, and degree of behavioral specialization represented by CF traces indicates that continental organisms in the Late Devonian exhibited behaviors nearly as complex as those exhibited by Mesozoic to recent continental organisms.

INTRODUCTION

The purpose of this paper is to ichnotaxonomically assess the trace fossils of the Frasnian–Famennian Catskill Formation (CF) of north-central Pennsylvania, U.S.A., and to document their paleoenvironmental occurrences in CF deposits and alluvial paleosols. We here describe an assemblage of 14 traces, representing disparate behaviors and preservational styles of rhizoliths that suggest a high degree of trophic and environmentally dependent behavioral specialization of continental invertebrates, vertebrates, and plants by the Late Devonian.

The majority of CF ichnotaxonomic work is greater than 20 years old, and no complete ichnotaxonomic assessment of CF alluvial traces has been completed. Gordon (1988) assessed the ichnotaxonomy and paleoenvironmental occurrences of traces from the Middle to Late Devonian Catskill Magnafacies (CM) of New York. Berg (1972), Thoms and Berg (1985), Bridge et al. (1986), and Driese et al. (1997) made assessments of CF and CM bivalve burrows, rhizoliths, and *in situ* progymnosperm stump casts, respectively. CF traces, however, have not been evaluated in the context of the modern understanding of continental ichnology (e.g., Bown

and Kraus, 1983; Smith, 1993; Hasiotis, 1998, 2002, 2003, 2004, 2007, 2008 Smith and Mason, 1998; Hembree and Hasiotis, 2007, 2008; Smith et al., 2008a). Analysis of CF trace fossils indicates that the distribution of Devonian continental organisms was controlled by paleohydrology, and that continental organisms contributed greatly to pedogenesis, as is observed in Mesozoic to recent continental ecosystems (e.g., Hasiotis, 2002, 2004, 2007, 2008; Hasiotis et al., 2007).

Trace fossil assemblages from pre-Mississippian continental deposits have historically been considered to be of low diversity and representative of simple, unspecialized behaviors (e.g., Buatois et al., 1998). Trace and body fossil evidence suggests that invertebrates and plants colonized land during the Late Ordovician (Retallack and Feakes, 1987; Johnson et al. 1994). This evidence is contentious, however. By the Late Devonian, continental organisms had been evolving separate from marine organisms for as much as 100 million years, and a minimum of ~70 million years (Selden and Edwards, 1989; Shear and Kukulová-Peck, 1990). We hypothesize that CF traces should exhibit a high degree of specialization, reflecting evolution of continental organisms since that time.

GEOLOGIC SETTING

The CF in Pennsylvania comprises a 300–1,500 m thick package of alluvial channel sandstones and overbank mudstones pedogenically modified to varying degrees (Diemer, 1992; Driese, et al., 1993; Bridge, 2000). CF sediments were shed into a foreland basin from the Acadian orogenic center to the east (Ettensohn, 1985). Paleogeographic reconstructions place the state of Pennsylvania at ~20° south (Ziegler et al., 1979; Boucot and Gray, 1983) or ~35° south latitude (Joachimski et al., 2002) during the Late Devonian. The CF alluvial plain

apparently experienced wet-dry seasonality as evidenced by the development of vertic paleosols with pedogenic carbonate horizons, pedogenic slickensides, and pseudoanticlines (Woodrow et al., 1973; Driese et al., 1993).

The CF is divided into the Irish Valley, Sherman Creek, and Duncannon members in the study area (Sevon and Woodrow, 1985). The Irish Valley Member consists of 180–300 m of interfingering alluvial mudstones and sandstones, and marine mudstones. The Sherman Creek Member is 300 to >600 m thick and includes intervals of marine sedimentation, containing brachiopods and marine bivalves (Cotter and Driese, 1998); it, however, contains less evidence of marine influence than the Irish Valley Member. Paleosols in the Sherman Creek Member dominantly represent immature soils, whose development was frequently retarded by high rates of sedimentation (Elick, 2006). The Duncannon Member is ~300 m thick and contains no evidence of marine influence. Paleosols of the Duncannon Member are commonly better developed than those of the Sherman Creek Member and more commonly exhibit pedogenic pseudoanticlines, angular blocky peds, and well-developed pedogenic carbonate horizons (Driese et al., 1993; Elick, 2006).

CF pointbar deposits are commonly 3–5 m thick and are composed of scour-based, trough cross-bedded, very fine- to fine-grained muscovite-rich sandstone, separated by low angle lateral accretion surfaces frequently topped by 5–20 cm of silty mudstone. These are termed storied sandstones by Bridge (2000). Pointbar deposits are green, purple or red, and vary in degree of pedogenic modification. Cross bedding is retained in even the most strongly pedogenically modified CF pointbar deposits. They fit the criteria for Protosols, *sensu* Mack et al. (1993), or Entisols, *sensu* US Soil Taxonomy.

Overbank deposits are composed of mudstones and mudstone-very fine-grained

sandstone interbeds that are red, purple, or rarely green. These deposits are finely laminated, weakly laminated, platy, structureless, or dominated by angular blocky to prismatic peds and pseudoanticlines (Diemer, 1992; Driese et al., 1993). Centimeter-scale pedogenic slickensides occur in weakly laminated to platy mudstones and along the boundaries of peds in thoroughly homogenized paleosols. Traces are more abundant in weakly laminated to thoroughly homogenized paleosols than in finely laminated paleosols. Finely to weakly laminated mudstone and sandstone-mudstone interbeds are often current or oscillation ripple laminated, and rarely trough cross-stratified.

Finely laminated and weakly laminated to platy overbank mudstones are often interbedded with very fine-grained, micaceous sandstones. These are interpreted as proximal floodplain and levee deposits, based on the prevalence of remnant lamination, which indicates that high sedimentation rates retarded soil formation. These paleosols fit the criteria for Protosols, *sensu* Mack et al. (1993), and Entisols–Inceptisols, *sensu* US Soil Taxonomy (Soil Survey Staff, 2010).

Mudstones and claystones with well-developed angular blocky peds, clay skins, pedogenic pseudoanticlines, well-developed pedogenic carbonate horizons, and no remnant lamination are interpreted as calcic Vertisols, *sensu* Mack et al. (1993), and also Vertisols *sensu* US Soil Taxonomy. Those that do not exhibit well-developed pseudoanticlines fit the criteria for calcic Argillisols, *sensu* Mack et al. (1993), based on the presence of pedogenic carbonate horizons and illuvial clay skins.

METHODS AND MATERIALS

Stratigraphic sections were measured at individual roadcut outcrops along U.S. Highway

15 in Southern Lycoming County, Pennsylvania, and at the Red Hill outcrop on PA Route 120, ~1 km southeast of North Bend, Pennsylvania (Fig. 1). Individual lithological units were discerned based on grain size, sedimentary structures, color, and pedogenic features. Depositional and postdepositional (pedologic) environments were interpreted using these features. The stratigraphic position of trace-fossil occurrences was documented to discern their paleoenvironmental occurrences, associations, and distribution (Figs. 2–4).

Trace fossils were photographed, measured, and collected for further analysis in the laboratory when possible. Thin sections and polished slabs containing burrows and rhizoliths were prepared in the University of Kansas Geology Department thin section laboratory to analyze burrow internal morphology and paleosol micromorphology. Thin sections were examined using a Nikon model E6000W POL petrographic polarizing light microscope. Slabbed sections were examined in hand sample or using a Nikon model SMZ1000 binocular light microscope. Architectural and surficial morphologies of traces were examined in hand sample and under the binocular light microscope, and compared to those previously described from continental and marine deposits. Existing ichnotaxa were used when possible and 2 new ichnogenera and 3 new ichnospecies were erected for CF traces that did not conform to previously erected ichnotaxa. Rhizolith morphologies were described using the terminology of Cannon (1949) and Fitter (1987). The root magnitude ordering, and root angle measurement schemes of Fitter (1987) were also used to describe rhizoliths (Fig. 5).

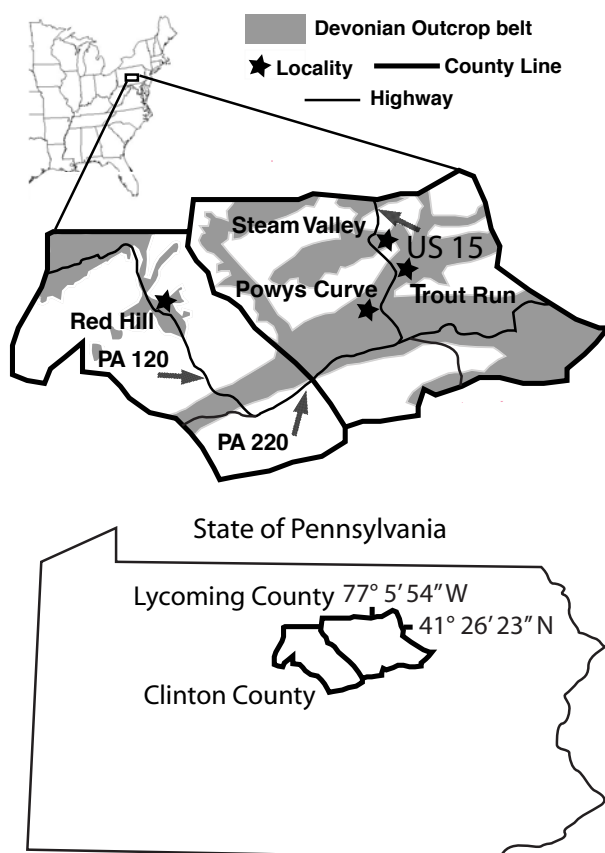
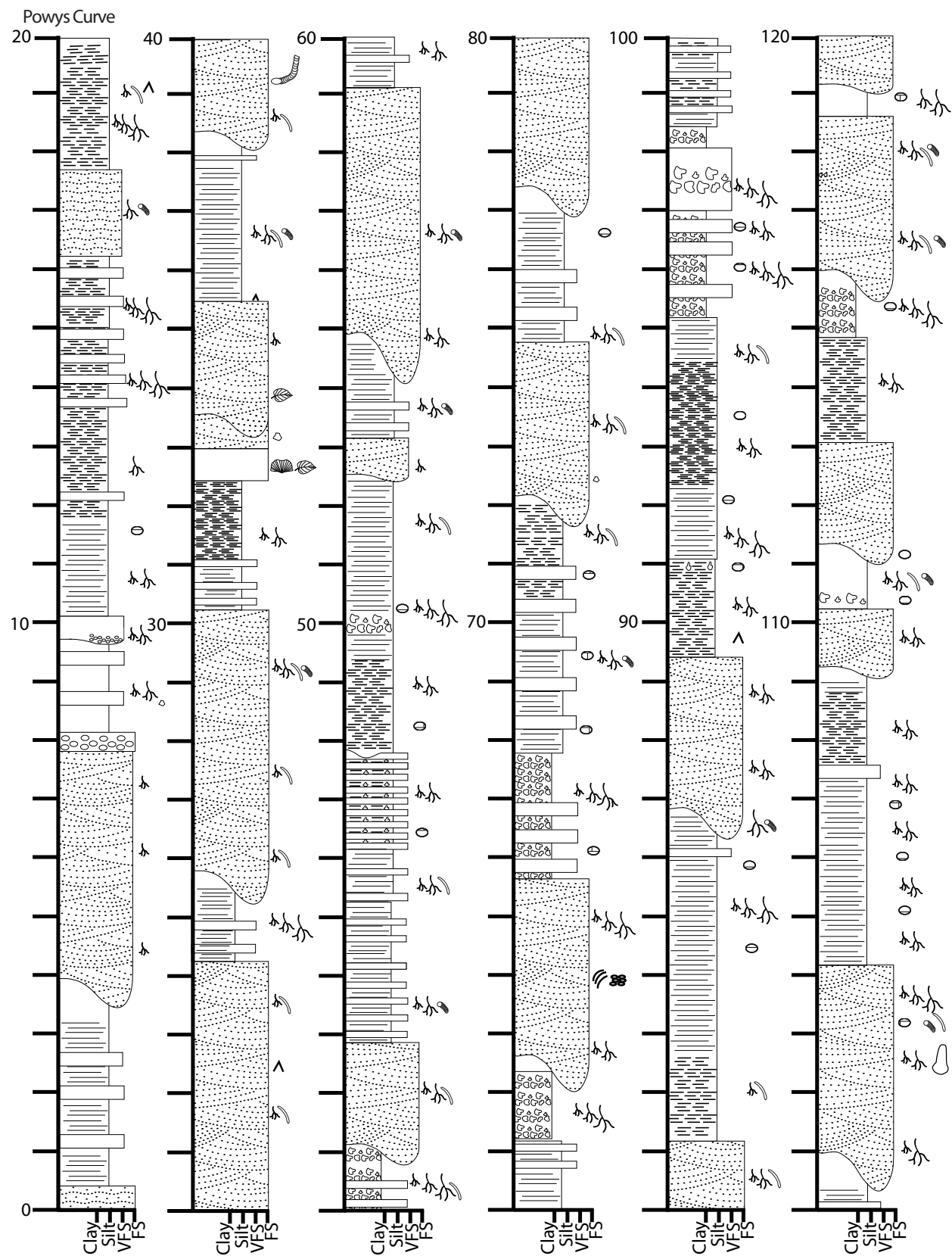


FIGURE 1—Map of Clinton and Lycoming Counties, Pennsylvania, with localities examined during this study.



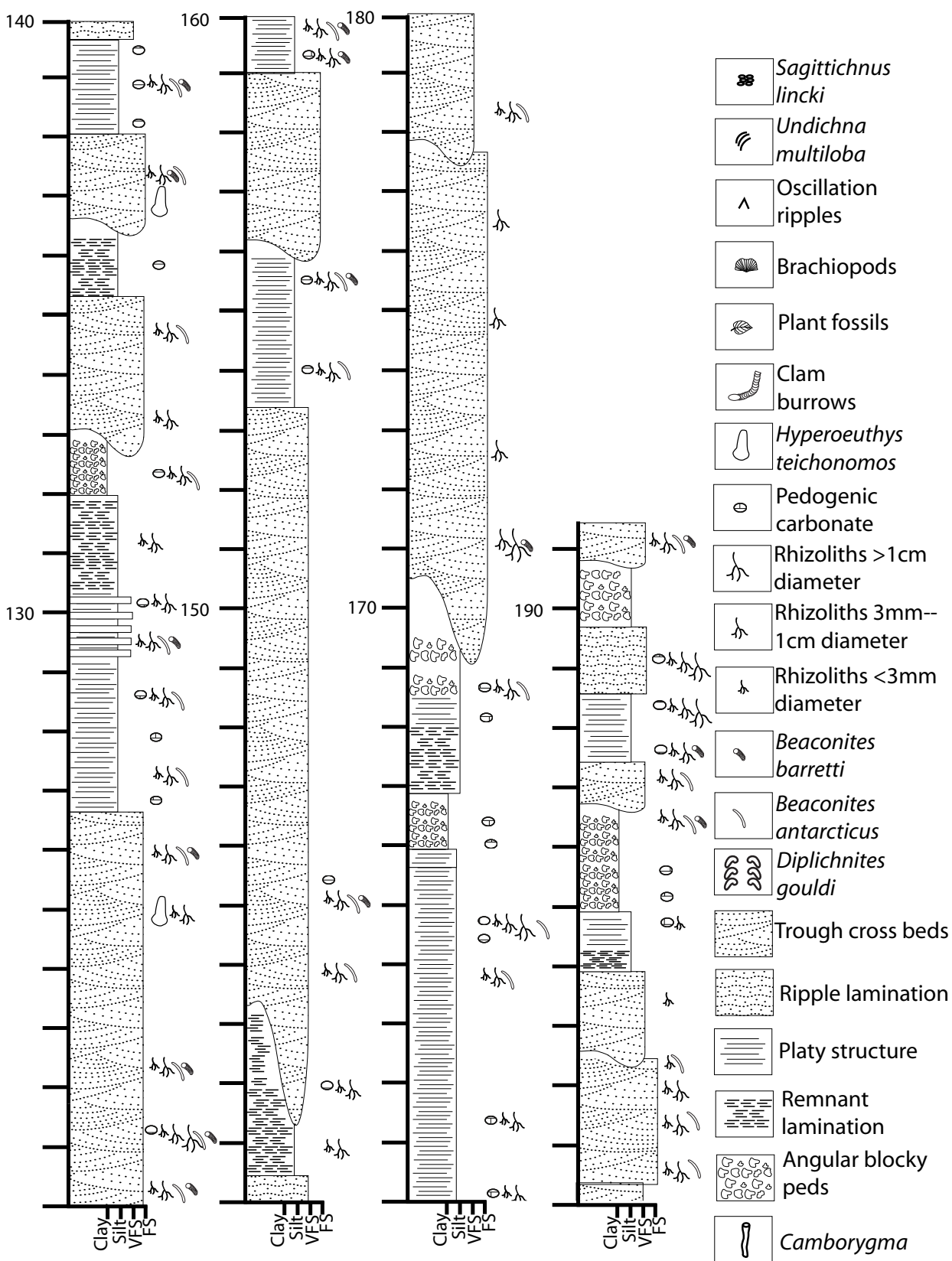


FIGURE 2— Measured section at Powys Curve showing stratigraphic position of traces.

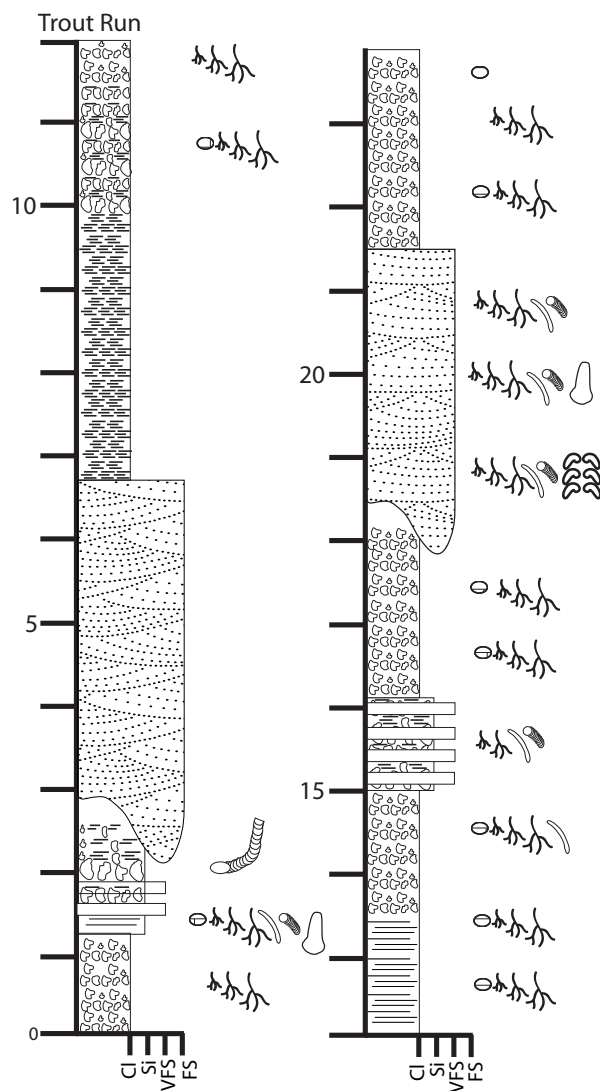


FIGURE 3— Measured section at Trout Run showing stratigraphic position of traces.

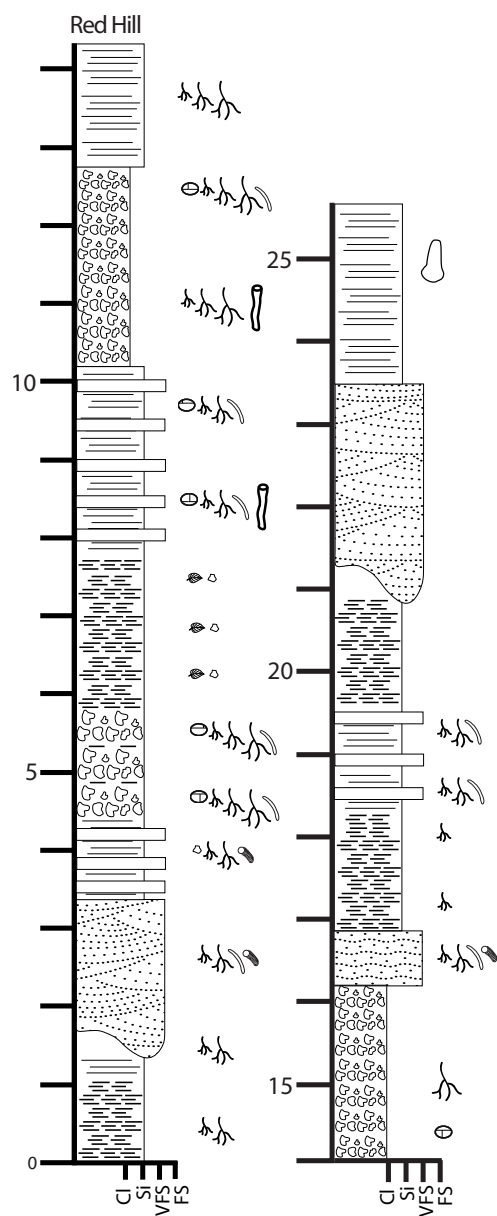


FIGURE 4— Measured section at Red Hill showing stratigraphic position of traces.

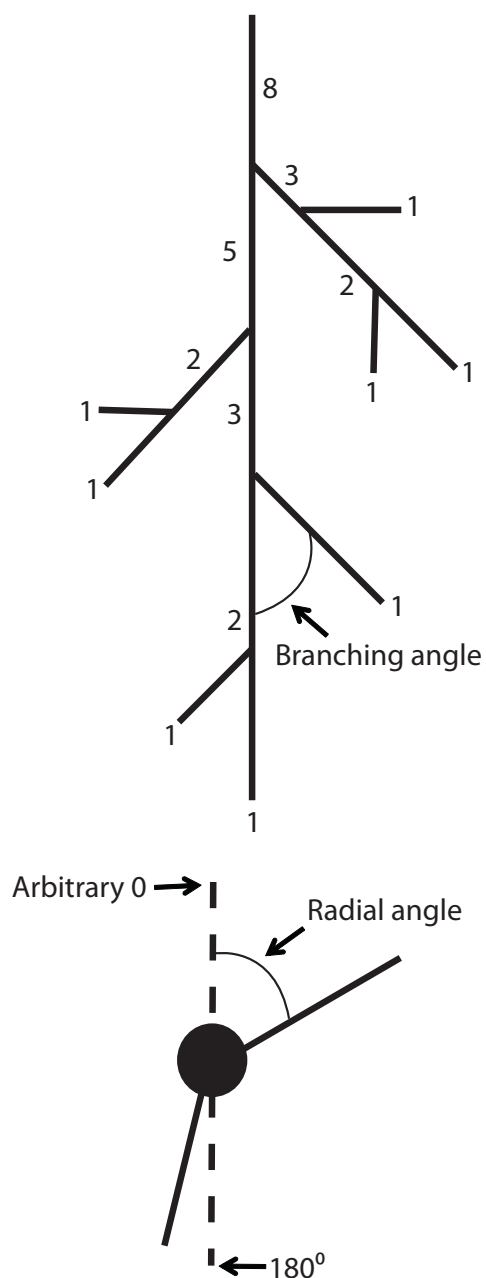


FIGURE 5—Diagram of the root rank ordering and angle measurement scheme modified from Fitter (1987); rank order of a root=the number of branches emanating from the root.

SYSTEMATIC ICHNOLOGY

Ichnogenus BEACONITES Vialov, 1962

Type Ichnospecies.—BEACONITES ANTARCTICUS, emended Bradshaw, 1981

Figure 6 A–J

Description.—Vertical to horizontal; highly sinuous; elongate; elliptical cross-section; 2–6 mm in diameter (Fig. 7); up to 3 cm long; composed of poorly organized packets of meniscus-shaped, structureless backfill; backfill organized into 1–3 mm thick packets; backfill identical to host sediment; thinly and discontinuously lined with very fine sand or silt grains; lining thickness variable; surficial morphology smooth.

Occurrence.—Finely ripple-laminated mudstone-sandstone interbeds, weakly laminated–platy mudstone-sandstone interbeds, pedogenically modified pointbar deposits, thoroughly homogenized vertic claystones, in bedding plane concentration up to hundreds per dm² (Figs. 2–4).

Discussion.—*Beaconites antarcticus* was erected by Vialov (1962) and emended by Bradshaw (1981) to describe backfilled burrows from the Devonian of the Beacon Supergroup of Antarctica. Similar burrows from Devonian continental strata were attributed to *B. antarcticus* by Gevers et al. (1971), Bradshaw (1981), and Gordon (1988). Previously described *B. antarcticus* are 10–30 mm in diameter, filled with thick, weakly arcuate backfill packets and thinly lined with sand grains (Gevers et al., 1971; Bradshaw, 1981).

Backfill packets in CF *B. antarcticus* are rarely visible without cutting and polishing, or thin sectioning burrows, likely because the burrow lining obscures them. CF *B. antarcticus* differs from those previously described (Gevers et al., 1971; Bradshaw, 1981) in being smaller in diameter and apparently more variable in orientation.

CF *B. antarcticus* only occurs in intervals that have been pedogenically modified. When found in abundance in weakly laminated to thoroughly homogenized paleosols, burrows crosscut rhizoliths, are crosscut by rhizoliths, and crosscut one another. Burrows in well-developed paleosols also crosscut angular blocky peds. High concentrations of crosscutting burrows suggest that paleosols experienced either multiple seasonal burrowing episodes, or prolonged, continuous pedogenesis by burrowing. Crosscutting relationships with rhizoliths indicate that *B. antarcticus* was constructed in actively forming soils on the CF floodplain.

Modern burrows in soils that contain packeted backfills are constructed by such soil arthropods as larval and nymphal insects (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009). These organisms excavate small dwelling chambers in moderately to well-drained alluvial soils in order to consume plant roots, or deposit feed on organics, and represent temporary soil biota *sensu* Wallwork (1970) and Hasiotis (2007)—an organism that hatches from an egg underground and spends its juvenile state underground, only to exit as an adult. When organics have been consumed, the burrower moves forward, removing sediment from its anterior and deposited it posteriorly, resulting in packets of burrow backfill. Packeted backfills in CF *B. antarcticus* indicate a similar behavior by its tracemakers, which may also have been temporary soil organisms. Whether CF *Beaconites* represented rhizophagous herbivory or deposit feeding on soil organic matter is unclear.

Trace fossil and modern biological evidence suggests that backfilled burrow production in modern and ancient soils is largely attributable to hygrophilic to terraphilic organisms—organisms that dwell in the upper, and intermediate to lower vadose zone, respectively—such as cicada nymphs and beetle larvae (Smith and Hasiotis, 2008; Smith et al., 2008a; Counts and Hasiotis, 2009). We interpret CF *B. antarcticus* to represent terraphilic to hygrophilic organisms

for this reason, as well as their co-occurrence and crosscutting relationships with rhizoliths. Further evidence that CF *Beaconites antarcticus* represents terraphilic to hygrophilic organisms is the red or purple color of nearly all CF paleosols, which indicates that they represent well-drained to moderately well-drained soils.

The morphology of CF *B. antarcticus* suggests an arthropod tracemaker, based on comparison to burrow morphologies in modern soils. Devonian insect body fossils are rare and Devonian hexapod assemblages are dominated by entognaths, which share a common ancestor with insects (Labandeira et al., 1988; Engel and Grimaldi, 2004; Grimaldi and Engel, 2005). The similarity of CF *B. antarcticus* to burrows constructed by modern rhizophagous holometabolous and hemimetabolous insects suggests that insects may have been much more common constituents of Late Devonian soil faunas than is indicated by the body fossil evidence. Alternatively, the burrows represent soil-dwelling arthropods of unknown taxonomic affinity, with no body fossil record.

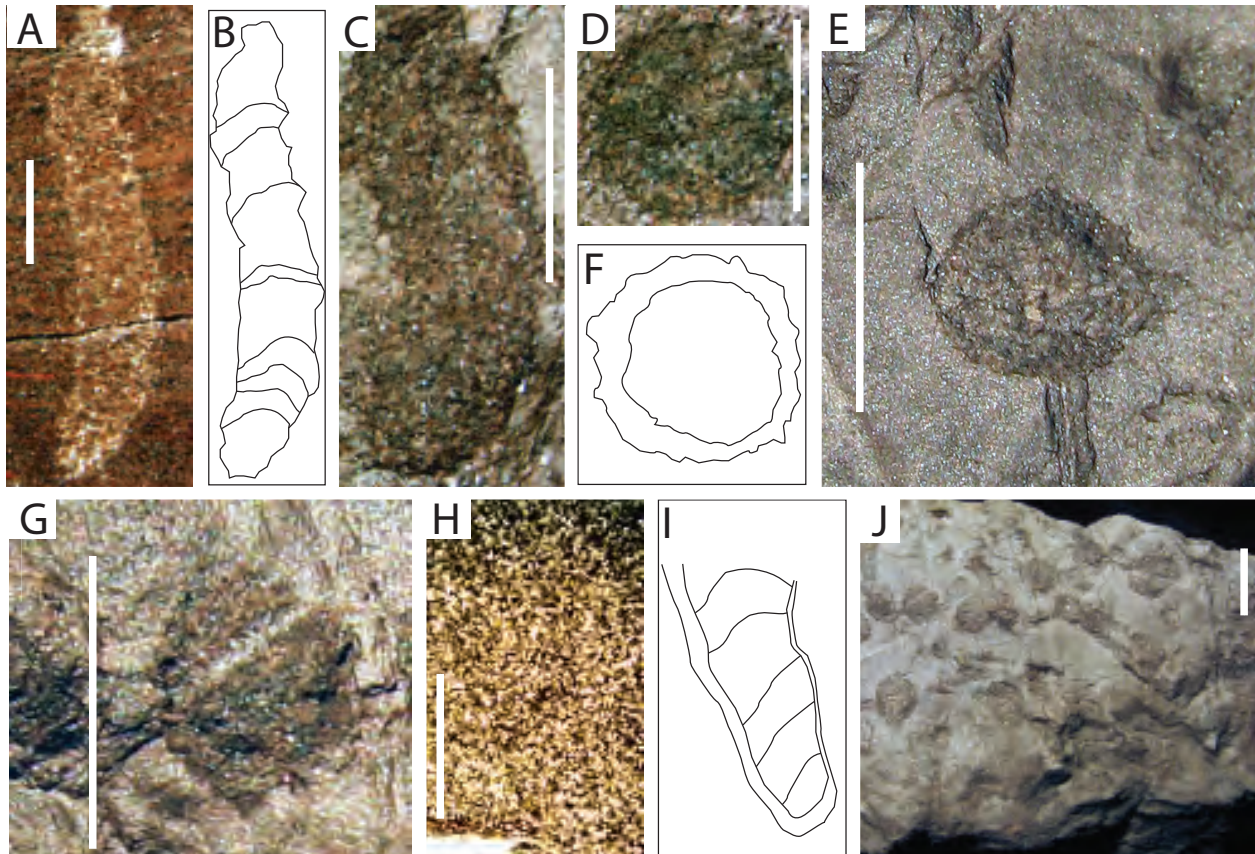


FIGURE 6—*Beaconites antarcticus*; Scale=5 mm. A. Closeup of *Beaconites antarcticus* in slabbed section. B. Line drawing of 4A showing backfill packets. C. Close-up of subhorizontal *Beaconites antarcticus*. D. Close-up of subvertical *Beaconites antarcticus* in cross section. E. Close-up of *Beaconites antarcticus* crosscutting a rhizolith. F. Line drawing of 4D showing burrow lining. G. Rhizolith crosscutting *Beaconites antarcticus*. H. *Beaconites antarcticus* in thin section. I. Line drawing of 4H showing backfill packets and lining. J. Multiple *Beaconites antarcticus* and rhizoliths on a very fine sandstone slab.

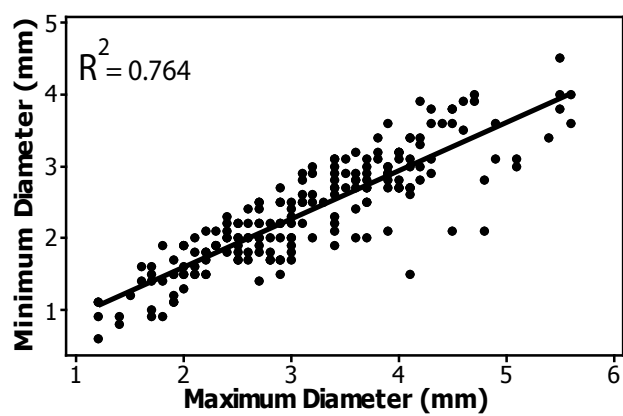


FIGURE 7— Maximum vs. minimum diameter of *Beaconites antarcticus*.

Ichnospecies BEACONITES BARRETTI, Bradshaw, 1981

Figure 8 A–F

Description.—Subhorizontal to subvertical; highly sinuous; surface unornamented to slightly rugose; 7–63 mm diameter (Fig. 9); may be > 300 mm long; strongly elliptical in cross section; preserved in full relief; filled with arcuate backfill meniscae; burrow fill identical in composition to host rock; meniscae 1–3 mm thick; menisci do not merge laterally to form burrow lining.

Occurrence.—Finely ripple-laminated mudstone-sandstone interbeds, weakly laminated–platy mudstone-sandstone interbeds, pedogenically modified pointbar deposits, thoroughly homogenized vertic claystones in bedding plane concentrations up to ten per dm².

Discussion.—*Beaconites* isp. are reported from nearly all Devonian continental ichnoassemblages (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004; Davies et al., 2006). The worldwide distribution of *Beaconites* indicates that its tracemakers were worldwide in distribution.

Bennettarthra annwnensis, Fayers et al. (2010) has been suggested as a possible tracemaker of *B. barretti*. Its size (carapace width >100 mm) is consistent with reported sizes of *B. barretti*, which often exceeds 100 mm diameter (Bradshaw, 1981; Morrissey and Braddy, 2004). *B. annwnensis* appears to have been a scorpion, however (W. D. I. Rolfe *in litt.* to P. A. Selden). *B. annwnensis* is an unlikely tracemaker for of *B. barretti*, as such, because scorpions are only known to make open burrows and are not known to backfill (Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006). Eoarthropleurid myriapods have also been suggested to be possible *B. barretti* tracemakers (Rolfe, 1980; Morrissey and Braddy, 2004), however,

neoichnological experiments with burrowing millipedes have not yielded meniscus-filled burrows (Hembree, 2009).

CF *B. barretti* differs morphologically from *B. antarcticus* in being much larger in diameter, more sinuous, and lacking the characteristically thick backfill packets of *B. antarcticus* (Bradshaw, 1981). Keighley and Pickerell (1994) attributed *B. barretti* to the ichnogenus *Taenidium* and erected the ichnospecies *Taenidium barretti*. *B. barretti* differs substantially, however, from *Taenidium* isp., as originally described, because *Taenidium* contains thick or pelleted meniscate backfills (Smith et al., 2008). Burrows from the Old Red Sandstone of Norway assigned to *B. barretti* by Davies et al. (2006) and reassigned to *Taenidium barretti* by Keighley and Pickerill (1994), and Davies et al. (2006) should be reassigned to *Beaconites barretti*.

Morphological similarity of *B. barretti* to *B. antarcticus* indicates that *B. barretti* represents a similar behavior. The difference in backfill morphology, however, suggests a different tracemaker and slightly different behavior. How the behavior of the *B. barretti* and *B. antarcticus* tracemakers differed is unclear.

Similarity of *Beaconites* isp. to meniscate burrows of soil insects that represent temporary soil biota *sensu* Wallwork (1970) and Hasiotis (2007) (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009) suggests an arthropod tracemaker, possibly an insect or an unknown soil arthropod. These burrows may also represent behavior of temporary soil organisms. We interpret CF *B. barretti* to represent behavior of hygrophilic to terraphilic soil arthropods for the same reason that we interpret *B. antarcticus* to represent hygrophilic to terraphilic soil arthropods.

Frequent co-occurrences and crosscutting relationships with *B. antarcticus* indicate that

the *B. antarcticus* and *B. barretti* tracemakers coexisted in CF soils. *Beaconites barretti* are nearly always crosscut by rhizoliths and *B. antarcticus*, and often crosscut one another, suggesting that heavily burrowed intervals were subject to multiple seasons of burrowing, or prolonged biotic pedoturbation.

The presence of *Beaconites* isp. in the CF indicates that shallow to intermediate-depth deposit feeding occurred in alluvial paleosols in the Late Devonian. This is significant, because the occurrence of *Beaconites* in the Devonian places the inception of deposit feeding in soils in the Late Devonian, rather than in the Permian as part of the Scoyenia Ichnoguild (Buatois et al., 1998). Furthermore, the presence of *Beaconites* isp. in alluvial deposits of the CM of New York, USA (Gordon, 1988), and the Old Red Sandstone of Europe (Morissey and Braddy, 2004; Davies et al., 2006) suggest that deposit feeding on organic matter in soils had its inception as early as the Late Silurian to Early Devonian.

The Scoyenia Ichnoguild defined by Buatois et al. (1998) and later work (e.g., Buatois and Mángano, 2007) is problematic. It is composed of meniscate, infaunal burrows, and is interpreted to represent backfilled burrow production by shallow to intermediate depth soil infauna in ‘firmgrounds’. The term Scoyenia Ichnoguild, however, is misleading as no clear association is defined between behaviors represented by this ichnoguild and paleohydrology—whether traces occur in the vadose zone or phreatic zone—which is the most important control on the distribution of trace fossils in the continental realm (Hasiotis, 2002, 2004, 2007, 2008; Hasiotis et al., 2007). The Scoyenia Ichnofacies is also ambiguous, as no relationship between trace construction and pedogenesis is defined or discussed, which is essential to understanding the paleoenvironmental, paleoclimatic, and paleoecological context of continental trace fossils (e.g., Hasiotis, 2007; Hasiotis et al., 2007) is defined.

The Scoyenia Ichnofacies, *sensu* Buatois and Mángano (1995) is interpreted to represent moist to wet, slightly submerged to periodically submerged sediments, and is composed of backfilled burrows, crawling traces, cylindrical to irregular shafts, tracks, and trails. All of the traces indicative of the Scoyenia Ichnofacies can occur in deposits that exhibit little or no evidence of underwater submergence, or high soil moisture (Hasiotis, 2002, 2004, 2007; Hasiotis et al., 2007; Hembree and Hasiotis, 2007, 2008; Smith et al., 2008b). Most traces included in the Scoyenia Ichnofacies, *sensu* Buatois and Mángano (1995) can occur in moist environments and are representative of terraphilic to hygrophilic behavior (*sensu* Hasiotis, 2007). Those traces, however, are not exclusively characteristic of moist or periodically submergent environments—they can occur in any pedogenically modified sediment. The Scoyenia Ichnofacies should be abandoned, or its definition greatly modified to accommodate the actual associations of trace fossils and their paleoenvironmental interpretations based on paleohydrologic and paleopedologic evidence. We advocate a holistic—involving detailed facies analysis and behavioral interpretation of trace fossils—methodology to interpret continental trace fossils, rather than using an antiquated approach to define continental ichnofacies (e.g. Buatois and Mángano, 1995, 2007; Buatois et al., 1998; Genise et al., 2000).

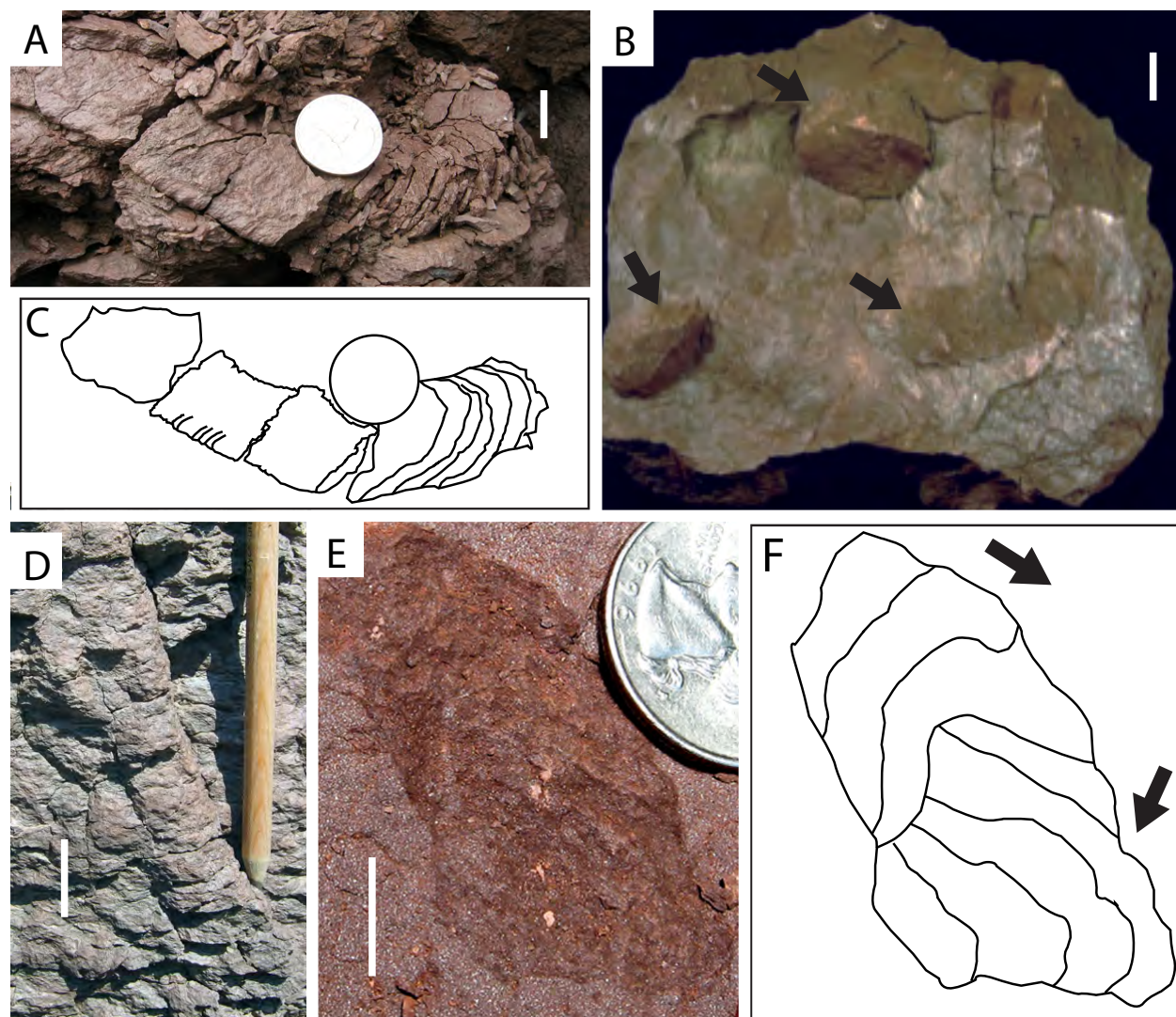


FIGURE 8— *Beaconites barretti*; scale=10 mm. A. Subhorizontal *Beaconites barretti* with well-defined arcuate menisci, Powys Curve. B. Several *Beaconites barretti* and multiple rhizoliths on a slab of very fine sandstone, Powys Curve. C. Line drawing of 9A showing burrow outline and menisci. D. Subvertical *Beaconites barretti* in a vertic claystone, Powys Curve. E. Horizontal *Beaconites barretti* in a very fine sandstone, Trout Run. F. Interpretive drawing of 8E.

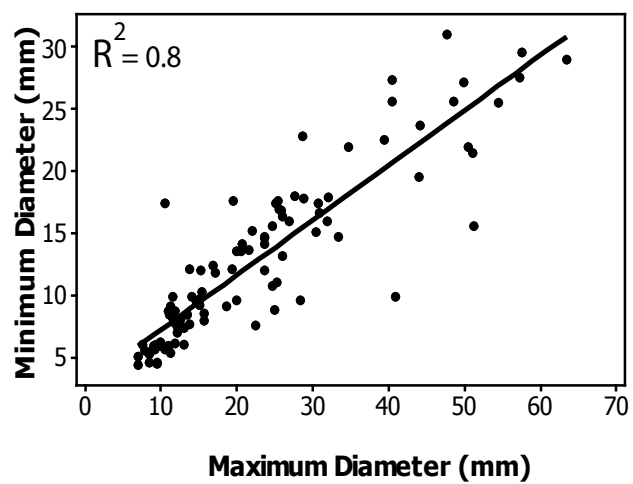


FIGURE 9— Minimum vs. maximum diameter of *Beaconites barretti*.

Ichnogenus CAMBORYGMA Hasiotis and Mitchell, 1993

Type ichnospecies CAMBORYGMA EUMEKONOMOS

Figure 10 E–G

Description.—Vertical to subvertical, sinuous, elongated burrows; burrow cross-section could not be seen; ~100 mm in diameter; up to 2 m long; presence or absence of burrow lining is unclear; termini blunt to tapering; fill is identical to host rock; surficial morphology characterized by transverse and longitudinal striations, and irregularly spaced knobby projections; striations spaced 1–15 mm apart and are ~1–20 mm wide (Fig. 10).

Occurrence.—Weakly laminated to platy mudstone-sandstone interbeds; only known to occur at the Red Hill outcrop (Fig. 3). Specimens are rare and do not weather in full relief, making collection nearly impossible.

Discussion.—The ichnogenus *Camborygma* was erected by Hasiotis and Mitchell (1993) to describe vertical, elongated, simple to bifurcating, large-diameter burrows from the Upper Triassic Chinle Formation of the western USA. Hasiotis and Mitchell (1993) interpreted these burrows as freshwater crayfish (Decapoda: Cambaridae) in origin based on architectural and surficial burrow morphologies. CF *C. eumekonomos* is similar to those traces described by Hasiotis and Mitchell (1993) in being elongated, sinuous, simple in architecture, and having a surficial morphology characterized by transverse and longitudinal striations, and knob-like projections.

CF *C. eumekonomos* likely represents the dwelling trace of a hydrophilic organism, *sensu* Hasiotis (2002, 2007)—an organism that burrows to the phreatic zone. Similar burrow morphologies described from Mesozoic and Cenozoic continental deposits have been interpreted to represent fluctuating water table conditions, based on comparisons to modern burrows with

similar morphology (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993; Hasiotis and Honey, 2000; Hasiotis 2007).

We interpret CF *C. eumekonomos* to have been constructed by an arthropod similar to a freshwater crustacean based on similarity of their architectural and surficial burrow morphologies to previously described burrows (e.g. Hasiotis and Mitchell, 1989, 1993; Hasiotis et al., 1993). The tracemaker of CF *C. eumekonomos* is difficult to infer, because the oldest evidence of freshwater decapods is from the Upper Triassic Chinle Formation (Hasiotis and Mitchell, 1993). Marine decapods are known to have existed by the Late Devonian, however (Schram et al., 1978). CF *C. eumekonomos* may indicate that decapod crustaceans had already invaded freshwater and terrestrial habitats by the Late Devonian. The CF *C. eumekonomos* tracemaker may also have been a soil-dwelling, decapod-like arthropod.

The presence of highly penetrative burrows in the CF is significant, because it contradicts previous assertions that deeply penetrative burrowing did not evolve until the Triassic (e.g., Buatois et al., 1998). Our data indicate that the inception of deeply penetrative burrowing in alluvial environments occurred in the Devonian, and that such burrowing continued into the Triassic, although Devonian and Triassic tracemakers may not have been the same.

Burrowing crayfish (e.g., *Cambarus* and *Procambarus sp.*) construct seasonal and permanent burrows in alluvial and palustrine settings to seek protection and to fulfill physiological moisture needs (Grow and Merchant, 1980; Correia and Ferreira, 1995; Hobbs, 2001; Mazlum and Eversole, 2004). Juveniles are hatched in the burrow, and remain until burrows are flooded, later establishing burrows of their own (Correia and Ferreira, 1995; Mazlum and Eversole, 2004). Adults primarily dwell in the burrow but leave occasionally to forage (Penn, 1943), therefore, burrowing crayfish represent periodic soil organisms *sensu*

Wallwork (1970) and Hasiotis (2002, 2007). CF *Camborygma isp.* likely also represent domichnia of periodic soil arthropods, *sensu* Hasiotis (2002, 2007) with life habits similar to burrowing crayfish, although the CF *Camborygma* tracemaker is unknown.

Gordon (1988) reported burrows similar to *C. eumekonomos* from the Givetian to Frasnian CM of New York, USA. Figures and descriptions therein are insufficient to definitively place Gordon's (1988) burrows in *C. eumekonomos*, however. The presence of deeply penetrative, vertical burrows in Middle-to-Late Devonian-aged alluvial strata suggests that hydrophilic, soil-dwelling arthropods may have evolved by the Middle to earliest Late Devonian.

CAMBORYGMA LITONOMOS Hasiotis and Mitchell, 1993

Figure 10 A–C

Description.—Vertical to subvertical, straight-to-sinuuous, elongated burrows; elliptical in outline; 20–30 mm in diameter; up to 180 mm long; composed of burrow fill and a robust, but discontinuous wall lining, which comprises up to 40 percent of burrow thickness; termini blunt to tapering, and approximately the same diameter as burrow shaft; burrows begin and terminate at the same stratigraphic level within a single occurrence; fill and lining identical in composition to host rock; surficial morphology characterized by tranverse and longitudinal striations; striations 1–3 mm wide and spaced 1–3 mm apart (Fig. 10).

Occurrence.—Weakly laminated to platy mudstone-sandstone interbeds; thoroughly homogenized vertic claystones, in bedding plane concentrations up to 10 per m², in discrete horizons; only known to occur at the Red Hill outcrop.

Discussion.—We interpret CF *C. litonomos* to represent dwelling burrows of terraphilic, hygrophilic, or hydrophilic, periodic soil-dwelling arthropods of unknown taxonomic affinity.

The vertical orientation, elongated shafts, and surficial morphology characterized by transverse striations of *C. litonomos* are morphologically similar to previously described *C. litonomos*, interpreted to be freshwater decapod dwelling burrows (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993).

CF *C. litonomos* exhibits a lower length-to-width ratio and is more uniform in diameter than previously described examples of this ichnotaxon, which can be as much as 0.5 m long, and often exhibits a bulbous chamber at the terminus or middle of the burrow (Hasiotis and Mitchell, 1993). Previously described *C. litonomos* can also exhibit U-shaped chambers that form two entrances, or expanded portions of the shaft that form chambers. CF *C. litonomos* does not exhibit expanded chambers, or U-shaped double entrances, but instead consistently exhibits a simple cylindrical morphology. CF *C. litonomos* also lacks knobby and hummocky surficial morphology, interpreted to represent pereopod and cheliped marks in Triassic crayfish burrows (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). We interpret the difference in surficial morphology of *C. litonomos* from that of previously described *Camborygma* isp. to result from morphological and physiological differences between the CF *C. litonomos* tracemaker, and the tracemaker of previously described *C. litonomos* (freshwater crayfish). The nature of these morphological differences is unclear, however, because the tracemaker of CF *C. litonomos* is unknown.

C. litonomos exhibits a much smaller length to width ratio than CF *C. eumekonomos*, as well as exhibiting much less shaft sinuosity. CF *C. eumekonomos* also exhibits greater variability in shaft diameter than *C. litonomos*. The surficial morphology of *C. litonomos* is further characterized by narrower, more regular transverse striations than that of *C. eumekonomos*.

We interpret the morphological differences of CF *C. eumekonomos* and *C. litonomos* to reflect different tracemakers, both of which were probably, periodic, soil-dwelling arthropods. The *C. litonomos* tracemaker was likely much smaller than the *C. eumekonomos* tracemaker, as evidenced by the smaller diameter of *C. litonomos* than *C. eumekonomos*. The much greater length of CF *C. eumekonomos* than *C. litonomos* suggests that *C. eumekonomos* was constructed under much lower average water table conditions than *C. litonomos*, which was likely constructed under high water table conditions, or may have been constructed by a terraphilic to hygrophilic organism.

CF *C. litonomos* may represent the dwelling burrow of a terraphilic to hygrophilic, soil-dwelling arachnid. Modern arachnids, such as wolf spiders, construct vertically oriented, open dwelling burrows in soils (e.g., Hasiotis and Bourke, 2006). Wolf spider burrows are similar in architectural morphology to CF *C. litonomos* (e.g., Hasiotis and Bourke, 2006), suggesting that the *C. litonomos* tracemaker may have been an arachnid. Trigonotarbid, phalangiotarbid, amblypygid, scorpionid, and uraraneid arachnids all existed in the Devonian (Shear and Selden, 2001; Poschmann et al., 2005; Selden and Penny, 2010) and are potential tracemakers of CF *C. litonomos*. Trigonotarbids are known to occur in the CF (Shear, 2000), possibly making them a more likely tracemaker than the other groups.

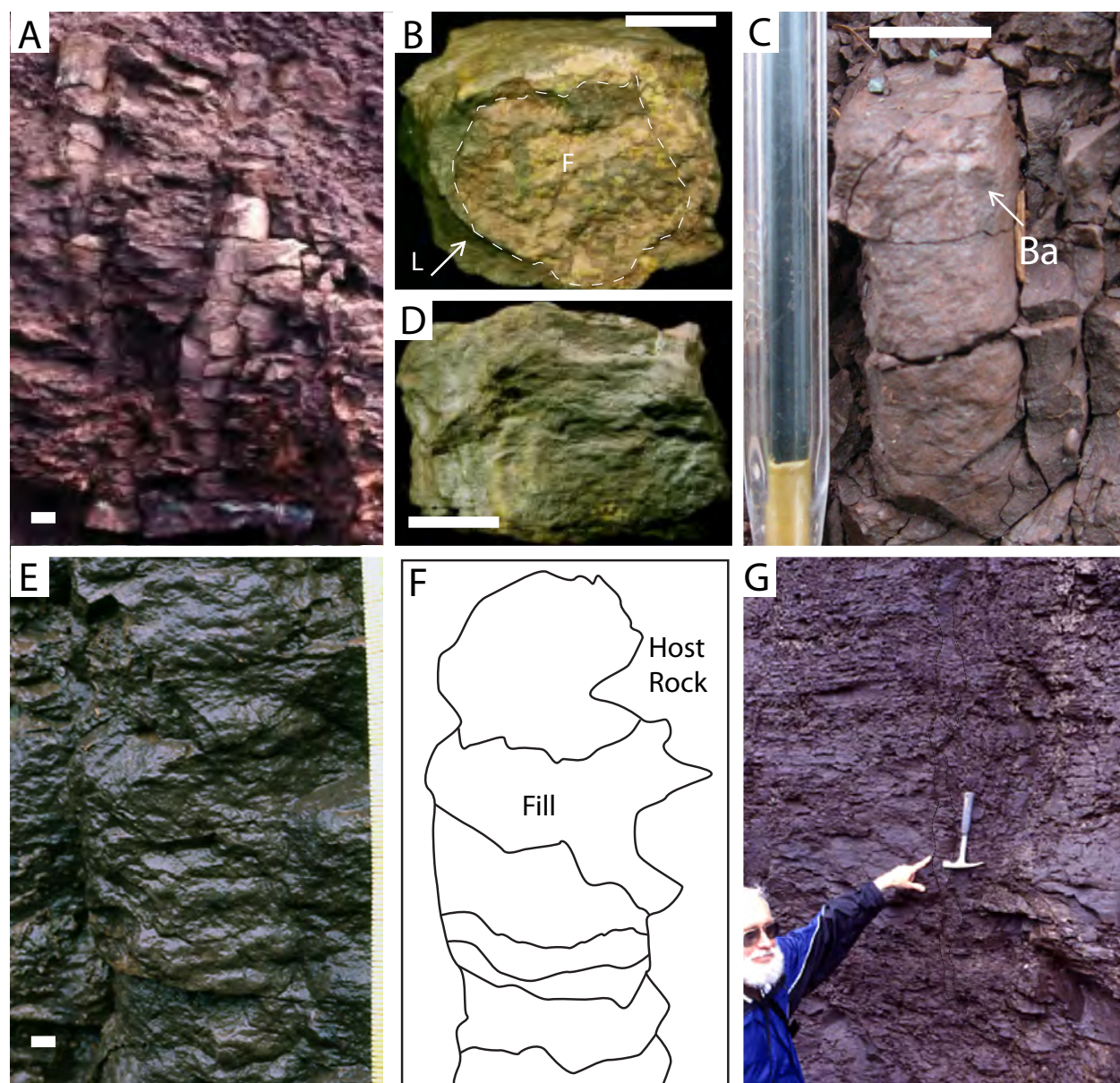


FIGURE 10—*Camborygma eumekonomos* and *C. litonomos*; scale= 10 mm. A. *C. litonomos* in outcrop, Red Hill. B. Cross section of *C. litonomos*; L= lining; F= fill. C. Closeup of *litonomos* in outcrop; Ba= *Beaconites antarcticus*. D. Surficial morphology of *C. litonomos*. E. Closeup of *C. eumekonomos*. F. Interpretive line drawing of E. G. *C. eumekonomos* in outcrop, Red Hill.

Ichnogenus DIPLICHNITES Dawson, 1873

Ichnospecies DIPLICHNITES GOULDI Gevers, 1973

Figure 11 A–G

Description.—Simple trackways composed of parallel sets of tracks; tracks evenly spaced; stride length uniform; tracks elongated, and slit-like (morphotype 1) to comma-shaped (morphotype 2); posterior of comma-shaped tracks bounded by a sediment mound; concavity of track curvature faces inferred direction of movement; comma-shaped tracks are deeper and wider than slit-like tracks; total trackway width is approximately twice the stride length; total trackway width is approximately 1.5 times inside width; 0.79–61.2 mm in total width; trackways divisible into two size classes; size class 1 is 0.79 to 1.92 cm wide and includes both morphotypes; size class 2 is represented by one example that is 61.2 mm wide and belongs to morphotype 2.

Occurrence.—Finely laminated mudstone-sandstone interbeds, at Steam Valley; trough crossbedded, red, rhizoturbated very fine-grained sandstone-mudstone interbeds, Trout Run. Occurrences are rare and trackways are fragmentary.

Discussion.—We interpret CF *Diplichnites gouldi* to represent repichnia of 2 size classes of myriapod-like arthropods. The great size difference in size class 1 and 2 suggests tracemakers of differing taxonomy. The morphological similarity of the size class 2 trackway to other morphotype 2 trackways, however, indicates that the tracemakers may have been individuals of the same or closely related species that differed greatly in size, perhaps representing juveniles and adults.

We attribute CF *D. gouldi* morphotype 1 and 2 to the same ichnotaxon and similar tracemakers because: 1) type 1 and type 2 trackways exhibit nearly identical track spacing; 2) the orientation of tracks in both morphotypes is very similar; 3) tracks in both morphotypes are

similar in morphology, despite the pronounced curvature of type 2 trackways; and 4) we lack sufficient material to make complete analyses of both trackway morphotypes. CF *D. gouldi* morphotypes 1 and 2 may represent different sediment moisture conditions, 1 representing dry, relatively firm sediment, and 2 representing moist to nearly saturated conditions. If the two morphotypes represent differing moisture conditions, the curved tracks of morphotype 2 represent sediment being pushed back by the tracemaker's tarsal claws as they contacted the sediment. This is evidenced by sediment mounds on the posterior side of morphotype 2 tracks.

The linear feature associated with the trackway in figure 11a is not included in the description of the trackways, because we do not interpret that feature to be part of the trackway. We do not interpret linear feature to be part of the trackway because: 1) the curvature of the feature differs from that of the trackway, and 2) the feature does not occur in the center of the trackway.

Arthropod trackways are a constituent of nearly all Paleozoic continental ichnoassemblages (Briggs and Rolfe, 1983; Walker, 1985; Pearson, 1992; Buatois et al., 1998; Smith et al., 2003; Lucas et al., 2004; Morrissey and Braddy, 2004). Diverse arthropod trackways, interpreted to indicate unique morphologies, and locomotor styles of tracemaking organisms, and sediment consistency have been recognized (Johnson et al., 1994; Morrissey and Braddy, 2004; Davis et al., 2007). The ichnogenus *Diplichnites* is most characteristic of Devonian ichnoassemblages (e.g., Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004).

Ichnotaxonomic assessments of trackways similar to *Diplichnites* have been met with considerable confusion, resulting from the construction of numerous ichnogenera for trackways of myriapod-like organisms (Briggs et al., 1979; Smith et al., 2003). This ichnogenus is,

however, readily distinguishable from: (1) *Octopodichnus*, which consists of straight series of four grouped, discrete tracks (Brady, 1947); (2) *Paleohelcura*, which consists of straight or triangular series of two to three tracks (Brady, 1961; Lucas et al., 2004; Davies et al., 2006); and (3) *Diplopodichnus* in which individual footprints are indistinguishable (Brady, 1947; Lucas et al., 2004; Morrissey and Braddy, 2004).

Diplichnites isp. trackways are consistently composed of two parallel sets of discrete, elongate, tracks that are not arranged in an echelon, triangular, etc. groupings (e.g., Briggs et al., 1979; Ryan, 1986; Lucas et al., 2004; Morrissey and Braddy, 2004; Davies et al., 2006). We here ascribe trackways to the ichnospecies *Diplichnites gouldi* based on similarity of these trackways to *D. gouldi* described in the literature (e.g., Gevers et al., 1971; Gevers, 1973; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004).

Diplichnites is most commonly ascribed to a myriapod or myriapod-like tracemaker. The applicability of *Diplichnites* to trackways of trilobites, as has occurred in the past, has been doubted (Briggs et al., 1979). Archipolypodan millipedes are known to occur in the CF (Wilson et al., 2005), however, those described are too small to have made the trackways described here. For these reasons, we attribute CF *D. gouldi* to a myriapod-like tracemaker of unknown taxonomic affinity.

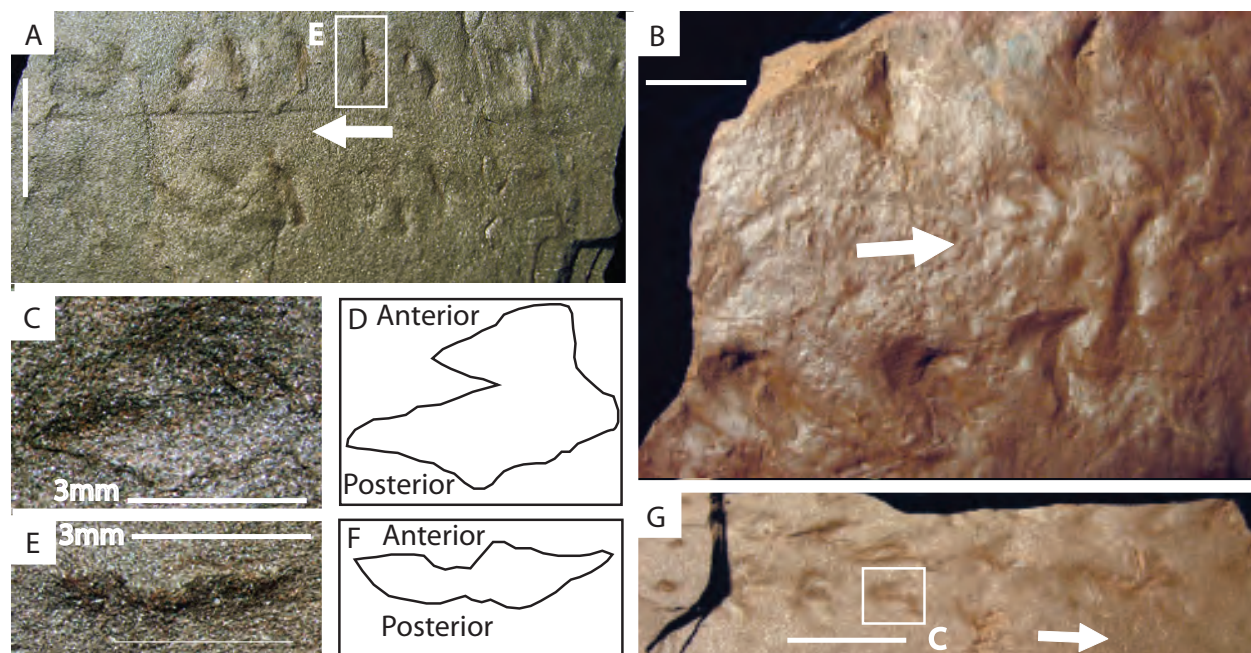


FIGURE 11— *Diplichnites gouldi*; scale=10 mm. A. *Diplichnites gouldi* type 1. B. Large *Diplichnites gouldi* type 2. C. *Diplichnites gouldi* type 2 track. D. Line drawing of *Diplichnites gouldi* type 2 track. E. *Diplichnites gouldi* type 1 track. F. Line drawing of *Diplichnites gouldi* type 1 track. G. Small *Diplichnites gouldi* type 2.

HYPEROEUTHYS TEICHONOMOS, Jones and Hasiotis (In review)

Figure 12 A–G

Description.—A single, vertical to subvertical shaft with a bulbous terminus, resulting in overall club-shaped morphology; shaft is inclined < 10 degrees; variably thick wall lining or multiple wall linings present around periphery of shaft; lining thins around the terminus; elliptical in cross section (26.4 to 145.4 mm minimum diameter and 21.2–121.6 mm maximum diameter) D1/D2 ratio 1.026 to 1.537; termini are 20–30 per cent greater in diameter than shaft, but equally elliptical in outline; termini comprise ~20 per cent of burrow height; burrows are up to 400 mm long; surficial morphology is characterized by sets of evenly spaced, transverse striations; striations are 1–5 mm wide and spaced 1 to 10 mm apart; striations are more prominent on the shaft than the terminus.

Occurrence.—Finely ripple-laminated mudstone-sandstone interbeds, weakly laminated–platy mudstone-sandstone interbeds, pedogenically modified pointbar deposits, thoroughly homogenized vertic claystones, rarely in bedding plane concentrations > 5 per m².

Discussion.—We interpret these trace fossils to be lungfish estivation burrows based on similarity to those reported in the literature (Romer and Olson, 1954; Vaughn, 1964; Carroll, 1965; Carlson, 1968; Woodrow and Fletcher, 1969; Olson and Bolles, 1975; Berman, 1976; Dalquest and Carpenter, 1977; Hasiotis et al., 1993; Hasiotis et al., 2002), and burrows of the Permian lungfish *Gnathorhiza* housed in the University of Kansas Ichnology collections, many of which contain lungfish skeletal material (Hasiotis et al., 2002). CF *Hyperoeuthys teichonomos* exhibits all of the morphological features of lungfish estivation burrows established by Hasiotis et al. (1993): 1) club-shaped morphology; 2) vertical to subvertical orientation; 3) the presence of transverse striations on the burrow surface; and 4) the presence of a sediment rind

and structureless fill.

Burrows are constructed by the modern African lungfish *Protopterus* and *Lepidosiren* on alluvial floodplains and lake margins for the purpose of estivation—a period of suspended animation, similar to hibernation to avoid desiccation during the dry season (Kerr, 1898; Carter and Beadle, 1930; Johnels and Svennson, 1954; Buillon, 1961; Greenwood, 1987). This behavior is most consistent with that of transient soil biota in the sense of Wallwork (1970), and Hasiotis (2002, 2007).

Lungfish skeletal material in the form of toothplates and cranial bone has been reported from several localities in the CF, indicating that lungfish did live on the CF floodplain (Friedman and Daeschler, 2006) (Table 1). Lungfish burrows and lungfish skeletal material also occur at some of the same localities (Table 1). Lungfish burrows are more common than skeletal material in the CF, indicating that CF lungfish were more common than is evidenced by the body fossil record.

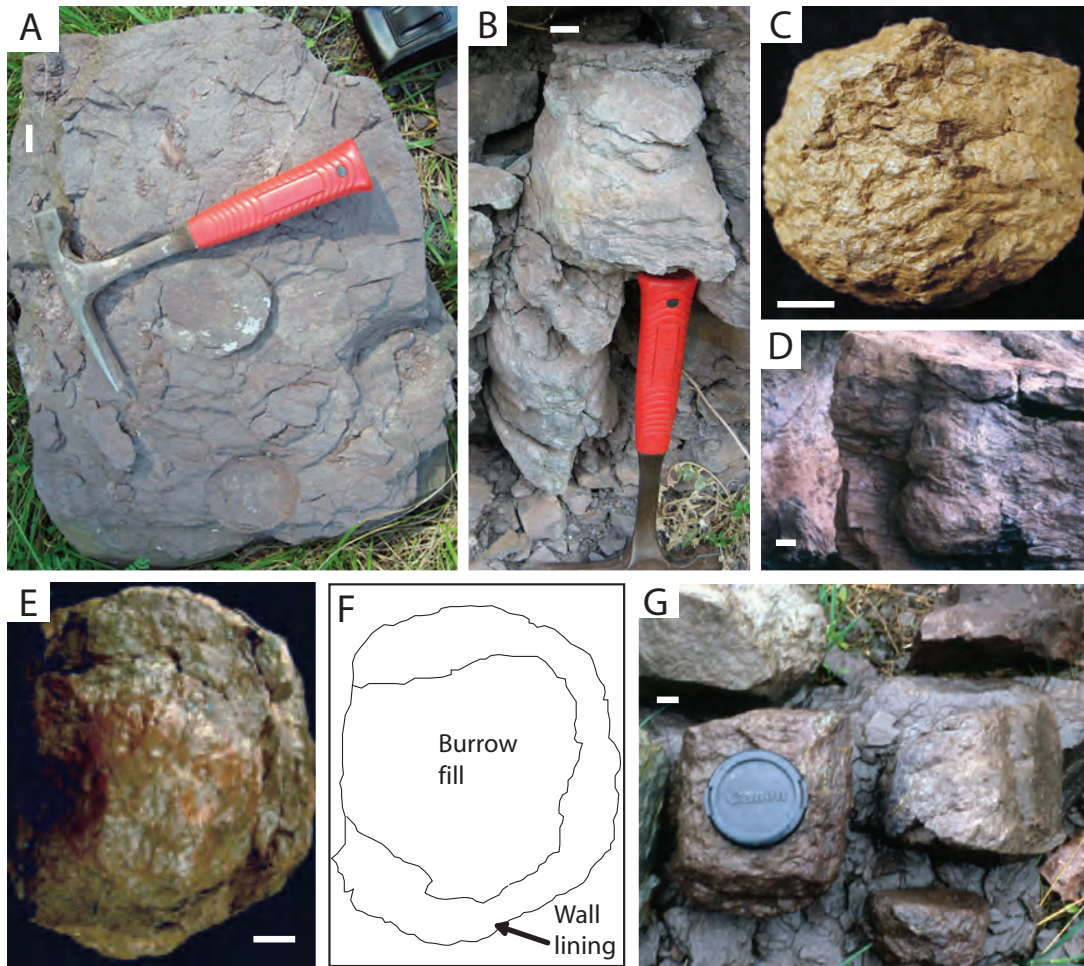


FIGURE 12— *Hypero euthys teichonomos*; scale=10 mm. A. *H. teichonomos* in a slab of very fine sandstone, Trout Run. B. Large, nearly complete *H. teichonomos*, Steam Valley. C. Terminus of *H. teichonomos*, Trout Run. D. Nearly complete *H. teichonomos*, Powys Curve. E. *H. teichonomos* with well-defined lining and fill. F. Line drawing of E. G. Shaft pieces of *H. teichonomos*, Powys Curve.

Author	Member	Year	Location
Daeschler and Mullison	?Irish Valley	2004	Tioga, Pennsylvania*
Friedman and Daeschler	Sherman Creek	2006	Hyner, Pennsylvania (Red Hill)*; Powys Township*, Pennsylvania; Mansfield, Pennsylvania; Southern Tioga County, Pennsylvania

TABLE 1—Locations from which lungfish skeletal material has been recovered; * indicates localities where we found *Hyperoeuthys teichonomos*.

Ichnogenus LOCKEIA James, 1879

Ichnospecies LOCKEIA ORNATA Bandel, 1967

Figure 13 B, E, G

Description.—Sinuous, elongated traces; 20–40 mm in diameter; 100–300 mm long; variable in diameter; portions of burrows composed of series of connected ellipsoidal cubichnia separated by narrower, elongated hypichnia; hypichnia between cubichnia are 0.25–0.5 times the width of ellipsoidal structures; surficial morphology characterized by knobby and rib-like structures; not filled with regular series of rib-like menisci; bedding parallel; preserved in convex hyporelief.

Occurrence.—The traces occur on the sole of a large block that can be traced to the bottom of a 4-m-thick package of trough crossbedded, very fine-grained sandstone at Trout Run. The traces crosscut abundant flute casts that occur on the sole of the block.

Discussion.—Bivalve burrows are commonly reported from nearshore marine and fluvial channel environments (Archer and Maples, 1984; Mangano et al., 1998; Radley et al., 1998; de Gibert and Ekdale, 1999; Schlirf et al., 2001; Hasiotis, 2002, 2004; Uchman et al., 2004; Uchman and Gazdzicki, 2006). The freshwater bivalve *Archanodon*, generally considered the tracemaker of CM bivalve burrows, has long been known to occur in the Middle to Late Devonian of New York, Pennsylvania, and Europe and has been interpreted as a shallow nonsiphonate suspension feeder based on the morphology of body fossils and subvertical meniscus-filled burrows (Newton, 1899; Gordon, 1988; Berg, 1972; Thoms and Berg, 1985).

L. ornata was originally described by Bandel (1967) as *Pelecypodichnus ornatus*, but was attributed to a new *Lockeia* ichnospecies because *Pelecypodichnus* is not a valid ichnogenus (Maples and West, 1989). CF *L. ornata* are similar to those described by Bandel (1967). CF *L.*

ornata differ from *Lockeia serialis* in lacking very well defined, keeled, almond-shaped cubichnia (Seilacher and Seilacher, 1994; Radley et al., 1998; Goldring et al., 2005).

Bivalve locomotion in sediment is composed of three phases: 1) gaping of the valves and protraction of the foot, 2) swelling of the foot and closing of the valves, and 3) retraction of the foot, which results in pulling the closed valves toward the foot (Trueman, 1966). We interpret these series of weakly almond-shaped impressions and thinner hypichnial trails to represent such locomotory cycles, with the roughly almond-shaped traces representing phase 1, during which the bivalve rested while gaping its valves, and the thinner, elongated hypichnia representing phases 2 and 3.

Ichnospecies LOCKEIA SILIQUARIA James, 1879

Figure 13 A

Description.—Almond-shaped structures; 31.9–61.5 mm in maximum diameter; 18.8–32.3 mm in minimum diameter; individual traces are isolated from others; may be weakly keeled; occur in high concentrations; preserved in convex hyporelief; traces do not exhibit a preferred orientation.

Occurrence.—These traces occur in abundance, preserved in convex hyporelief at the bottom of a bed of trough cross-bedded, scour-based, very fine-grained mica-rich sandstone at Steam Valley.

Discussion.—*Lockeia siliquaria* is the most common *Lockeia* ichnospecies reported in the literature and is interpreted to be the resting trace (cubichnion) of an infaunal bivalve (Archer and Maples, 1984; Seilacher and Seilacher, 1994; Schlirf et al., 2001; Goldring et al., 2005; Gaillard and Racheboeuf, 2006). Whether this trace represents an external mold of a bivalve

shell, or an impression of its foot has been debated (Seilacher and Seilacher, 1994). The only occurrence of *L. siliquaria* found during our fieldwork was at the Steam Valley locality and did not co-occur with *L. ornata*.

CF bivalve body fossils and burrows are normally attributed to the Devonian freshwater bivalve *Archanodon* (Berg, 1972; Thoms and Berg, 1985; Bridge, 1986). No bivalve body fossils were found during fieldwork for this study. *L. siliquaria* described here, however, are similar in size and proportions to *Archanodon* body fossils figured by Berg (1972), and Bridge (1986). We interpret CF *L. siliquaria* to represent a cubichnion produced by *Archanodon*.

PLEUROCURVUS new ichnogenus

Figure 13 C, D, F, H

Diagnosis.—Subvertical, J-shaped traces; filled with thin, continuous, arcuate meniscus-like structures; elliptical in outline; surficial morphology rugose.

Description.—Traces filled with 2.5–5 mm thick meniscus-like structures. Meniscus-like structures are oriented normal to the long axis of the burrow; preserved in full relief, subvertical in orientation and roughly J-shaped.

Etymology.—Greek, *Pleuron* rib, in reference to meniscus-like burrow fill; Latin, *Curvus* bent.

PLEUROCURVUS ARENAORTE new ichnospecies, Figure 15 B, C, D, F, H

Sand Plugged Pipes, Allen, 1961

Pelecypodichnus, Eagar, 1974

Beaconites antarcticus, Allen and Williams, 1981

Bivalve trace fossils, Thoms and Berg, 1985

Beaconites isp., Bridge et al., 1986

Large vertical burrows, Gordon, 1988

Escape traces, Sarkar and Chauduri, 1992

Etymology.—Latin, *Arena* sand; Greek, *Aorte* pipe.

Diagnosis.—As for ichnogenus; only known ichnospecies.

Types.—No types were repositied, because the only examples found occur on a boulder too large to collect on the southern end of the Trout Run outcrop.

Type Stratum.—Upper Devonian Catskill Formation

Type Locality.—East side of US Highway 15, ~1 km north of Trout Run, Pennsylvania, U.S.A. (41° 23' 31'' N, 77° 03' 31'' W).

Description.—Of the Trout Run burrows, one is 24 cm long, elliptical in cross section and crosscuts the entire thickness of the block perpendicular to bedding. The burrow is apparently incomplete. This burrow is poorly preserved, however, badly weathered meniscus-like structures are distinguishable on the burrow surface. The other two examples are preserved at the bottom of the block and apparently crosscut bedding with a slightly subhorizontal to subvertical orientation as evidenced by the orientation of menisci and the exposure of only what appear to be the termini of the burrows. Burrow surficial morphologies are weakly to strongly rugose, reflecting the presence of meniscus-like internal structure.

Occurrence.—The burrows described here occur in a block of mica-rich, very fine-grained sandstone traced to the bottom of a 4-m-thick interval of very fine-grained, trough cross-bedded sandstone at Trout Run.

Discussion.—Meniscus-filled, subvertical bivalve burrows have been reported from middle Paleozoic alluvial channel deposits by Allen (1961), Berg (1973), Eagar (1974), Allen

and Williams (1981), Bridge and Dingman (1981), Thoms and Berg (1985), Bridge et al. (1986), and Gordon (1988) and interpreted to represent readjustment of freshwater bivalves following sedimentation events, based on comparisons with burrows of the modern unionid bivalve *Margaritifera margaritifera* (Thoms and Berg, 1985; Bridge et al., 1986).

Bridge and Dingman (1981) and Bridge et al. (1986) attributed similar burrows to *Beaconites*. Bridge et al. (1986) suggested that they differed from known *Beaconites* isp. Eagar (1974) attributed meniscus-filled bivalve burrows to *Pelecypodichnus*, however, these burrows do not conform to that ichnogenus, because Seilacher (1953) described the ichnogenus to represent almond-shaped cubichnia (Maples and West, 1989). *Pelecypodichnus* is also not a valid ichnogenus (Maples and West, 1989).

Pleurocurvus arenaorte differs from known ichnospecies of *Beaconites* as described by Vialov (1962) and Bradshaw (1981) in that they are: 1) nearly always sub-vertical in orientation; and 2) lack true arcuate backfill menisci, reflecting a different behavior than *Beaconites* and other burrows containing backfill menisci. Meniscus-filled bivalve burrows of Devonian to recent deposits represent re-equilibration of bivalves after sedimentation in order to maintain constant burial depth (Thoms and Berg, 1985; Bridge, 1986), rather than active backfilling by a burrowing organism, as in Smith and Hasiotis (2008) and Counts and Hasiotis (2009).

Pleurocurvus arenaorte meniscus-like structures represent offset laminae that were disrupted by the bivalve after burial. The lack of analogy of *P. arenaorte* to all *Beaconites* ichnospecies indicates that this new ichnotaxon is necessary.

Subhorizontal portions of burrows interpreted to represent *P. arenaorte* (Fig. 13 B, F, H) are interpreted to represent the most basal portion of the trace. The slight curvature of CF *P. arenaorte*, as can be seen in Figure 13D, is the result of the lowermost portions of burrows

crosscutting the bedding tangentially. These lowermost portions of the burrows crosscut the sole of the bed at a subhorizontal to subvertical orientation and can be preserved in convex hyporelief. The subhorizontal to subvertical lowermost portions of the burrows represent initial readjustment of the bivalve in response to sedimentation. Bivalves exhibit a rocking motion when readjusting their position in the sediment column, resulting in a horizontal and vertical component of locomotion (Stanley, 1975). We interpret the subhorizontal to subvertical, lowermost portions of *P. arenaorte* to represent both horizontal and vertical locomotion, resulting from this rocking motion.

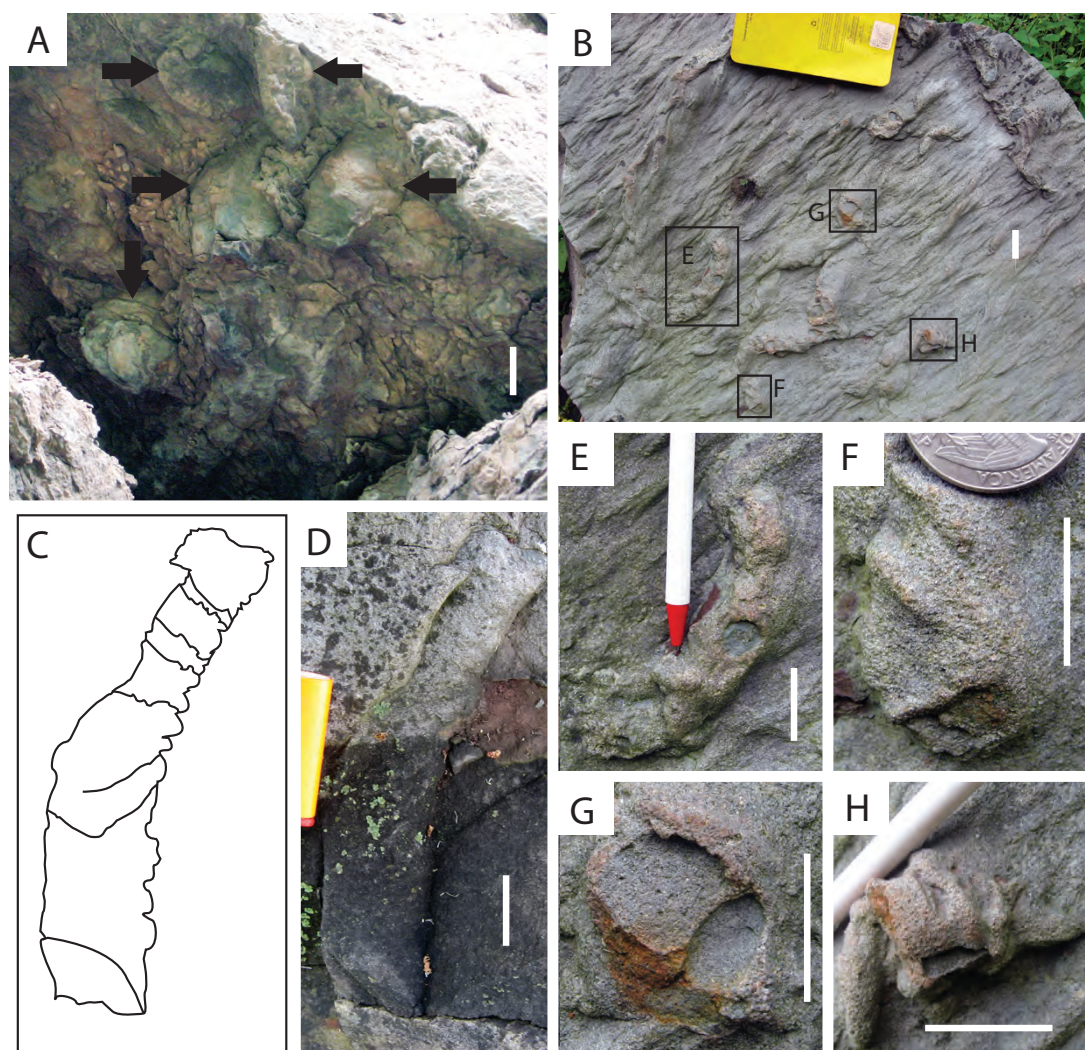


FIGURE 13— Bivalve burrows; scale=20 mm. A. Multiple *Lockeia siliquaria* on the sole of a fine sandstone bed, Steam Valley. B. Multiple *Lockeia ornata* and *Pleurocurvus arenaorte* on the sole of a very fine sandstone bed, crosscutting a fabric of flute casts, Trout Run. C. Line drawing of D. D. *Pleurocurvus arenaorte*, Trout Run. E. *Lockeia ornata* on the sole of a very fine sandstone bed, Trout Run. F. *Pleurocurvus arenaorte* from the sole of the very fine sandstone bed, Trout Run. G. Cross section of *Lockeia ornata*, Trout Run. H. *Pleurocurvus arenaorte* on the sole of a bed, Trout Run.

Ichnogenus SAGITTICHNUS Seilacher, 1953

Type ichnospecies SAGITTICHNUS LINCKI Seilacher, 1953

Figure 14 A–C

Description.—Keeled, arrowhead-shaped to rice-grain-shaped traces; 1–3 mm wide and 2–4 mm long; occur in great abundance when found; keel is not usually prominent; long axis often slightly curved.

Occurrence.—Preserved in convex hyporelief at the bottom of a purple, very fine-grained sandstone bed on the west side of US Highway 15 at Powys Curve, Pennsylvania (41° 20' 08.91" N, 77° 04' 52.99" W).

Discussion.—*Sagittichnus lincki* was described by Seilacher (1953) and is thought to be the resting trace of an unknown organism (Garvey and Hasiotis, 2008). Literature on *Sagittichnus* is rare but the trace has usually been reported from continental environments (e.g., Gluszek, 1995; Garvey and Hasiotis, 2008) in association with other small resting traces and bedding-parallel repichnia (Bromley and Asgaard, 1979; Gluszek, 1995; Garvey and Hasiotis, 2008). Traces similar in morphology to *Sagittichnus* have been produced by modern freshwater ostracodes under experimental conditions (Retrum et al., 2011, in press). We, however, cannot definitely ascribe CF *S. lincki* to ostracode behavior.

Ostracodes and conchostracans have been reported from Middle and Upper Devonian CM rocks of New York; however, there is debate about whether the ostracodes were freshwater or marine (Gordon, 1988; Friedman and Lundin, 1998; Knox and Gordon, 1999). The association of CM ostracodes and conchostracans with lingulid brachiopods and *Spirophyton* traces suggests that they are from a brackish water environment (Knox, 2001). The CF *S. lincki* tracemakers may have been ostracodes, based on the trace fossil morphology. This would

indicate that freshwater ostracodes first evolved in the Late Devonian. The tracemaker of CF *S. lincki* is indeterminate, and other occurrences of *Sagittichnus* are generally not ascribed to a specific tracemaker (Garvey and Hasiotis, 2008).

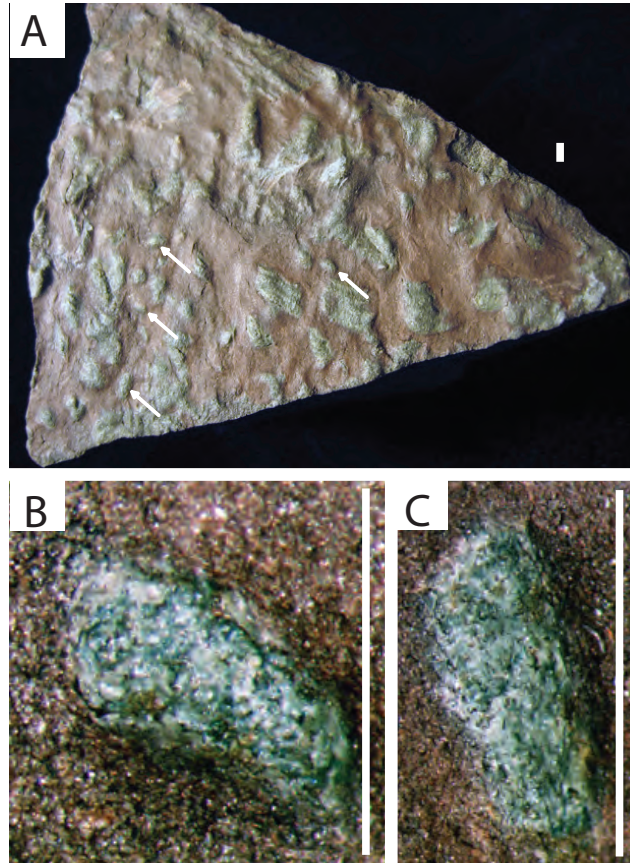


FIGURE 14— *Sagittichnus lincki*; scale=5 mm. A. Multiple *Sagittichnus lincki* on the sole of a very fine sandstone block, Powys Curve. B. Close-up of *Sagittichnus lincki*—same block as 14A. C. Close-up of *Sagittichnus lincki*—same block as 14A.

Ichnogenus UNDICHNA Anderson, 1976

UNDICHNA MULTILOBA new ichnospecies.

Figure 15 A–D

Diagnosis.—Horizontal, straight to sinuous paired sets of scratch marks; scratch marks in a set equal in diameter; sets composed of three to five scratches; scratch marks may be continuous or are composed of discontinuous sets.

Etymology.—*Multi* Latin, many; *Lobos* Greek, lobe.

Holotype.—KUVP152193

Paratype.—KUVP152192

Type stratum.—Upper Devonian Catskill Formation.

Type locality.—West side of US Highway 15, Powys Township, Pennsylvania, ~10 km south of the village of Trout Run, Pennsylvania, U.S.A., (41° 20' 08.91" N, 77° 04' 52.99" W).

Repository.—Division of Vertebrate Paleontology, Museum of Natural History and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, U.S.A.

Description.—Sets of 3–5 horizontal, paired sets of scratch marks; sets are composed of discontinuous scratch marks < 10 mm long, or continuous scratch marks up to 79.1 mm long; surficial morphology smooth; sets within a pair are spaced 8–15 mm apart; each scratch is 0.6–1.4 mm in diameter; sets are 1.8–6.1 mm wide and spacing within each set is the same; preserved in convex hyporelief.

Occurrence.—Two blocks at Powys Curve recovered from float traced to part to a ~0.3-m-thick purple, very fine-grained sandstone bed, 1.5 m from the base of a 3.6-m-thick channel filled with green and purple very fine, muscovite-rich, low angle trough cross-bedded sandstone with bedsets bounded by low angle lateral accretion surfaces.

Discussion.—The multilobate nature of *U. multiloba* differentiates it from all described *Undichna* isp. (Anderson, 1976; Turek, 1989; Lu et al., 2003; Wisshak et al., 2004; Minter and Braddy, 2006). The *Undichna* isp. most similar to *U. multiloba* are *U. septemsulcata* and *U. bina*. Despite being similar in width and sinuosity to *U. multiloba*, *U. septemsulcata* exhibits bilobate, rather than multilobate pectoral fin trails, and includes a caudal fin trail (Wisshak et al., 2004).

Undichna bina is similar to *U. multiloba* in lacking a caudal fin trail, however, the paired fin (pectoral or pelvic) trails of *U. bina* are unilobate (Anderson, 1976; Minter and Braddy, 2006). *Undichna multiloba* differs from *Lunichnium rotterodium* and *Gracilichnium chlupaci*—amphibian swimming traces—in lacking foot impressions, and a central median groove (Turek, 1989; Minter and Braddy, 2006).

We interpret the continuous multilobate scratch marks described here to represent dragging of the pelvic or pectoral fins of a placoderm fish while it swam. This interpretation is based on: 1) the fact that they are paired; 2) their continuous nature; and 3) their sinuosity (Fig. 15). Discontinuous multilobate scratch marks likely represent a fish using its pectoral fins to push along the sediment surface, resulting in the production of trails as much as 3 cm long of discrete, scratch marks < 10 mm long (Fig. 16). Why a discernible caudal fin trace is absent is unknown.

The fish fauna of the CF includes representatives of the Placodermi, Sarcopterygii (Dipnoi and Rhipidistii), Acanthodii, and early Actinopterygii (Daeschler, 2000; Daeschler and Mullison, 2004; Davis et al., 2004; Friedman and Daeschler, 2006). The fish fauna of Powys Curve is composed of the antiarch placoderm *Bothriolepis* sp., a lungfish of indeterminate taxonomic affinity, Acanthodian fishes, the porolepiform *Holoptychius* sp., and the rhizodont

Sauripterus sp. (Friedman and Daeschler, 2006).

The inferred benthonic habit of such antiarch placoderms as *Bothriolepis* (Carrol, 1988) suggests that a placoderm similar to *Bothriolepis* may have been the tracemaker. The 8–15 mm spacing of pairs of scratch mark sets falls slightly below the low end of *Bothriolepis* sp. head shield widths figured by Thomson and Thomas (2001)—head shield width roughly corresponds to the spacing of the anterior margins of proximal pectoral fin segments in most *Bothriolepis* sp. reconstructions (e.g., Patton, 1904; Denison, 1941; Thomson and Thomas, 2001). This may indicate that the tracemaker was a juvenile, or a smaller placoderm similar to *Bothriolepis*. Proximal pectoral fin segments of *Bothriolepis* sp. often exhibit a scalloped anterior margin (Patton, 1904; Denison, 1941), which may be responsible for the multilobate morphology of *U. multiloba*.

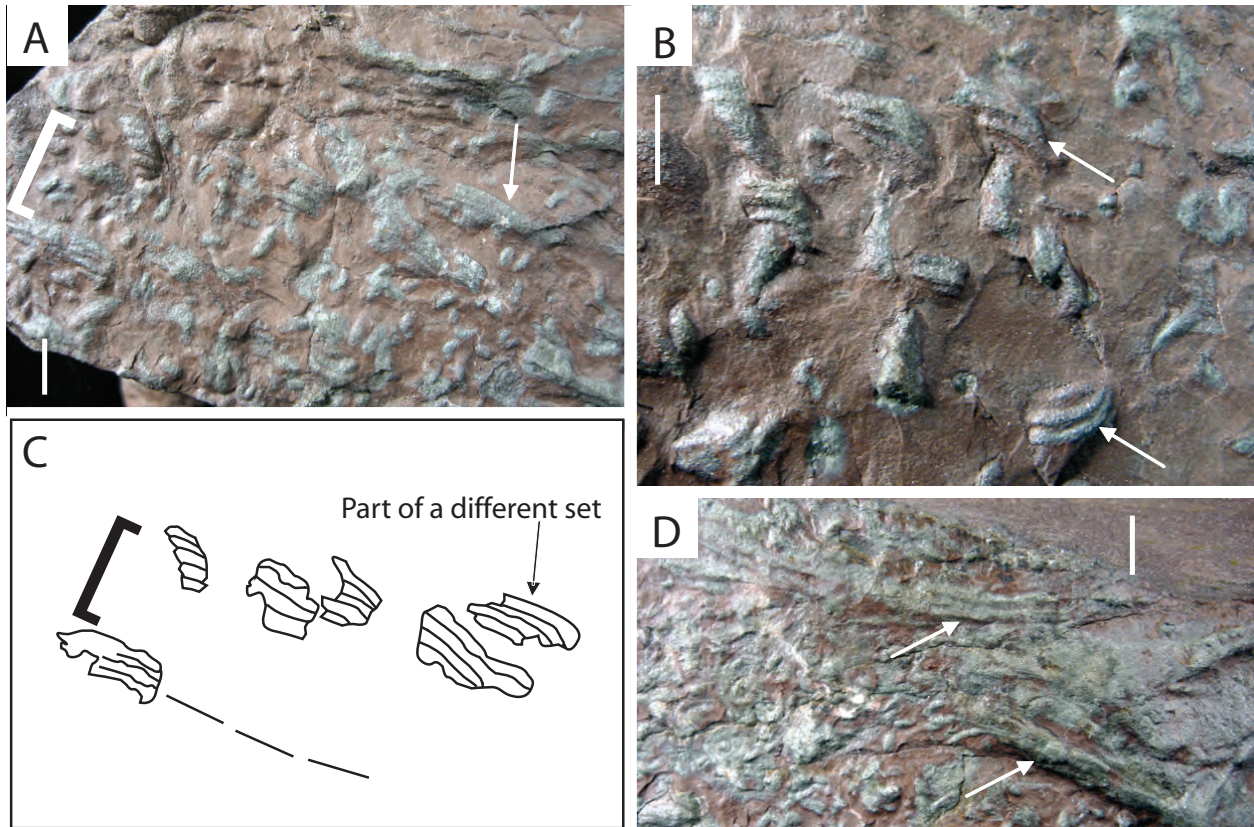


FIGURE 15—*Undichna multiloba*; scale=10 mm. A. The Holotype with discontinuous *Undichna multiloba* and *Sagittichnus lincki*. B. The Paratype with discontinuous *Undichna multiloba*. C. Line drawing of 12A. D. The Holotype with continuous *Undichna multiloba*.

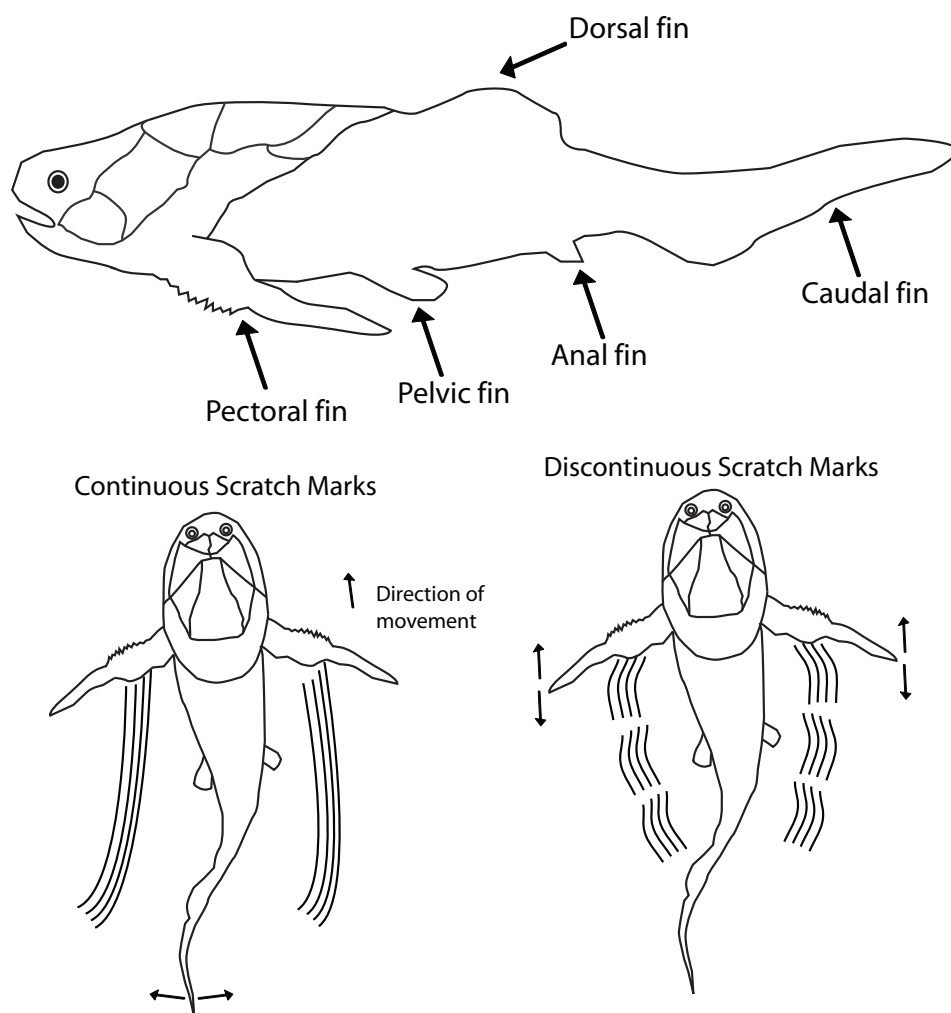


FIGURE 16— Interpretive drawing of *Undichna isp.* production.

RHIZOLITHS

Clay-filled, hematite-rich rhizoliths

Figure 17 A, F, H

Description.—Diameter 2–20 mm; exhibit minimal downward-tapering, downward and laterally fractal-branching, dominantly dichotomous structures; structures bifurcate, trifurcate, or rarely exhibit multiple 0.5–1 mm diameter branches; branches emanate from multiple 2–5 mm-diameter branches, rather than a single primary branch; branches range from first to approximately 20th order; lateral roots diverge from and aggregate around larger roots; individual branch lengths range from 10 mm to 200 mm; branching angles range from 10°/170° to 55°/125°; radial angles range from 20°/160° to 80°/100°; fill is composed of a hematite-rich clay lining that exhibits high relief in thin section, and frequently a core of translucent-to-vitreous, sparry or micritic calcite, or quartz silt grains; clay linings contain inclusions of quartz silt and muscovite; clay often exhibits an apparently fibrous or layered texture in thin section; rhizoliths may lack a core; individual rhizoliths may have carbonate-cored, sediment cored and coreless portions; penetrative up to 300 mm, but normally less than 200 mm; individual root systems may be > 500 mm in lateral extent; occur in concentrations of 10's to 100's per dm².

Occurrence.—Ripple-laminated mudstone-sandstone interbeds, weakly laminated to platy mudstone-sandstone interbeds, pedogenically modified trough cross-bedded sandstones, thoroughly homogenized vertic claystones.

Discussion.—The presence of a carbonate or quartzose silt core in portions of nearly all clay-filled, hematite-rich rhizoliths suggests that rhizolith preservation was a process involving two or more stages. The clay-filled portions of rhizoliths always surround the carbonate or silt core when the core is present. This suggests that the hematite and clay accumulated around the

root, which later decayed, leaving space to be filled with pedogenic carbonate, or silt depending on predominant physicochemical conditions at the time of replacement.

Rhizoliths often exhibit evidence of complex formational histories, resulting in petrographic and compositional heterogeneity of individual rhizoliths (e.g., Cohen, 1982; Mount and Cohen, 1984; Kraus and Hasiotis, 2006). CF clay-filled hematite-rich rhizoliths differ from those described by Cohen (1982) and Mount and Cohen (1984), however, in that the outermost portion of CF rhizoliths is composed of clay, rather than micrite.

Evidence of illuviation of clay in soil channels, such as root channels, is common in soils and paleosols (Retallack, 2001). Illuvial clay rinds on rhizoliths have been recognized in paleosols (e.g., Fernandes and Basilici, 2009). The clay in the outer rinds of CF clay-filled, hematite-rich rhizoliths is likely of illuvial origin.

Architectural morphologies of clay-filled, hematite-rich rhizoliths are similar to fibrous roots in the terminology of Pfefferkorn and Fuchs (1991), Hasiotis (2002), and to Type V fibrous roots of Cannon (1949). The similarity of clay-filled, hematite-rich rhizolith morphology to that of Cannon's (1949) Type V roots is the presence of multiple primary roots, rather than a single primary root.

Multiple primary roots have been described from the CF in association with the isotalean lycopsid *Otzinachsonia beerboweri*. Photographs of *O. beerboweri* roots from Cressler and Pfefferkorn (2005) show that, in addition to radiating from multiple primary roots, *O. beerboweri* roots exhibit a dominantly dichotomous branching pattern, and a radial pattern similar to those of CF clay-filled, hematite-rich rhizoliths. Reconstructions of the roots of *Selaginella fraiponti*, a small Carboniferous lycopod (Shankler and Leisman, 1969), lower Mississippian lycopod roots attributed to *Protostigmara eggertiana* figured by Jennings et al. (1983), roots of the modern

lycopod *Selaginella selaginoides* figured by Karrfalt (1981), are also similar to CF clay-filled, hematite-rich rhizoliths in exhibiting multiple dichotomously branched primary roots.

CF clay-filled, hematite-rich rhizoliths were not found in association with plant body fossils, or structures similar to lycopod rooting organs, making definitive identification of the tracemaker impossible. We interpret CF clay-filled, hematite-rich rhizoliths to represent lycopod root systems based on their similarity to lycopod roots. The presence of lycopod roots in CF paleosols is consistent with the occurrence of lycopod body fossils at Red Hill (Cressler and Pfefferkorn, 2005; Cressler, 2006).

Neither Cressler and Pfefferkorn (2005), nor Cressler (2006) included estimates of the height of CF lycopods, likely because the material that they examined was fragmentary. Cressler and Pfefferkorn (2005), however, identified two size classes of *O. beerboweri*, the first ranging from 2.5 to 3.5 cm in maximum diameter, and the second ranging from 8.0 to 10.3 cm in diameter. This suggests that *O. beerboweri* was a relatively small (at least not arborescent) plant. The relatively shallow penetration depth and small aerial extent of CF clay-filled, hematite-rich root systems is consistent with similarly small plants.

Plant rooting depth is largely dependent on the moisture preferences and tolerances, and physiology of different plant species (Schultze et al., 1996; Shenk and Jackson, 2002), although average plant root depths tend to be greatest in arid environments (Jackson et al., 1996). Root oxygenation is an extremely important physiological process in root systems, and root morphology is strongly influenced by root oxygen needs in a given plant species (Cannon, 1949; Shenk and Jackson, 2002). Water table depth exerts strong control on rooting depth because of the interplay of plant roots' need for both moisture and oxygen for woody riparian vegetation in alluvial environments (Shafroth et al., 2000). For example, shallow water table depth can result

in shallow rooting depth, whereas deep or variable water table depth can result in deeply penetrative rooting in the same plant species.

The shallow penetration depth of CF clay-filled, hematite-rich rhizoliths indicates that they represent plant rooting in the upper vadose zone of actively forming CF alluvial soils. Plants represented by CF clay-filled, hematite-rich rhizoliths were likely dependent on well-drained, well-oxygenated soil conditions and represent organisms with terraphilic or hygrophilic affinities *sensu* Hasiotis (2002, 2007). The plants' need for well-drained, well-oxygenated conditions, in addition to explaining the shallow rooting depth of clay-filled, hematite-rich rhizoliths, is consistent with the predominance of oxidized, rather than reduced iron in these rhizoliths (e.g., Kraus and Hasiotis, 2006; Smith et al., 2008b).

Rhizohaloes

Figure 17 C, G

Description.—5BG 8/4 chroma, 3–50 mm diameter downward and laterally fractal-branching, dichotomous structures; dominantly 30–50 mm in diameter; branches range from second to approximately fifth order; branching angles range from 20°/160 to 90°; penetrative up to 800 mm; up to 1,000 mm long; infilled with silt, clay, mud, or sand; sometimes contain pedogenic carbonate; composition is similar to host rock; termini of branches are somewhat rounded; may be vertical or horizontal; boundaries sharp to diffuse but normally sharp; occur in concentrations of tens per m² in thoroughly homogenized vertic claystone paleosols.

Occurrence.—Weakly laminated–platy mudstone-sandstone interbeds, thoroughly homogenized vertic claystones.

Discussion.—Redoximorphic mottling results from the presence of multiple Fe oxidation

states in paleosols (PiPujol and Buurman, 1997; Scheinost and Schwertmann, 1999) and reflects the hydrologic regime under which soil formation occurred (PiPujol and Buurman, 1997; Kraus and Hasiotis, 2006). Roots create channels in soils that facilitate water percolation through the soil profile (Cohen, 1982; Mount and Cohen, 1984; PiPujol and Buurman, 1997; Kraus and Hasiotis, 2006). This water movement can produce gley features (pseudogley) in channels and pores of dominantly well-drained soils during periods of seasonal waterlogging (PiPujol and Buurman, 1994; Retallack, 2001). This results from the reduction and removal of iron from sediment filling soil channels during waterlogged periods (PiPujol and Buurman, 1994; Kraus and Hasiotis, 2006).

PiPujol and Buurman (1994) established a six-stage qualitative assessment of the degree of pseudogley of paleosols. CF rhizohaloes exhibit strong depletion of iron and a 1–2 mm thick bleached rim around the halo that can be identified in thin section and is composed of the same sediment as the rest of the host rock and rhizohalo. CF rhizohaloes do not include a rim of red neoneoferrans. CF rhizohaloes, thus, best conform to pseudogley stage 4 of PiPujol and Buurman (1994). Stage 4 pseudogley features of PiPujol and Buurman (1994) exhibit strong depletion of iron in the root or other soil macrochannel, as indicated by greenish gray colors, and partial dissolution of neoferrans associated with the pseudogley feature (PiPujol and Buurman, 1994). CF rhizohaloes, despite lacking partially dissolved neoferrans, do not appear to exhibit as much gleying as PiPujol and Buurman's (1994) stage 5, because stage 5 pseudogley features exhibit complete removal of iron resulting in wide, gray soil macrochannels and complete removal of iron from the channel. The green color of CF rhizohaloes indicates incomplete removal of iron from the root channel.

Analysis of thin sections and slabbed sections indicates that CF rhizohaloes are often

associated with micritic and sparry carbonate rhizoliths and pedogenic carbonate nodules. Kraus and Hasiotis (2006) described gleyed rhizohaloes with carbonate accumulations and attributed the rhizolith redoximorphic features to surface water gley. Carbonate accumulations, including small carbonate rhizoconcretions in rhizohaloes from the Paleocene Willwood Formation have been interpreted to result from seasonal wetting and drying of soils (Kraus and Hasiotis, 2006). We make the same interpretation for carbonate in CF rhizohaloes, consistent with the presence of vertic structures in CF paleosols.

The large diameter and highly penetrative nature of CF rhizohaloes suggests that they represent highly penetrative, primary taproots of a large plant. Physiological water and oxygen preferences exert a strong control on root morphology and penetration depth (Cannon, 1949; Shultze et al., 1996; Shafroth et al., 2000; Shenk and Jackson, 2002). The deeply penetrative nature of CF rhizohaloes suggests that they represent rooting deep in the vadose zone to allow for exploitation of deep water sources in dry soil conditions. Driese et al. (1997) suggested that deeply penetrative roots associated with CF stump casts at Trout Run represent the same behavior in response to dry soil conditions. Penetration of CF rhizohaloes to the lower vadose zone or phreatic zone is consistent with behavior of hygrophilic organisms *sensu* Hasiotis (2002, 2007). The differential penetration depth of CF clay-filled, hematite-rich rhizoliths and rhizohaloes is significant, as it indicates that CF plants exhibited both terraphilic and hygrophilic behaviors.

Although CF rhizohaloes are composed of multiple large-diameter, primary roots, as is similar to clay-filled, hematite-rich rhizoliths, the greater size and penetration depth of CF rhizohaloes suggests that they do not represent the same plants. Driese et al. (1997) suggested that large-diameter, deeply penetrative rhizoliths associated with stump casts represent rooting of

the arborescent progymnosperm *Archaeopteris*. *Archaeopteris* is, however, not the only arborescent plant reported from the CF, as the arborescent lycopod *Lepidodendropsis* has also been reported from Red Hill (Cressler, 2006). We interpret CF large-diameter, deeply penetrative CF rhizohaloes to represent deep primary taproots of an arborescent plant, probably *Archaeopteris*, but perhaps *Lepidodendropsis*.

Carbonate Rhizocretions

Figure 17 D

Description.—Downward and laterally fractal-branching, dichotomous structures; < 1–15 mm in diameter; penetrative less than 100 mm; highly fragmentary; composed of micritic and sparry calcite; boundaries are sharp to diffuse; may be composed of a rim of sparry calcite and micritic core; occur in concentrations up to thousands in hand sample; difficult to distinguish in outcrop.

Occurrence.—Finely ripple-laminated mudstone-sandstone interbeds, weakly laminated to platy mudstone-sandstone interbeds, pedogenically modified trough cross-bedded sandstone, thoroughly homogenized vertic claystones.

Discussion.—Carbonate rhizocretionss have been reported from the CF by Driese and Mora (1993); Driese et al. (1993,1997); and Retallack et al. (2009). Carbonate rhizoliths are associated in all of these facies with clay-filled, hematite-rich rhizoliths and green rhizohaloes; however, they are most commonly associated with rhizohaloes, especially when rhizohaloes contain carbonate accumulations. Carbonate rhizoliths associated with rhizohaloes are generally much smaller in diameter than the rhizohaloes (1–3 mm) and occur in dense accumulations.

The significance of carbonate rhizoliths has been discussed by Kraus and Hasiotis (2006),

who suggest that their formation is indicative of seasonal wetting and drying of soils, even when evapotranspiration does not exceed precipitation (Farrel, 1987; Aslan and Autin, 1988). Cohen (1982) asserted that carbonate rhizoliths form in voids left after root decay, with precipitation beginning in the root channel and extending outward. This mode of formation seems most likely for CF carbonate rhizoliths, because they exhibit sharp boundaries and contain few inclusions of quartzose silt or clay, and do not contain root body fossils.

The occurrence of carbonate rhizoliths is consistent with inferred wet-dry seasonality on the CF alluvial plain (Woodrow et al., 1973; Driese et al., 1993) and is corroborated by the presence of vertic structures and angular blocky peds in CF paleosols. Driese and Mora (1993) asserted that carbonate rhizoliths broken by argilloturbation in CF soils provided nuclei around which carbonate nodules formed. The presence of carbonate rhizoliths in actively forming CF vertic soils contributed to the formation of subsoil carbonate horizons, as such.

The fragmentary nature of CF carbonate rhizcretions makes analysis of their root architecture difficult. The shallow penetration depth and dichotomous architecture of these traces suggests that they represent shallow rooting by terraphilic plants with a physiological need for well-drained, well-oxygenated soils.

The fragmentary nature of CF rhizcretions further makes identification of the tracemaker(s) difficult; we cannot propose a well-supported hypothesis of the identity of the tracemaker. Small (0.5–1 mm) diameter rhizcretions are often found associated with large-diameter rhizohaloes. This suggests that some CF rhizcretions may represent root hairs of large, arborescent plants, however, this interpretation is speculative. These small-diameter rhizcretions may also represent rooting by relatively small plants that coexisted with arborescent plants on the CF alluvial plain.

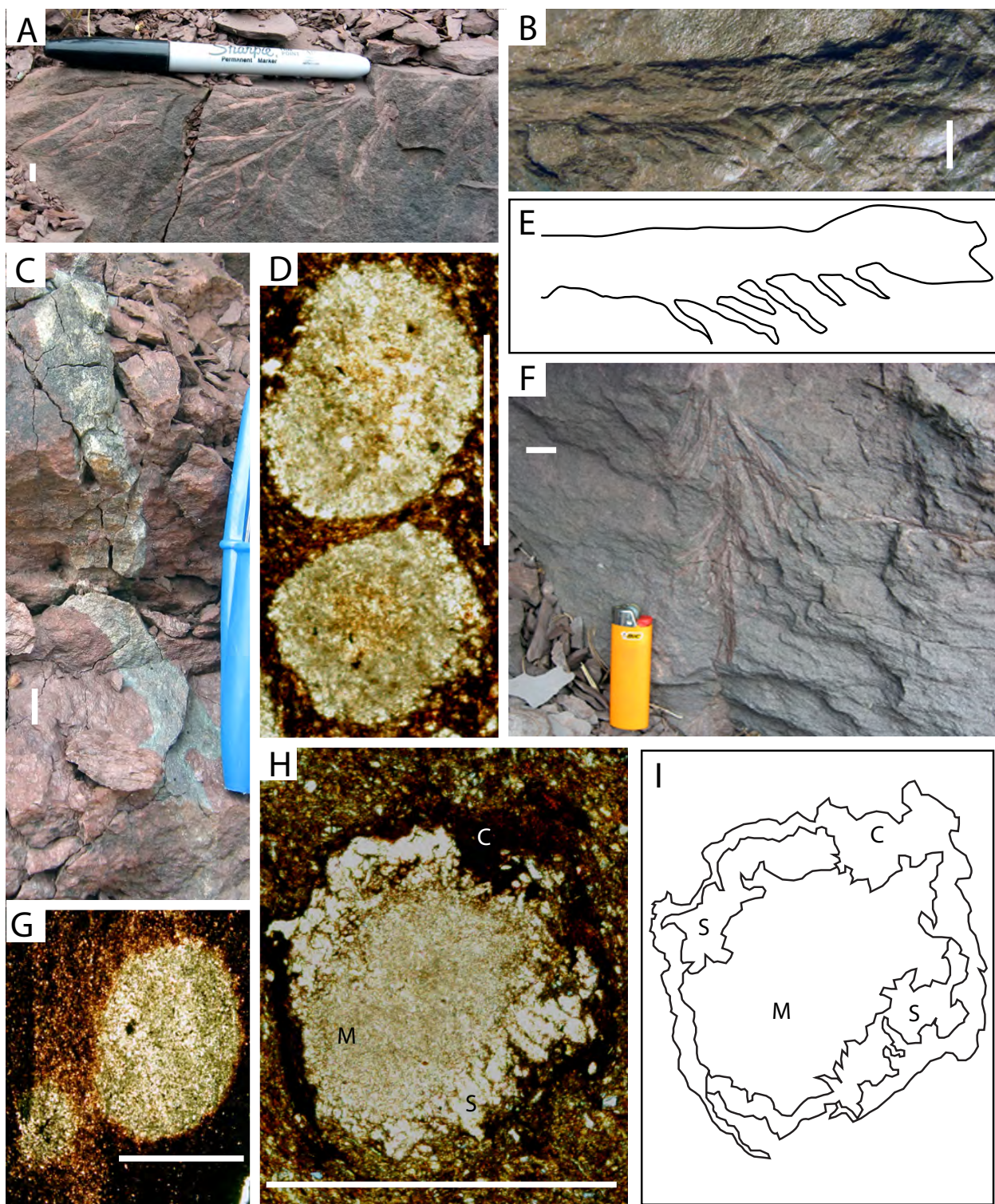


FIGURE 17—Rhizoliths; scale=5 mm. A. Clay-filled, hematite-rich rhizoliths penetrating a very fine sandstone bed, Powys Curve. B. Closeup of a clay-filled, hematite-rich rhizoliths, Trout Run. C. Rhizohalo, Steam Valley. D. Carbonate rhizocretions in thin section, Trout Run. E. Line drawing of B showing branching pattern of rootlets. F. Clay-filled, hematite-rich rhizoliths, Powys Curve. G. Cross section of small rhizohaloes in thin section, Powys Curve. H. Cross section of carbonate-cored, clay-filled hematite-rich rhizoliths, Powys Curve; M=micrite, C=hematite-rich clay, S=sparry calcite.

In Situ Stump Casts

Figure 18

Description.—Vertically oriented, cylindrical, sediment-filled structures; base of structures characterized by downward and laterally fractal-branching, dichotomous, sediment-filled rhizoliths; may exhibit a deeply penetrative, central tap root or multiple deeply penetrative primary taproots; fill material similar to host rock.

Occurrence.—Pedogenically modified, trough cross-bedded sandstones, weakly laminated-to-platy sandstone-mudstone interbeds, thoroughly homogenized vertic claystones.

Discussion.—*In situ* stump casts have been described in the CF by Driese et al. (1997) from a pedogenically modified channel sandstone at Trout Run, Pennsylvania. The stump casts of Driese et al. (1997) were: 1) vertical in orientation, 2) filled with material similar to the host rock, 3) exhibited reticulate internal structure of unknown significance, and 4) associated with abundant carbonate rhizoliths. These stump casts occurred in a discrete horizon in a paleosol interpreted as a protosol, *sensu* Mack et al. (1993).

The stump casts described here are similar to those of Driese et al. (1997) in being similar in orientation, having fill that is similar in composition to the host rock, and being associated with carbonate rhizocretions. Whether or not the stump casts exhibit reticulate internal structure is unclear, because samples could not be collected. The stump casts described by Driese et al. (1997) were attributed to the arborescent progymnosperm *Archaeopteris*. CF stump casts may represent rooting by *Archaeopteris*, *Lepidodendropsis*, or both plants. Stump casts with and without large, single, primary taproots may represent different species of *Archaeopteris*, but may also represent rooting by *Archaeopteris* and *Lepidodendropsis*.

In situ stump casts are important, because they occur in life position, allowing for analysis of their paleoenvironmental context. Stump casts reported here occur in paleosols of differing maturity (Protosols to Vertisols, *sensu* Mack et al., 1993). These stump casts occur in paleosols representing moderately to well-drained soils. Inferred paleohydrologic relationships of deeply penetrative CF rhizohaloes are discussed above and we make the same interpretation for CF *in situ* stump casts—that they represent rooting in the lower vadose zone or upper phreatic zone by arborescent plants with hygrophilic to hydrophilic affinities.

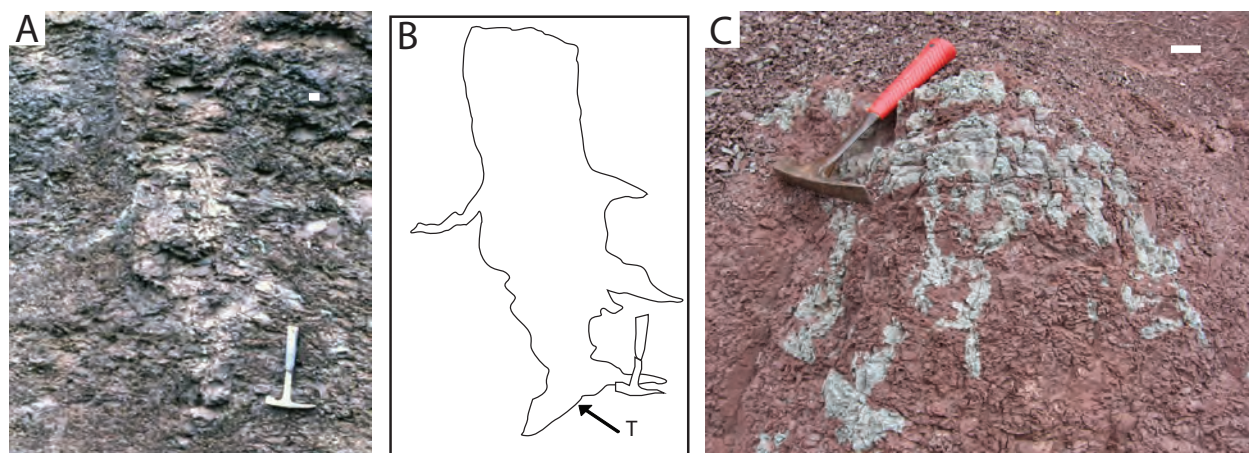


FIGURE 18—*In situ* stump casts. A. *In situ* stump cast with taproot, Red Hill. B. Interpretive line drawing of A. C. *In situ* stump cast without taproot, Red Hill.

DISCUSSION

The CF ichnoassemblage is similar in composition to previously reported Devonian continental ichnoassemblages (e.g., Gevers et al., 1971; Berg, 1972; Bradshaw, 1981; Walker, 1985; Thoms and Berg, 1986; Gordon, 1988; Driese and Mora, 1993; Driese et al. 1997; Morrissey and Braddy, 2004; Wisshak et al., 2004), which are composed of *Beaconites* isp., bivalve burrows (*Lockeia* isp., and *Pleurovurvus arenaorte*), arthropod trackways (e.g., *Diplichnites* isp.), fish swimming traces (*Undichna* isp.), and rhizoliths. The CF ichnoassemblage differs from other Devonian continental ichnoassemblages in that it contains probable lungfish estivation burrows (*Hypero euthys teichonomos*) and arthropod dwelling burrows (*Camborygma eumekonomos* and *C. litonomos*).

The traces that comprise the CF, as well as previously reported Devonian continental ichnoassemblages, represent the behavior of aquatic as well as subaerial and soil-dwelling (terrphilic to hygrophilic, and hydrophilic) organisms. The behavioral specialization of soil-dwelling organisms into terrphilic, hygrophilic, and hydrophilic organisms in the CF indicates that Devonian continental organisms exhibited tiering in response to paleohydrology, consistent with Mesozoic to recent continental organisms (e.g. Hasiotis, 2002, 2007, 2008; Hasiotis et al., 2007).

The behavioral complexity of Devonian continental organisms, as evidenced by the CF ichnoassemblage, and previously described Devonian continental ichnoassemblies (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004; Davies et al., 2006) contrasts with previous assessments of behavioral complexity and ecospace utilization in Devonian continental ecosystems (e.g., Buatois et al., 1998). The results of our study, and previous studies of Siluro-Devonian continental ichnoassemblages indicate that the *Scoyenia* Ichnofacies and

Scoyenia Ichnoguild of Buatois et al. (1998) occur in Siluro-Devonian alluvial strata worldwide (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004; Davies et al., 2006).

The *Scoyenia* Ichnofacies comprise occurrences of backfilled burrows in alluvial deposits, most of which exhibit evidence of pedogenesis, although evidence of pedogenesis is not always explicitly described, nor included in behavioral and paleoecological interpretations of traces. The CF does not contain the oldest evidence of backfilled burrows in alluvial paleosols, despite containing much older evidence of backfilled burrows in continental environments than was recognized by Buatois et al. (1998). Studies by Morrissey and Braddy (2004) and Davies et al. (2006) reported backfilled burrows in Upper Silurian to Lower Devonian strata from the Old Red Sandstone of Europe. The *Scoyenia* Ichnofacies initiated in the Late Silurian, as such.

Our study and that of Gordon (1988) further demonstrate that deeply penetrative burrowing behavior had evolved by the Late, if not the Middle Devonian. Buatois et al. (1998) asserted that the evolution of deep burrowing behavior—and thus implicitly the evolution of hydrophilic, soil-dwelling organisms—in continental environments occurred in the Triassic. Buatois et al. (1998) cited the presence of deeply penetrative burrows from the Upper Triassic Chinle Formation, interpreted to be freshwater decapod burrows by Hasiotis et al. (1993) and Hasiotis and Mitchell (1993) as the earliest evidence of this behavior. Gordon (1988), however, described vertically oriented burrows from the Middle to Late Devonian CM of New York, USA that occur in alluvial deposits. Gordon's (1988) burrows were ~50 to 150 mm in maximum diameter and greater penetrative for greater than 1 m. The presence of Gordon's (1988) burrows in Givetian to Frasnian alluvial deposits indicates that deeply penetrative burrowing occurred in Middle to lowest part of Upper Devonian alluvial deposits as well, and that the inception of

deeply penetrative burrowing in alluvial deposits began in the Middle to earliest Late Devonian, rather than the Triassic, as was asserted by Buatois et al. (1998).

The presence of burrows of terraphilic, hygrophilic, and hydrophilic soil organisms in the CF indicates that Frasnian to Famennian soil organisms exhibited nearly as much behavioral complexity and tiering as Mesozoic to recent soil-dwelling organisms. The results of this study indicate that tiering of traces, representing differing behavioral and physiological responses of soil organisms to paleohydrology must have evolved before the Late Devonian. The evolution of specialized moisture preferences and tolerances resulted in vertical tiering of traces in paleosol profiles with shallowly penetrative rhizoliths and burrows representing terraphilic to hygrophilic organisms that inhabited the upper to lower vadose zone, highly penetrative rhizoliths as hygrophilic behaviors, and burrows representing organisms with hydrophilic behaviors that inhabited, or made connections with the phreatic zone.

Previous analyses of the evolution of ecospace utilization and trace-fossil distribution with respect to the development of Phanerozoic continental ecosystems (e.g., Buatois et al., 1998) have suggested that terrestrialization occurred gradually, culminating in the development of complex ecosystems in the Mesozoic. Our results, and those of previous studies of Siluro-Devonian continental trace fossil assemblages (e.g., Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morissey and Braddy, 2004; Davies et al., 2006) indicate that organisms colonized land quickly, and that the spatial distribution and tiering of organisms in alluvial sediments was similar to that reported for Mesozoic to recent continental ecosystems (e.g., Bown and Kraus, 1983; Hasiotis, 1998, 2002, 2003, 2004, 2007, 2008; Hembree and Hasiotis, 2007, 2008; Smith and Mason, 1998; Smith and Hasiotis, 2008; Smith et al., 2008b, 2009).

The earliest trace and body fossil evidence for life on land occurs in Middle to Upper

Ordovician paleosols and shallow marine environments (Retallack and Feakes, 1987; Johnson et al., 1994; Strother et al., 1996; Retallack, 2001). Ordovician continental trace fossil assemblages are characterized by rare, moderately penetrative subvertical structures (Retallack and Feakes, 1987; Retallack, 2001) and rare arthropod trackways (Johnson et al., 1994). Whether or not these traces truly represent behavior of continental organisms has been contentious (e.g., Davies et al., 2010). Ordovician continental body fossil assemblages are characterized by plant spores, which are worldwide in distribution and may have been produced by liverwort-like plants (Strother et al., 1996; Kenrick and Crane, 1997).

The nature and timing of the colonization of land by plants and animals is still unresolved. The world-wide distribution of plant spores in Middle to Upper Ordovician marginal marine strata, and the presence of trace fossils in Upper Ordovician paleosols as well as apparent subaerial deposits, however, suggests that both plants and animals colonized land in the Middle to Upper Ordovician. The presence of myriapod, arachnid, and plant body fossils (Selden and Edwards, 1989; Jeram et al., 1990; Edwards and Selden, 1993; Edwards et al., 1995; Shear and Selden, 1995; Shear et al., 1998), as well as abundant backfilled burrows and trackways in continental settings by the Late Silurian (Morrissey and Braddy, 2004; Davies et al., 2006) indicates that continental ecosystems were well established by the Late Silurian and must have exhibited rapid evolution between the Late Ordovician and Late Silurian.

CONCLUSIONS

Alluvial channel and overbank strata of the upper Devonian CF in north-central Pennsylvania, USA, contain an assemblage of 14 distinct trace fossils, as well as *in situ* progymnosperm stump casts. Burrow and trackway ichnotaxa each represent the unique

behavior of an animal that inhabited the CF alluvial plain.

The backfilled burrows *Beaconites antarcticus* and *B. barretti* represent dwelling and feeding by soil arthropods of unknown taxonomic affinity. These burrows may represent rhizophagous herbivory, based on crosscutting relationships with rhizoliths, or soil detritivory. The shallow penetration depth of CF *Beaconites* isp. suggests that they represent terraphilic to hygrophilic soil-dwelling organisms. The occurrence of tens to hundreds of *Beaconites* isp. burrow per dm² indicates that the tracemakers of these burrows were abundant in CF soils.

Camborygma eumekonomos and *C. litonomos* represent the dwelling burrows of soil-dwelling decapods, or decapod-like crustaceans. The presence of these burrows in the CF indicates that soil-dwelling decapods may have evolved by the Late Devonian, and that hydrophilic soil organisms had evolved by the Late Devonian. Marine decapods are known from this same time period, so the presence of freshwater burrowing continental crustaceans is not impossible.

Diplichnites gouldi represents locomotion by an arthropod of unknown taxonomic affinity, perhaps a myriapod. The presence of this trace is consistent with constituents of other Devonian continental ichnoassemblages.

Hypero euthys teichonomos represents estivation of lungfish that inhabited ephemeral wetlands during the wet season when the CF alluvial plains were flooded. This behavior has been well documented in the Paleozoic continental fossil record.

Lockeia ornata, *L. siliquaria*, and *Pleurocurvus arenaorte* represent three distinct behaviors of freshwater bivalves living in pedogenically unmodified CF pointbar deposits. *Lockeia siliquaria* represents resting of an infaunal bivalve. *Lockeia ornata* represents bedding-parallel locomotion, punctuated by periods of resting by an infaunal bivalve. *Pleurocurvus*

arenaorte represents readjustment of a shallow infaunal siphonate bivalve in response to sedimentation. These traces represent the behavior of freshwater bivalves.

Sagittichnus lincki represents resting of an unknown organism, possibly a small crustacean (?ostracode) or other arthropod. Although previous purported Devonian freshwater ostracodes were later determined to be brackish-water dwellers, these traces may support the evolution of freshwater ostracodes by the Late Devonian.

Undichna multiloba represents swimming behavior of a small benthonic fish, possibly an antiarch placoderm. This trace is morphologically distinct from known *Undichna* ichnospecies, and merits a new ichnospecies *U. multiloba*.

Rhizoliths and stump casts represent rooting in CF soils by plants. The presence of rhizoliths in the most weakly developed CF paleosols indicates that plants were early colonizers of CF soils. Clay-filled rhizoliths with a quartzose silt or carbonate core occur in very weakly to very strongly developed CF paleosols. Carbonate rhizoliths occur in weakly to strongly developed CF paleosols, but are most common in strongly developed vertic claystone paleosols. Rhizohaloes occur rarely in weakly developed paleosols, but are very common and occur in high abundance in well-developed vertic claystone paleosols, in association with carbonate rhizoliths. Stump casts occur in paleosols representing immature to mature, and moderately well-drained to well-drained soils.

Disparate rhizolith morphologies represent unique preservational styles of plant roots that penetrated CF soils, as well specialized behaviors and moisture preferences that allowed plants to root in the upper and lower vadose zone of CF alluvial soils. *In situ* stump casts likely represent the life position of one or more species of the arborescent progymnosperm *Archaeopteris*, or arborescent lycopods. The presence of deeply penetrative taproots on CF stump casts indicates

that they represent plants with the ability to access phreatic zone water sources.

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**CHAPTER 3. PALEOENVIRONMENTAL DISTRIBUTION OF TRACE FOSSILS IN
THE FRASNIAN–FAMENNIAN CATSKILL FORMATION, NORTH-CENTRAL
PENNSYLVANIA, USA: AN ASSESSMENT OF A LATE DEVONIAN SOIL
ECOSYSTEM AND INITIATION OF ECOSYSTEM ENGINEERING BY MIDDLE
PALEOZOIC SOIL BIOTAS**

WADE T. JONES^{*}, STEPHEN T. HASIOTIS

FORMATTED FOR PALAIOS

ABSTRACT

The purpose of this paper is to assess the facies distribution, paleoecological, and paleopedological implications of trace fossils of the Frasnian–Famennian Catskill Formation (CF) of north-central Pennsylvania, USA. The CF contains a moderately diverse suite of trace fossils interpreted to represent behavior of soil-dwelling, surface dwelling and aquatic animals, as well as rooting by plants with terraphilic to hydrophilic affinities. As in other continental successions, CF traces represent behaviors specific to continental organisms and different from those of marine organisms. Traces of soil-dwelling organisms occur in weakly developed (Protosols) to moderately well-developed and well-developed (Vertisols and Argillisols) paleosols. Subaerial trackways occur in weakly developed paleosols. Aquatic traces occur in pointbar deposits. We interpret traces in CF paleosols to represent behavior of terraphilic to hygrophilic (*Beaconites antarcticus* and *B. barretti*) and terraphilic to hydrophilic organisms (*Camborygma*

lironomos and *C. eumekonomos*). The presence of these behavioral types indicates that tiering in CF paleosols was as sophisticated as tiering in Mesozoic to recent paleosols and soils. The abundance and degree of trace crosscutting increases in increasingly mature paleosols. This indicates that disparate CF paleosol ichnoassemblages, despite being controlled by paleohydrology, also represent stages of ecological succession, i.e. colonization of CF alluvial soils. Continental organisms of Mesozoic to recent age are known to have exhibited behaviors that beneficially modified their environment (ecosystem engineering) by modulating resource flow paths (allogenic engineering) or modifying their bodies in ways that create new or improved habitats for themselves or other organisms (autogenic engineering). The idea that behaviors of middle Paleozoic continental organisms significantly modified the environments in which they lived has not been examined in detail. Our data suggest, however, that Devonian continental organisms beneficially modified the physicochemical environment in which they lived, and that the inception of allogenic ecosystem engineering in continental environments occurred as early as the Late Devonian.

INTRODUCTION

The purpose of this paper is to assess the paleoenvironmental distribution, paleoecology, and paleopedological implications of alluvial trace fossils in the Late Devonian Catskill Formation (CF), north-central Pennsylvania, USA. Previous studies of Devonian continental ichnoassemblages (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004) have assessed the ichnotaxonomy and facies distribution of Devonian continental ichnoassemblages, as well as the behaviors that they represent. These studies, however, did not

examine Devonian continental traces in the context of our most recent understanding of the controls on continental trace fossil distribution.

CF alluvial deposits contain a moderately diverse suite of trace fossils, representing behaviors characteristic of continental organisms. Backfilled burrows, rhizoliths, and lungfish estivation burrows occur in nearly all pedogenically modified CF alluvial deposits. We interpret these traces to represent behavior of soil-dwelling organisms. CF arthropod trackways (*Diplichnites gouldi*) represent locomotion of arthropods on undeveloped to poorly developed CF paleosols. Bivalve traces, fish swimming traces, and resting traces produced by an unknown tracemaker (*Sagittichnus lincki*) represent the behavior of aquatic organisms that lived in CF fluvial channels.

Continental trace fossil distribution is controlled by factors distinct from those that control the distribution of marine traces (Smith, 1993; Smith and Mason, 1998; Hasiotis, 2002, 2007; Hembree and Hasiotis, 2007; Hasiotis, 2008; Hembree and Hasiotis, 2008; Smith et al., 2008). The most important of these controls is the level of the water table, which is largely responsible for vertical tiering of burrowing, soil-dwelling organisms (Hasiotis, 2002, 2007). Hasiotis (2002, 2007) categorized soil organisms by their relationship of burrowing depth to the depth of the water table. Soil organism distribution is also controlled by soil oxygenation which can be strictly a function of the physicochemical environment, or can be substantially modified by densely distributed soil invertebrates (Villani et al., 1999).

According to Hasiotis (2002, 2007), hydrophilic organisms burrow below the water table to fulfill physiological moisture needs. For similar reasons, hygrophilic organisms remain in the moist lower vadose zone and terraphilic organisms remain in the upper vadose zone. The CF trace fossil assemblage suggests that Late Devonian continental organisms exhibited behaviors

characteristic of all three behavioral categories of Hasiotis (2002, 2007). This indicates that middle Paleozoic soil organism behavior was nearly as complex as that of Mesozoic to recent soil organisms.

Soil organism behavior has also been categorized based on organisms' residence times in soil. Residence time of organisms in soils varies depending on the life cycle and life habits of juvenile and adult forms of an organism (Wallwork, 1970; Hasiotis, 2002, 2007). The CF ichnoassemblage suggests that temporary, transient, and periodic soil organisms, *sensu* Wallwork (1970), and Hasiotis (2002, 2007) were integral parts of Late Devonian soil biotas.

Bioturbation by soil biotas is known to be a major contributor to pedogenesis in Mesozoic–recent continental environments via modifications of soils that affect their physical, chemical and biotic properties (Reichle, 1977; Lavelle et al., 1992, 2006; Chauvel et al., 1999; Konaté et al., 1999; Dauber et al., 2001; Hasiotis, 2003; Johnson et al., 2005; Jouquet et al., 2006). Soil organisms can modify soil properties so significantly that they strongly influence spatial and temporal heterogeneity of biomass and species distribution (Lavelle et al., 1992; De Deyn et al., 2003; Jouquet et al., 2006; Lavelle et al., 2006).

Organisms exhibiting behaviors that substantially beneficially modify their physical environment have been termed ecosystem engineers by Jones et al. (1994). Jones et al. (1994) established two main categories for ecosystem engineers: 1) allogenic engineers, which modify the physicochemical environment by modulated one or more resource flow paths (e.g., beavers blocking stream flow to create large, semi-permanent wetlands); and 2) autogenic engineers, which modify the physicochemical environment by modify their own bodies (e.g., trees blocking sunlight, which creates shady patches that benefit their own root system in addition to creating habitat for understory vegetation).

Evidence of ecosystem engineering in Mesozoic–recent continental (predominantly soil) environments, by social insects and other arthropods is common (Hasiotis, 2002, 2003, 2007; Jouquet et al., 2006; Jones et al., 2006). Fossil evidence of ecosystem engineering is predominantly evidence of allogenic engineering by modification of soil pore space, and improvement of soil drainage via creation of macropores and macrochannels by plants and soil-dwelling invertebrates and vertebrates (Hasiotis 2002, 2003, 2007; Hasiotis et al., 2007). The idea that middle Paleozoic continental organisms may have been ecosystem engineers has not been examined, however. In addition to their paleoenvironmental distribution, we also assessed CF traces as potential evidence of ecosystem engineering by Devonian soil organisms. Ichnologic evidence from the CF suggests that soil ecosystem engineering by plants and animals was both prevalent, and influential on community structure and biomass distribution by the Late Devonian.

GEOLOGIC SETTING

The CF comprises a 300–1,500 m thick package of alluvial channel sandstones and overbank mudstones, pedogenically modified to differing degrees (Diemer, 1992; Driese et al., 1993; Bridge, 2000). CF sediments were shed westward into the Appalachian retroarc foreland basin from the Acadian orogenic center (Ettensohn, 1985). Paleogeographic reconstructions have placed Pennsylvania at roughly 20° south (Boucot and Gray, 1983; Ziegler et al., 1979), or ~35° south latitude during the Late Devonian, (Joachimski et al., 2002). The CF alluvial plain apparently experienced wet-dry seasonality, evidenced by the development of vertic paleosols with weakly to strongly developed pedogenic carbonate horizons, pedogenic slickensides, and pseudoanticlines (Woodrow et al., 1973; Driese et al., 1993).

The CF is divided into the Irish Valley, Sherman Creek, and Duncannon members in the study area (Sevon and Woodrow, 1985). The Irish Valley Member consists of 180–300 m of interfingering alluvial mudstones and sandstones, and marine mudstones. The Sherman Creek Member is 300–600 m thick and contains little evidence of marine influence, however, it includes intervals of marine sedimentation, containing brachiopods, and marine bivalves. Paleosols in the Sherman Creek Member are dominantly Entisols and Inceptisols *sensu* US soil taxonomy, or Protosols *sensu* Mack et al. (1993), whose development was frequently retarded by high rates of deposition (Elick, 2006). The Duncannon Member is ~300 m thick and contains no evidence of marine influence. Paleosols in the Duncannon member are commonly better developed than those in the Sherman Creek Member and more commonly exhibit pedogenic pseudoanticlines, angular blocky peds, and well-developed pedogenic carbonate horizons (Driese et al., 1993; Elick, 2006).

METHODS AND MATERIALS

Stratigraphic sections were measured at individual roadcut outcrops along US Highway 15 between Powys Township and Steam Valley, Pennsylvania, and at Red Hill, on Pennsylvania Highway 120, ~1 km southeast of North Bend, Pennsylvania (Fig. 19) using a Jacob's staff. Individual lithologic units were discerned based on grain size, sedimentary structures, color, and pedogenic features. The stratigraphic position of trace fossil occurrences was documented to discern paleoenvironmental occurrences and associations.

Thin sections were prepared in the University of Kansas Geology Department thin section laboratory to examine micromorphology of trace fossils and paleosols, and were examined using a Nikon model E6000W POL petrographic polarizing light microscope.

Surficial morphologies of traces were examined using a Nikon model SMZ1000 binocular light microscope. Variability in the degree of homogenization of paleosols by burrows and rhizoliths was assessed using a visual compositional estimate chart from Terry and Chilingar (1955).

Rhizolith architectural morphologies were characterized using the rank ordering, branch angle measurement, and radial angle measurement schemes of Fitter (1987) (Fig. 20). We also used the qualitative terminology of Cannon (1949) to characterize rhizoliths.

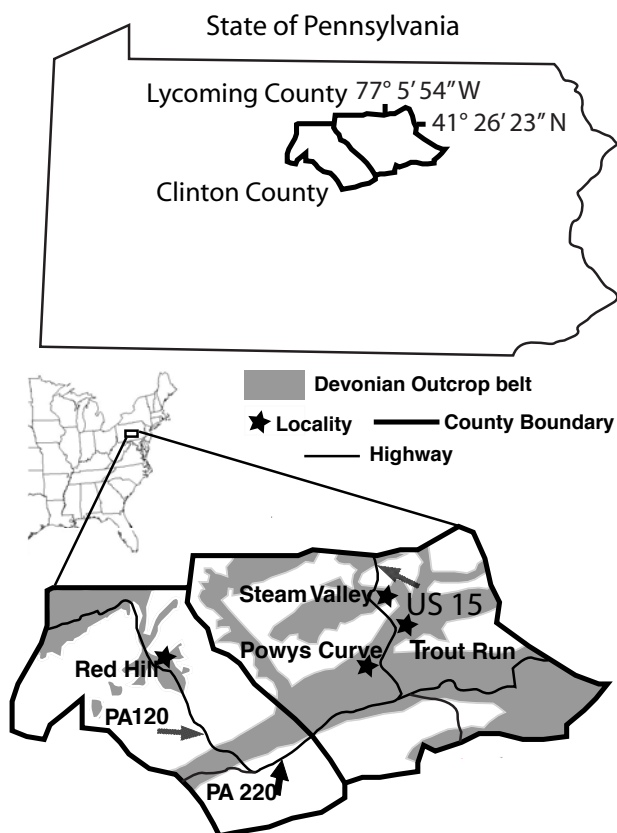


FIGURE 19—Map of Clinton and Lycoming Counties, Pennsylvania with localities examined during this study.

FACIES DESCRIPTIONS AND INTERPRETATIONS

Finely Laminated Mudstone-Sandstone Interbeds

Description.—Finely laminated siltstone, claystone, and clay-rich mudstone-sandstone interbeds commonly occur in the CF (Fig. 21 A–D). These intervals are normally > 2 m thick and commonly occur in overbank successions, and in channels, between intervals of low–high-angle trough cross-bedded, very fine–medium-grained sandstone. Finely laminated mudstone is normally interbedded with decimeter-scale beds of very fine-grained, micaceous sandstone. Both sandstone and mudstone in finely laminated intervals are current or wave ripple cross-laminated (Fig. 21 D) (Table 2), and rarely trough cross-bedded. These intervals sometimes contain 10–20 cm thick horizons of 1–3-mm-diameter pedogenic carbonate nodules.

Interpretation.—Finely laminated mudstone-sandstone interbeds of the CF are most consistent with natural levee deposits and very proximal floodplain deposits, because the paucity of pedogenic features indicates high rates of sedimentation, inhibiting pedogenesis (e.g. Kraus and Bown, 1988). The presence of primary sedimentary structures and paucity of pedogenic features in finely laminated mudstone-sandstone interbeds is consistent with features seen in poorly developed soils (Retallack, 2001). These paleosols are interpreted as Entisols *sensu* US Soil Taxonomy, or Protosols *sensu* Mack et al. (1993).

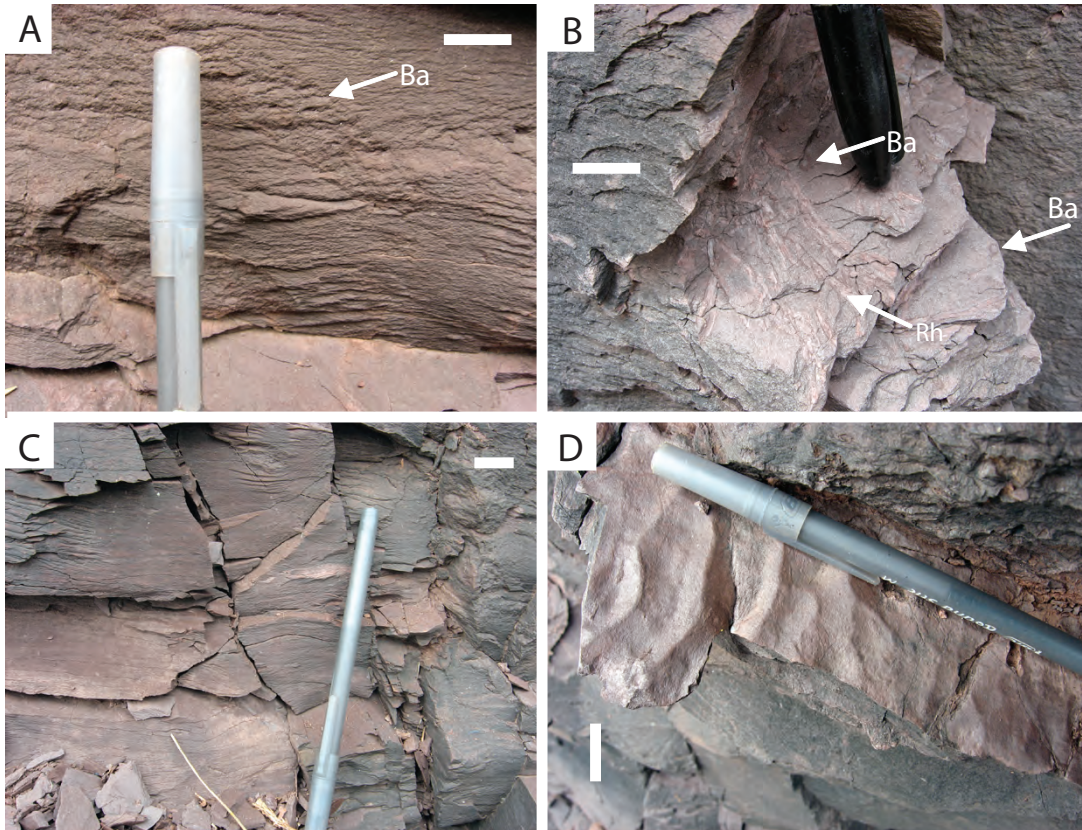


FIGURE 21—Finely laminated mudstone-sandstone interbeds; Ba=*Beaconites antarcticus*; Rh=rhizolith; scale=10 mm. A) Finely laminated siltstone crosscut by *Beaconites antarcticus*, Powys Curve, PA. B) Finely laminated siltstone crosscut by *Beaconites antarcticus*, and clay-filled hematite-rich rhizoliths, Powys Curve, PA. C) Finely laminated mudstone, Powys Curve, PA. D) Oscillation Ripples in Finely laminated mudstone, Powys Curve, PA.

Facies	Sedimentary Structures	Pedogenic Features	Traces
Finely laminated sandstone-mudstone interbeds	Oscillation ripple lamination, Current ripple lamination, Parallel lamination, Trough cross-beds (rare)	Lamination weakly disrupted	Clay-filled, hematite-rich rhizoliths, Carbonate rhizoliths, <i>Beaconites antarcticus</i> , <i>Beaconites barretti</i> , Lungfish burrows
Weakly laminated sandstone-mudstone interbeds	Weak remnant ripple lamination	Platy structure, strongly disrupted laminae, Pedogenic carbonate horizons, Small-scale pedogenic slickensides	Clay-filled hematite-rich rhizoliths, Carbonate rhizoliths, <i>Beaconites antarcticus</i> , <i>Beaconites barretti</i> , Lungfish burrows, Rhizohaloes, <i>Camborygma eumekonomos</i> , <i>Camborygma litonomos</i>
Thoroughly churned vertic claystone	Not preserved	Angular blocky peds, Pseudoanticlines, Small-scale pedogenic slickensides, Pedogenic carbonate horizons, Clay-skins	Clay-filled hematitic rhizoliths, Carbonate rhizoliths, <i>Beaconites antarcticus</i> , <i>Beaconites barretti</i> , Lungfish burrows, Rhizohaloes
Pedogenically modified pointbar deposits	Trough cross-beds, Current ripple lamination	Weakly to strongly disrupted lamination	Clay-filled hematitic rhizoliths, Carbonate rhizoliths, <i>Beaconites antarcticus</i> , <i>Beaconites barretti</i> , Lungfish burrows, Rhizohaloes
Pedogenically unmodified pointbar deposits	Trough cross-beds, Current ripple lamination	None developed	<i>Lockeia ornata</i> , <i>Lockeia siliquaria</i> , Subvertical bivalve equilibrichnia, <i>Sagittichnus lincki</i> , <i>Undichna isp.</i>

TABLE 2—Associations of lithofacies, sedimentary structures, pedogenic features, and trace fossils.

Weakly Laminated–Platy Mudstone–Sandstone Interbeds

Description.—Weakly laminated mudstone, claystone, and clayey siltstone exhibiting platy structure commonly occur in the CF (Fig. 22 A–D) (Table 2). These lithologies may or may not be interbedded with decimeter-scale, very fine-grained, micaceous sandstone beds. Very fine-grained sandstone beds retain current and wave ripple cross-lamination when they occur in this facies (Table 2), however, identifiable sedimentary structures are destroyed in clay-rich lithologies. Clay-rich lithologies in these intervals exhibit centimeter-scale, discontinuous pedogenic slickensides that give the rocks a smooth, glossy appearance in hand sample (Fig. 22C). Pedogenic slickensides are usually bedding-parallel. Pedogenic carbonate horizons developed in weakly laminated mudstone paleosols are composed of 2–3 mm diameter carbonate nodules. Clay-rich lithologies retain weak, discontinuous remnant laminae, resulting in platy soil structure (Fig. 22 A–D).

Interpretation.—The presence of weak remnant lamination, weakly developed vertic structures, and poorly developed pedogenic carbonate horizons indicates that weakly laminated to platy CF mudstones represent weakly developed soils. The greater abundance of burrows and better development of soil structure in these lithologies than in finely laminated mudstones indicates that they represent more strongly developed soils than finely laminated mudstone–sandstone interbeds. Development of soil structure in these intervals is variable; in the most strongly pedogenically modified intervals, nearly all lamination is destroyed, whereas in weakly pedogenically modified intervals, much remnant lamination is retained. We interpret these paleosols to represent Protosols *sensu* Mack et al. (1993), or Entisols–Inceptisols *sensu* US Soil Taxonomy, which formed on proximal floodplain deposits.

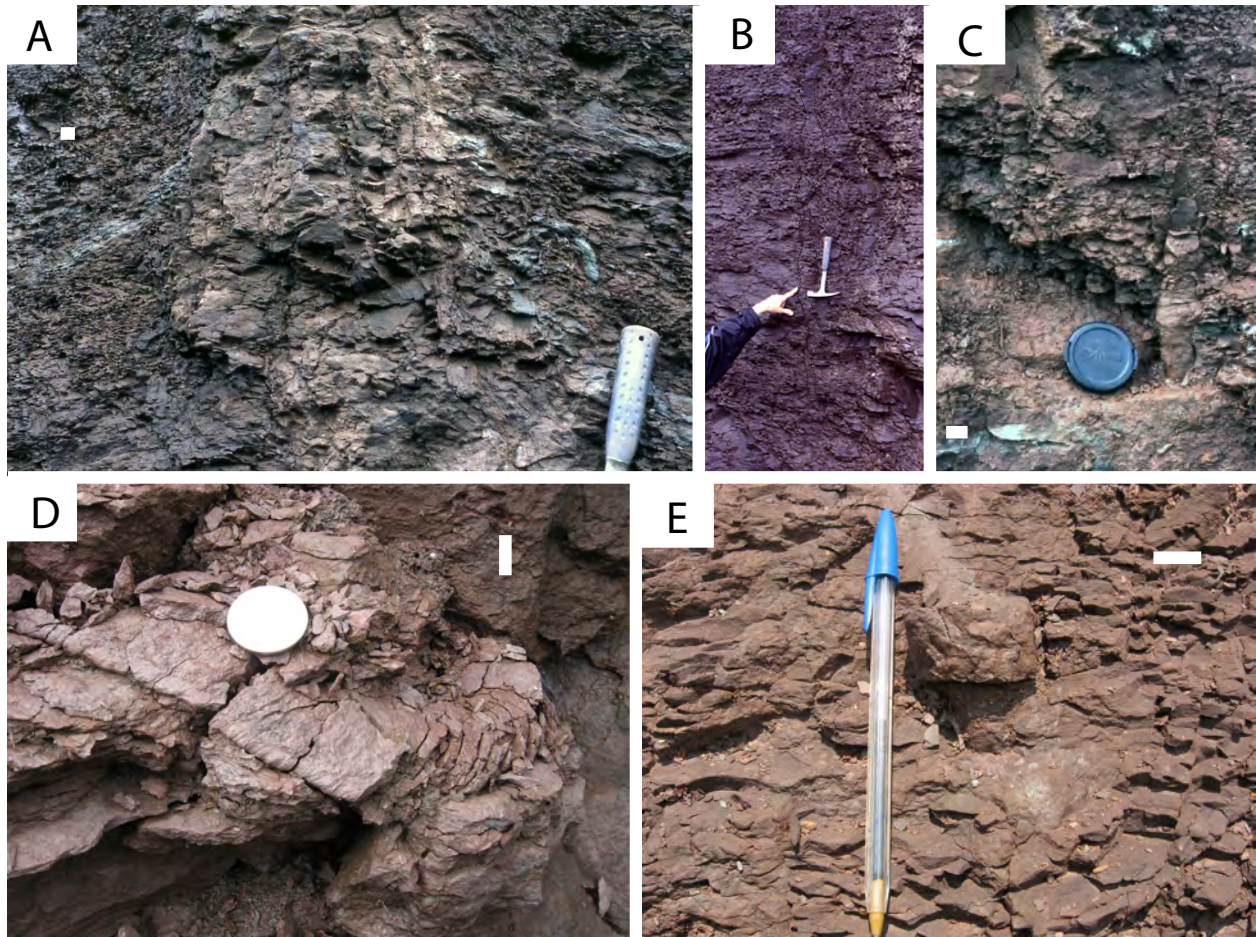


FIGURE 22—Weakly laminated–platy mudstone-sandstone interbeds; Ba=*Beaconites antarcticus*; Rh = rhizolith; scale bar =10 mm. A) *Camborygma eumekonomos* in platy mudstone, Red Hill. C) Platy mudstone with a prominent pseudoanticline, crosscut by *Camborygma litonomos.*, Red Hill. D) Platy mudstone crosscut by *Beaconites barretti*, Powys Curve. E) Platy mudstone crosscut by a lungfish estivation burrow, Red Hill.

Scour-Based Trough Cross-Stratified Sandstones

Description.—Weakly developed paleosols occur in CF trough cross-bedded, scour-based, very fine–medium grained sandstones (Fig. 23 A–D) (Table 2). Bedsets in these sandstones are bounded by erosional surfaces that occur every 0.5–2 m and exhibit decimeter-scale relief. Finely laminated siltstone beds 1–20 cm thick commonly occur along these surfaces. When traced laterally, sandstones truncate >3 m of underlying strata, which are most often overbank mudstone and siltstone–sandstone interbeds. Such sandstones are termed storied sandstones by Bridge (2000) and are interpreted to represent pointbar deposits. These sandstones may also be current ripple cross-laminated (Table 2).

Interpretation.—We interpret CF scour-based, trough cross-stratified sandstones to be pointbar deposits. Paleosol development on CF pointbar deposits is variable, although cross stratification is always preserved, indicating weak soil development, as can be seen in Driese et al. (1997). Better developed paleosols in pointbar deposits are characterized by development of platy structure or rare angular blocky peds in silty intervals and strong disruption of primary laminae in sandstone beds. Paleosols are also developed along the tops of CF channel sandstones, especially when they are overlain by paleosols developed on mudstone.

CF scour-based, trough cross-stratified sandstones commonly exhibit no evidence of pedogenesis. We interpret scour-based trough cross-stratified sandstones that lack evidence of pedogenesis to be pointbar deposits that were not subaerially exposed long enough for pedogenesis to begin.

Retention of primary sedimentary structure in paleosols developed on CF pointbar deposits indicates that they represent weakly developed soils. Failure of pedogenesis to destroy primary sedimentary structure and develop soil structure on pointbar deposits may also result

from the low clay content, which would have precluded churning by argilloturbation. Paleosols developed on CF pointbar deposits best conform to Protosols *sensu* Mack et al. (1993), or Entisols *sensu* US Soil Taxonomy.

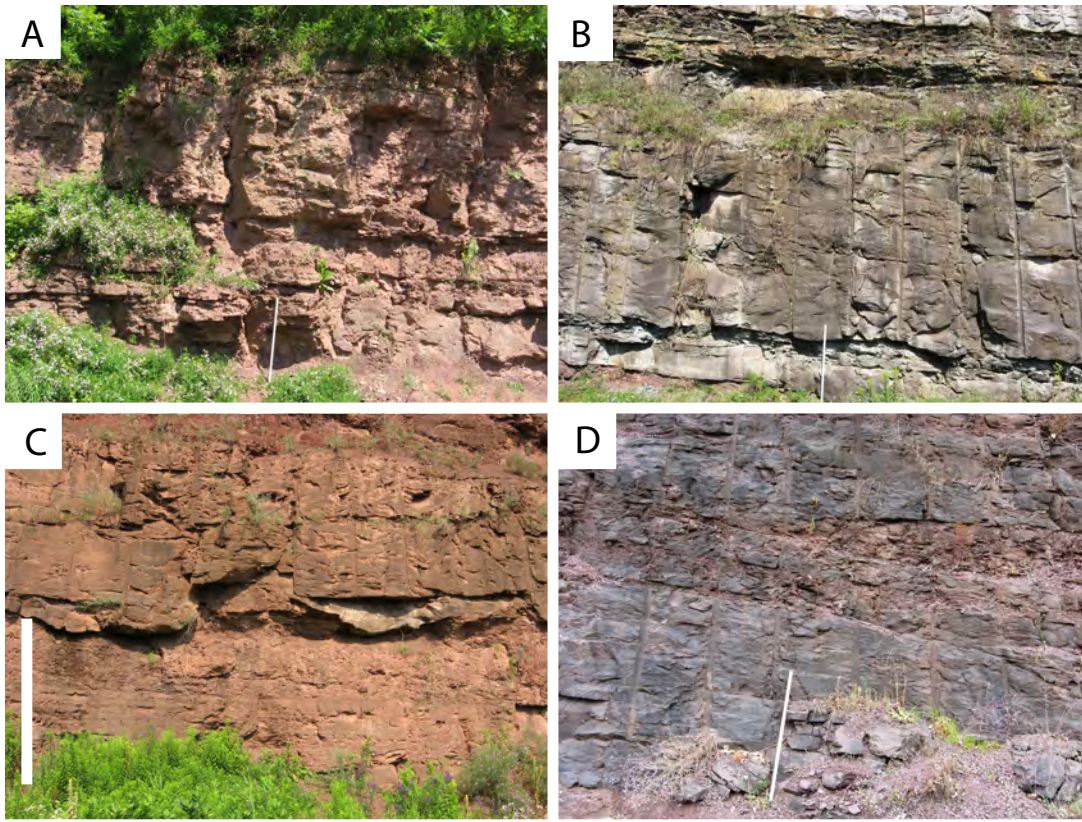


FIGURE 23—Trough cross-stratified, scour-based sandstones. A) Trout Run. B) Steam Valley. C) Trout Run. D) Powys Curve.

Thoroughly Homogenized Vertic Claystones

Description.—CF paleosols are commonly composed of claystone or silty, clayey mudstone, lack remnant lamination, and are dominated by a combination of: 1) subangular–angular blocky peds with clay skins; 2) prismatic peds; 3) meter-scale pedogenic slickensides and pseudoanticlines (gilgai); and 4) pedogenic carbonate horizons composed of carbonate nodules as large as 4 cm in diameter (Woodrow et al., 1973; Driese et al., 1993; Retallack et al., 2009) (Fig. 24 A–F) (Table 2). These paleosols are most common in the Duncannon Member of the CF (Elick, 2006).

Interpretation.—Thoroughly homogenized vertic claystone paleosols represent moderately well-developed to well-developed soils on the CF alluvial plain, in contrast to those described above and exhibit cumulic profiles (Driese and Mora, 1993). Retallack et al. (2009) estimated that well-developed CF paleosols were stable for > 4,000 years. CF vertic paleosols are normally interpreted as Vertisols, *sensu* US Soil Taxonomy, and Mack et al. (1993).

Some mature CF paleosols have been interpreted as Aridisols based on weak development of vertic structures and well-developed pedogenic carbonate horizons (Retallack et al., 2009) (Fig. 24 G). Other soil orders such as Alfisols, however, can be dominated by subangular to angular blocky peds and exhibit pedogenic carbonate horizons (Soil Survey Staff, 2010). CF vertic claystones that lack well-developed gilgai, as such, do not necessarily represent Aridisols. Well-developed CF vertic claystones without gilgai fit the criteria for vertic, calcic argillisols, *sensu* Mack et al. (1993).

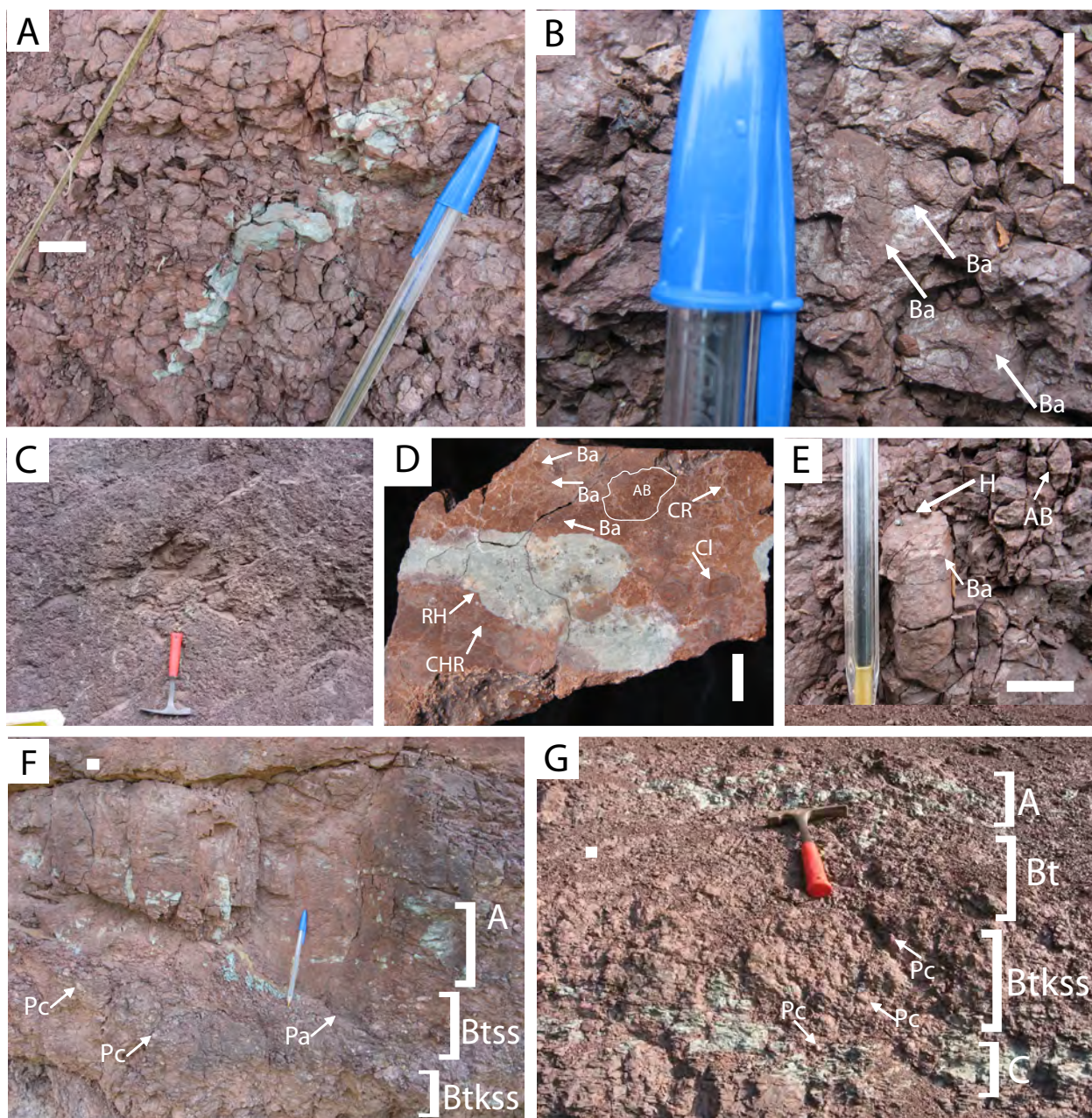


FIGURE 24—Thoroughly homogenized vertic claystones; Ba=*Beaconites antarcticus*, Pa=Pseudoanticline; Pc=Pedogenic carbonate; RH=rhizohalo, CR=carbonate rhizocretions, Cl= clayskin, AB= angular blocky ped, Clr- clayfilled rhizoliths. carbonate; scale bar=10 mm. A) Rhizohalo in a vertic claystone with well developed angular blocky peds, Steam Valley. B) Vertic claystone with angular blocky peds crosscut by *Beaconites antarcticus*, Red Hill. C) Pseudoanticlines in a Vertisol, Red Hill. D) Slabbed section of a vertic claystone paleosol; RH=rhizohalo, CR=carbonate rhizocretions, BF=backfilled burrow, Cl= clayskin, AB= angular blocky ped, Clr- clayfilled rhizoliths. E) *Camborygma litonomos* and backfilled burrows crosscutting a vertic claystone, Red Hill. F) Horizonation in a vertic claystone paleosol, Steam Valley. G) Horizonation in a vertic claystone paleosol, Red Hill.

ICHTHOLOGY

Type 1—*Beaconites antarcticus*, Figure 25 A–D, F

Description.—Vertical to horizontal; sinuous; elongated; elliptical cross-section; 2–6 mm in diameter; up to 3 cm long; composed of poorly organized packets of structureless backfill; packets weakly arcuate, poorly organized, and 1–3 mm thick; backfill identical to host sediment; thinly lined with very fine sand or silt grains; lining thickness variable; surficial morphology smooth.

Interpretation.—Modern backfilled burrows in soils are constructed by such arthropods as beetle larvae and cicada nymphs (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009). These organisms excavate dwelling chambers in moderately well-drained to well drained soils in order to consume plant roots and organics. When organics in proximity to the chamber have been consumed, the burrower moves forward, excavating a new chamber, removing sediment from in front of it and depositing the sediment behind it, resulting in arcuate packets of backfill (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009). Packeted backfills in CF *B. antarcticus* indicate a similar behavior by its trace maker. We further interpret the CF *B. antarcticus* tracemaker to have been a hygrophilic to terraphilic, soil-dwelling arthropod.

Type 2—*Beaconites barretti* Figure 25 A,B, G, H

Description.—Subhorizontal to subvertical, highly sinuous, surface unornamented to slightly rugose; 7–63 mm diameter; may be > 300 mm long; strongly elliptical in cross-section; preserved in full relief; filled with arcuate backfill meniscae; burrow fill identical in composition to host rock, meniscae unpacketed, 1–3 mm thick; menisci do not merge laterally to form burrow lining.

Interpretation.—The morphological similarity of *B. barretti* to *B. antarcticus* indicates that the two traces represent a similar behavior. The difference in backfill morphology, however, indicates that the traces represent slightly different behavior that may reflect a different trace maker. How behavior of the *B. barretti* and *B. antarcticus* trace makers differed is unclear.

Organisms that construct backfilled burrows in modern soils represent temporary soil biota *sensu* Wallwork (1970), and Hasiotis (2002, 2007) (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009). Trace fossil and modern biological evidence suggests that backfilled burrow production in modern and ancient soils is mostly attributable to hygrophilic to terraphilic organisms (Smith and Hasiotis, 2008; Smith et al., 2008a; Counts and Hasiotis, 2009). We interpret CF *B. antarcticus* and *B. barretti* to represent behavior of temporary, hygrophilic to terraphilic soil arthropods, based on this evidence.

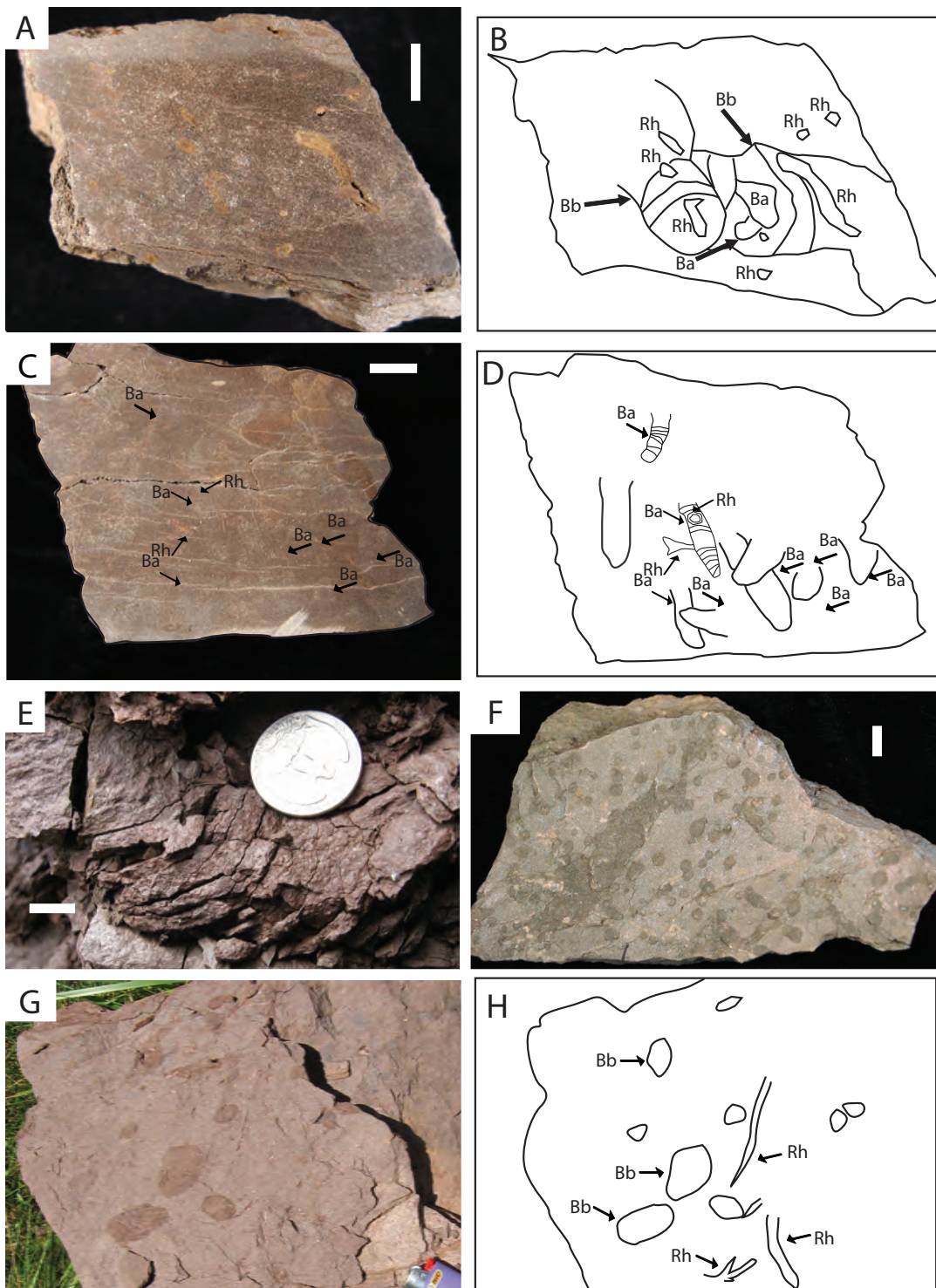


FIGURE 25—*Beaconites antarcticus* and *Beaconites barretti* Ba=*Beaconites antarcticus*; Bb=*Beaconites barretti*; Rh=rhizolith; scale=10 mm. A) Polished slab of siltstone crosscut by *Beaconites* and rhizoliths. B) Interpretive line drawing of A. C) Polished slab of very fine sandstone crosscut by multiple *Beaconites antarcticus* and rhizoliths. D) Interpretive line drawing of C. E) Multiple *Beaconites barretti* and rhizoliths on a slab of very fine-grained sandstone, Trout Run. F) Multiple *Beaconites antarcticus* crosscutting a block of very fine sandstone, Powys Curve.

Type 3—Bivalve equilibrichnia Figure 26 B

Description.—Burrows are preserved in full relief, subvertical in orientation and roughly J-shaped; filled with 2.5–5 mm thick meniscus-like structures. Meniscus-like structures are oriented normal to the long axis of the burrow.

Interpretation.—CF bivalve equilibrichnia are interpreted to represent readjustment of bivalves following sedimentation events, based on comparisons with burrows of the modern Unionid bivalve *Margaritifera margaritifera* (Thoms and Berg, 1985; Bridge et al., 1986). The apparent meniscus structure of these burrows is not analogous to that of actively backfilled, meniscate burrows, whose construction has been analyzed by Smith and Hasiotis (2008), and Counts and Hasiotis (2009). The meniscus structure, rather, represents offset laminae that were disrupted by the bivalve during escape from burial. CF bivalve equilibrichnia represent behavior of aquatic freshwater bivalves.

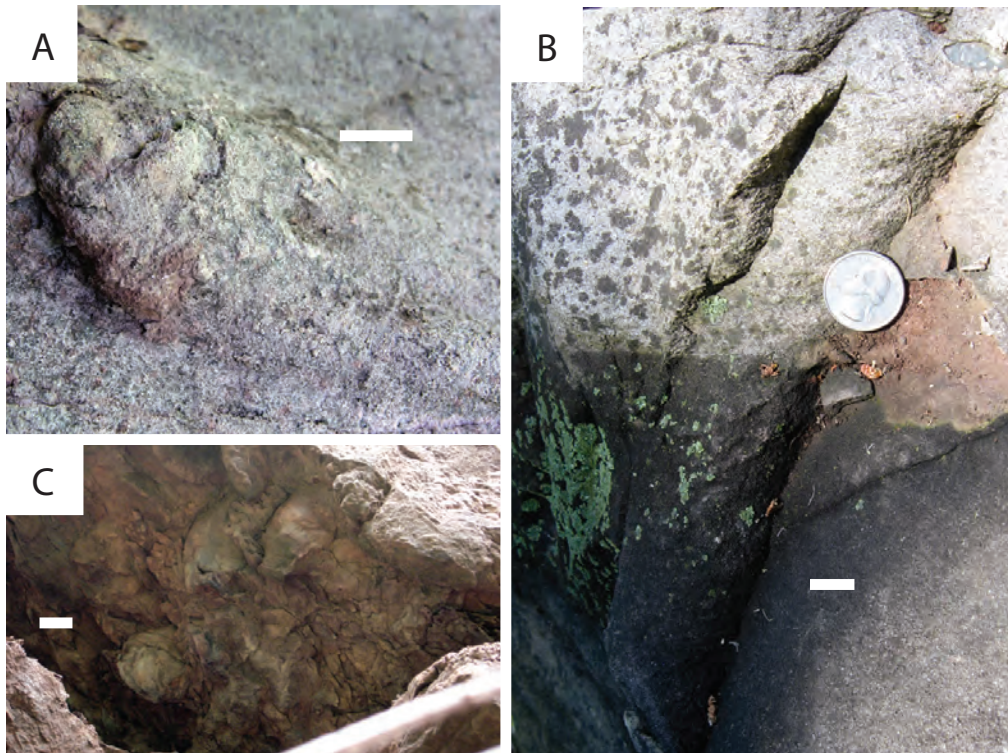


FIGURE 26—CF bivalve burrows; scale=1 cm. A) *Lockeia ornata*, Trout Run. B) Bivalve equilibrichnium, Trout Run. C) *Lockeia siliquaria*, Steam Valley.

Type 4—*Camborygma eumekonomos* Figure 22 B

Description.—Vertical to subvertical, sinuous, elongated burrows; burrow cross-section obscured; ~100 mm in diameter; up to 2 m long; presence or absence of burrow lining is unclear; termini blunt to tapering; fill is identical to host rock; surficial morphology characterized by transverse and longitudinal striations, and irregularly spaced knobby projections; striations spaced 1–15 mm apart and are ~1–20 mm wide.

Interpretation.—We interpret CF *C. eumekonomos* to be burrows of freshwater, crustacean-like arthropods based on similarity of their architectural and surficial morphologies to previously described burrows, interpreted to be freshwater decapod burrows (e.g. Hasiotis and Mitchell, 1989; Hasiotis et al., 1993 ; Hasiotis and Mitchell, 1993). CF *C. eumekonomos* likely represents the dwelling trace of a hydrophilic, soil-dwelling organism, *sensu* Hasiotis (2002, 2007) under fluctuating water table conditions (Hasiotis and Mitchell, 1993).

Burrowing crayfish (*Cambarus* and *Procambarus* sp.) construct seasonal and permanent dwelling burrows in alluvial and palustrine settings to seek protection and to fulfill physiological moisture needs (Grow and Merchant, 1980; Correia and Ferreira, 1995; Hobbs, 2001; Mazlum and Eversole, 2004). Juveniles are hatched in the burrow, and remain until burrows are flooded, later establishing burrows of their own (Correia and Ferreira, 1995 ; Mazlum and Eversole, 2004). Adults primarily remain in the burrow but leave periodically to forage (Penn, 1943). Burrowing crayfish represent periodic soil organisms *sensu* Wallwork (1970) and Hasiotis (2002, 2007) as such. CF *Camborygma* isp. likely represent domichnia of periodic soil arthropods, *sensu* Hasiotis (2002, 2007) with life habits similar to burrowing crayfish, although the CF *Camborygma* tracemaker is unknown.

Type 5—*Camborygma litonomos* Figure 22 C; Figure 24 E

Description.—Vertical to inclined, straight-to-sinuuous, elongated burrows; elliptical in cross-section; 20–30 mm diameter; up to 180 mm long; composed of burrow fill and robust, but discontinuous wall lining, which comprises up to 40 percent of burrow thickness; terminus blunt to tapering; burrows begin and terminate at the same stratigraphic level in a single occurrence; fill and lining identical in composition to host rock; surficial morphology characterized by tranverse and longitudinal striations; striations 1–3 mm wide and spaced at 1–3 mm intervals.

Interpretation.—We interpret CF *C. litonomos* to represent dwelling burrows of terraphilic, hygrophilic, or hydrophilic soil-dwelling arthropods of unknown taxonomic affinity. The vertical orientation, elongated shafts, and transversely striated surficial morphology of *C. litonomos* are morphologically similar to previously described *Camborygma litonomos*, interpreted to be freshwater decapod dwelling burrows (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). CF *C. litonomos* also exhibits architectural morphology similar to modern wolf spider burrows (Hasiotis and Bourke, 2006). Trigonotarbid, phalangiotarbid, amblypygid, scorpionid, and uraraneid arachnids all existed in the Devonian (Shear and Selden, 2001; Poschmann et al., 2005; Selden and Penny, 2010) and are potential tracemakers of CF *C. litonomos*. Trigonotarbids are known to occur in the CF (Shear, 2000), possibly making them a more likely tracemaker than the other arachnid groups.

Type 6—*Diplichnites gouldi* Figure 27 A, B

Description.—Simple trackways composed of parallel track sets; 7.9–61.2 mm wide; trackways are uniform in width; tracks are evenly spaced; stride length is uniform; trackways are not highly sinuous; tracks are elongate and slit-like to comma-shaped; the posterior of

comma-shaped tracks is bounded by a sediment mound; concavity of track curvature faces the inferred direction of movement; comma-shaped tracks deeper and wider than slit-like tracks; total width is approximately 2 times the stride length; total width is approximately 1.5 times inside width.

Interpretation.—CF *Diplichnites gouldi* is interpreted to represent locomotion of an unknown arthropod. *Diplichnites* is often interpreted as a repichnion of a myriapod-like tracemaker (Briggs, et al., 1979; Briggs, and Rolfe, 1983; Ryan, 1986; Pearson, 1992; Johnson, et al., 1994; Smith et al., 2003; Lucas et al., 2004). Myriapods are known to occur in the CF (Wilson et al., 2005); however, they are too small to have produced the trackways described here. That CF *Diplichnites* represents locomotion of one or more myriapod-like arthropods unrepresented in the CF body fossil record is probable.

We suggest that CF *D. gouldi* represents locomotion of a subaerial arthropod on newly deposited proximal floodplain and pointbar deposits. This is supported by the presence of *D. gouldi* in only weakly pedogenically modified CF deposits. Weak or no pedogenesis is likely requisite to the preservation of these trackways.

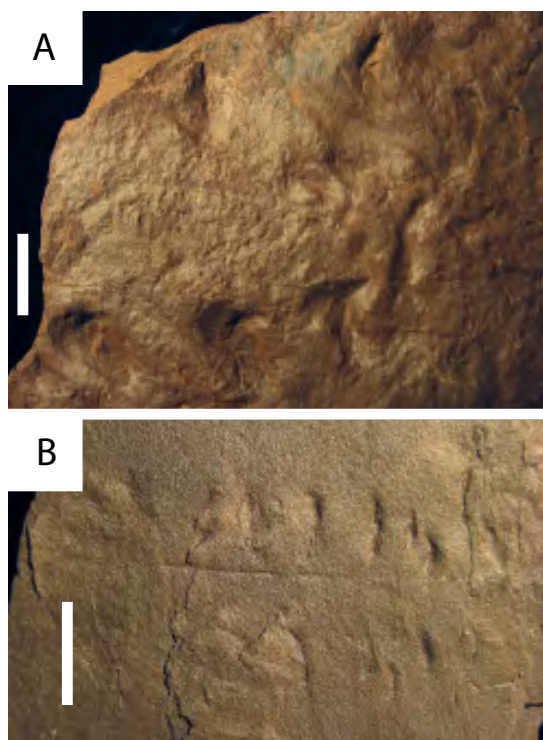


FIGURE 27—CF *Diplichnites gouldi*; scale bar=10 mm. A) Large Type 2 *Diplichnites gouldi*, Trout Run. B) Type 1 *Diplichnites gouldi*, Steam Valley.

Type 7—*Lockeia ornata* Figure 26 A

Description.—Sinuous, elongated traces; 20–40 mm in diameter; 100–300 mm long; variable in diameter; portions of burrows composed of series of connected ellipsoidal structures separated by narrower, elongated trails of bioturbated sediment; sediment trails between cubichnia are 0.25–0.5 times the width of ellipsoidal structures; surficial morphology characterized by knobby and rib-like structures; not filled with regular series of rib-like menisci; bedding parallel; preserved in convex hyporelief.

Interpretation.—*L. ornata* has historically been interpreted as the resting trace of a bivalve (Bandel, 1967; Mangano et al., 1998). Weakly almond-shaped impressions separated by thinner trails of deformed sediment that comprise *L. ornata* suggest that bivalves rested periodically during trace construction. The sinuosity and length of the burrows indicate that they represent bedding parallel locomotion, punctuated by periods of resting. We interpret CF *L. ornata* to represent behavior of freshwater bivalves, which are aquatic organisms.

Type 8—*Lockeia siliquaria* Figure 26 C

Description.—Almond-shaped structures, 31.9–61.5 mm in maximum diameter and 18.8–32.3 mm in minimum diameter; often weakly keeled; preserved in convex hyporelief.

Interpretation.—*Lockeia siliquaria* is interpreted as the resting trace (cubichnion) of an infaunal bivalve (Archer and Maples, 1984; Seilacher and Seilacher, 1994; Schlirf et al., 2001; Goldring et al., 2005; Gaillard and Racheboeuf, 2006). This trace may represent an external mold of a bivalve shell, or an impression of its foot, resulting from probing during the burrowing process (Seilacher and Seilacher, 1994). *L. siliquaria* also represents behavior of aquatic organisms.

Type 9—Lungfish aestivation burrows Figure 28 A–E

Description.—Elliptical in cross-section (13.8–121.6 mm minimum diameter and 15.0–142.6 mm maximum diameter); composed of a single vertical to subvertical shaft and bulbous terminus; overall club-shaped morphology; terminus 20–30 percent greater in diameter than the shaft, but equally elliptical in outline; periphery of burrow often characterized by a variably thick wall lining; wall lining is similar in composition to host sediment and fill; surficial morphology characterized by transverse striations; fill is massive.

Interpretation.—We interpret these traces to be lungfish aestivation burrows based on similarity to those reported in the literature (e.g. Romer and Olsen, 1954; Carrol, 1965; Berman, 1976; Hasiotis et al., 1993). CF lungfish aestivation burrows exhibit all of the morphological criteria for lungfish aestivation burrows outlined by Hasiotis et al. (1993).

Burrows are constructed by the modern South American and African lungfish *Lepidosiren* and *Protopterus*, respectively, on alluvial floodplains and lake margins for the purpose of aestivation (Kerr, 1898; Carter and Beadle, 1930; Johnels and Svennson, 1954; Buillon, 1961; Greenwood, 1987). Lungfish remain in the soil for months to several years until the floodplain is inundated again. Utilization of soil by modern lungfish as a temporary refugium, rather than a dwelling place during a life stage indicates that their burrowing behavior is most similar to that of transient soil organisms, *sensu* Wallwork (1970) and Hasiotis (2002, 2007).

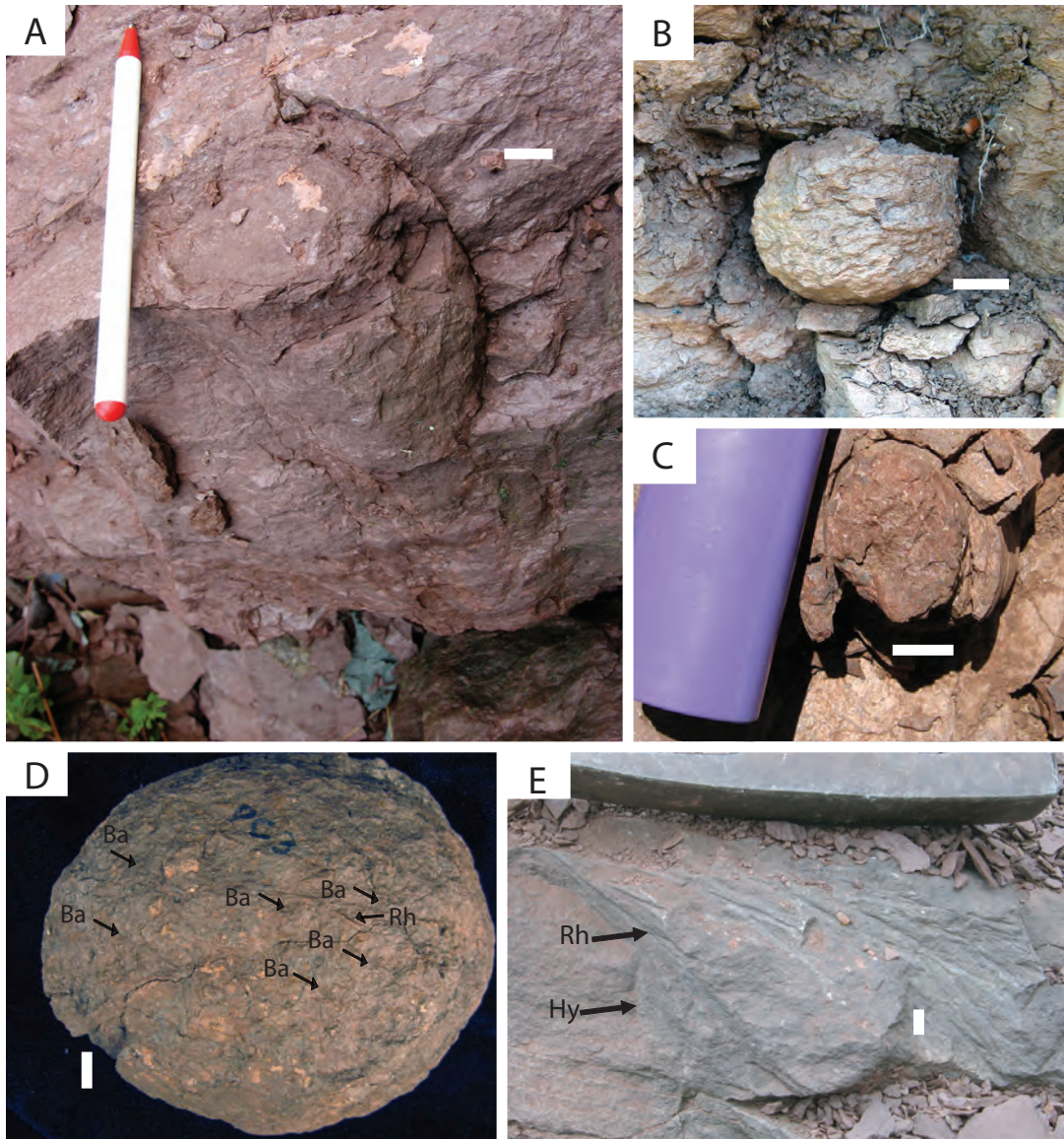


FIGURE 28—Lungfish estivation burrows; Ba= *Beaconites antarcticus*; Rh=rhizolith; scale=10 mm. A) Nearly complete shaft with a robust wall lining, Trout Run. B) Terminus *in situ*, Trout Run. C) Small shaft with robust wall lining in cross-section, Trout Run. D) Terminus crosscut by *Beaconites antarcticus* and clay-filled hematite-rich rhizoliths, Powys Curve. E) Portion of shaft in cross-section, crosscut by rhizoliths, Powys Curve.

Type 10—*Sagittichnus lincki* Figure 29 A, B

Description.—Keeled, arrowhead-shaped to rice grain-shaped traces; 1–3 mm wide and 2–4 mm long; occur in great abundance when found; preserved in convex hyporelief at the bottom of a purple very fine sand bed; keel is not usually prominent; long axis often slightly curved.

Interpretation.—*Sagittichnus lincki* is thought to be the resting trace of an unknown organism (Garvey and Hasiotis, 2008). Literature on *Sagittichnus* is rare but the trace is usually reported from continental environments in association with other small resting traces and bedding plane parallel repichnia (Gluszek, 1995; Garvey and Hasiotis, 2008). *Sagittichnus lincki* does not occur in pedogenically modified facies and is interpreted to represent resting behavior of a small aquatic organism.

Type 11—*Undichna isp.* Figure 29 A, B

Description.—Sets of 3–5 horizontal scratch marks; sets are paired and composed of discontinuous striations < 10 mm long, or continuous striations up to 79.1 mm long; surficial morphology smooth; sets within a pair are 8–15 mm apart; each mark 0.6–1.4 mm in diameter, diameter and spacing within each set is the same; preserved in convex hyporelief at the bottom of a very fine sandstone bed.

Interpretation.—We interpret continuous *Undicha isp.* scratch mark sets to represent drag marks of a placoderm fish's pelvic or pectoral fins while it swam. Discontinuous *Undichna isp.* likely represent a fish using its pectoral fins to push along the sediment surface, resulting in the production of trails of discrete scratch marks. Continuous *Undicha isp.* traces represent drag marks of a fish's pelvic or pectoral fins as it swam. Why a discernible caudal fin trace is absent

is unknown.

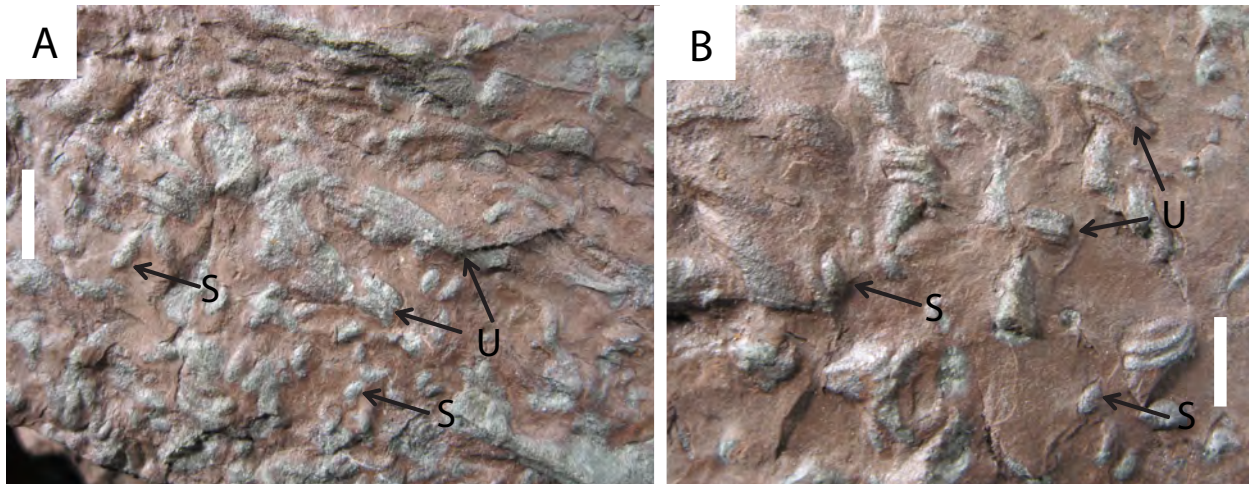


FIGURE 29—*Sagittichnus lincki* and *Undichna multiloba*; S= *Sagittichnus*; U= *Undichna*; scale=1 cm. A) *Sagittichnus lincki* and continuous *Undichna multiloba*, Powys Curve, PA. B) *Sagittichnus lincki* and discontinuous *Undichna multiloba*.

RHIZOLITHS

Type 12—Clay-filled, Hematite-rich Rhizoliths Figure 30 A, B

Description.—Diameter 2–20 mm; downward-tapering, downward and laterally fractal-branching, dominantly dichotomous structures; structures bifurcate, trifurcate, or rarely exhibit multiple 0.5–1 mm diameter branches; branches emanate from multiple 2–5 mm-diameter branches, rather than a single primary branch; branches range from first to approximately twentieth order; lateral roots diverge from and aggregate around larger roots; individual branch lengths range from 10 mm to 200 mm; branching angles range from 10°/120° to 55°/125°; radial angles range from 20°/160° to 80°/100°; fill is composed of a hematite-rich clay lining that exhibits high relief in thin section, and frequently a core of translucent-to-vitreous, sparry or micritic calcite, or quartz silt grains; clay linings contain inclusions of quartz silt and muscovite; clay often exhibits an apparently fibrous or layered texture in thin section; rhizoliths may lack a core; individual rhizoliths may have carbonate-cored, sediment cored and coreless portions; penetrative up to 300 mm, but normally less than 200 mm; individual root systems may be > 500 mm in lateral extent; occur in concentrations of 10's to 100's per dm².

Interpretation.—The presence of a core and lining in nearly all clay-filled, hematite-rich rhizoliths suggests that rhizolith preservation was a two-stage process. Clay-filled portions of rhizoliths always surround the core, when it is present. This indicates that the hematite and clay accumulated around the root, which later decayed, leaving space to be filled with crystalline carbonate, or silt. The clay lining in these rhizoliths is interpreted to be illuvial in origin.

Plant rooting depth is largely dependent on the moisture preferences and tolerances, and physiology of different plant species (Schultze et al., 1996; Shenk and Jackson, 2002), although average plant rooting depths tend to be greatest in arid environments (Jackson et al., 2002). Root

oxygenation is an extremely important physiological process in root systems, and root morphology is strongly influenced by root oxygen needs in a given plant species (Cannon, 1949; Shenk and Jackson, 2002). Water table depth exerts strong control on rooting depth because of the interplay of plant roots' need for both moisture and oxygen, as has been demonstrated by Shafroth et al. (2000) for woody riparian vegetation in alluvial environments—shallow water table depth can result in shallow rooting depth, whereas deep or variable water table depth can result in deeply penetrative rooting in the same plant species.

The shallow penetration depth of CF clay-filled, hematite-rich rhizoliths indicates that they represent plant rooting in the upper vadose zone of actively forming CF alluvial soils. The plants represented by CF clay-filled, hematite-rich rhizoliths were most likely dependent on well-drained, well-oxygenated soil conditions and represent organisms with terraphilic affinities *sensu* Hasiotis (2002, 2007). The plants' need for well-drained, well-oxygenated conditions, in addition to explaining the shallow rooting depth of clay-filled, hematite-rich rhizoliths, is consistent with the predominance of oxidized, rather than reduced iron in these rhizoliths (e.g., Kraus and Hasiotis, 2006; Smith et al., 2008a).

Type 13—Carbonate Rhizocretions Figure 30 E

Description.—Downward and laterally fractal-branching, dichotomous structures; < 1–15 mm in diameter; penetrative < 100 mm; highly fragmentary; composed of micritic and sparry calcite; boundaries are sharp to diffuse; may be composed of a rim of sparry calcite and micritic core; occur in concentrations up to thousands in hand sample; difficult to distinguish in outcrop.

Interpretation.—CF carbonate rhizocretions are interpreted to represent accumulations of pedogenic carbonate filling voids left after the decay of roots in dominantly well-drained,

seasonally wet-dry soils. These rhizcretions are precipitated in voids left after root decay (Cohen, 1982). Carbonate rhizcretions form in seasonally wet–dry environments, and can occur even when evapotranspiration does not exceed precipitation (Farrell, 1987; Aslan and Autin, 1988; Kraus and Hasiotis, 2006).

The presence of carbonate rhizcretions in CF paleosols is consistent with CF alluvial strata being deposited under a seasonally wet-dry climate (Woodrow et al., 1973). Driese and Mora (1993) asserted that carbonate rhizcretions broken by shrink-swell processes in CF soils provided nuclei around which carbonate nodules formed. The presence of carbonate rhizcretions in actively forming CF vertic claystones, as such, contributed to the formation of subsoil carbonate horizons.

The fragmentary nature of CF carbonate rhizcretions makes analysis of their root architecture difficult. The shallow penetration depth and dichotomous architecture of these traces suggests that they represent shallow rooting by terraphilic plants with a physiological need for well-drained, well-oxygenated soils.

The fragmentary nature of CF rhizcretions further makes identification of the tracemaker(s) difficult. A well-supported hypothesis of the identity of the tracemaker cannot be proposed, as such. Small (0.5–1 mm) diameter rhizcretions are often found in association with large-diameter rhizohaloes. This suggests that some CF rhizcretions may represent root hairs of large, arborescent plants, however, this interpretation is speculative. Small-diameter rhizcretions may also represent rooting by relatively small plants that coexisted with arborescent plants on the CF alluvial plain.

Description.—5BG 8/4 chroma, 3–50 mm diameter downward and laterally fractal-branching, dichotomous structures; dominantly 30–50 mm in diameter; branches range from second to approximately fifth order; branching angles range from 20°/160 to 90°; penetrative up to 800 mm; up to 1000 mm long; infilled with silt, clay, mud, or sand; sometimes contain pedogenic carbonate; composition is similar to host rock; termini of branches are somewhat rounded; may be vertical or horizontal; boundaries sharp to diffuse but normally sharp; occur in concentrations of tens per m² in thoroughly homogenized vertic claystone paleosols.

Interpretation.—Soil macrochannels facilitate down-profile percolation of water (Cohen, 1982; PiPujol and Buurman, 1997; Kraus and Hasiotis, 2006). Water movement can produce gley features (pseudogley) in soil channels of dominantly well-drained soils during periods of seasonal waterlogging (Pipujol and Buurman, 1994; Retallack, 2001). This results from the reduction and flushing of iron from sediment filling soil channels (Pipujol and Buurman, 1994; Kraus and Hasiotis, 2006). 5BG 8/4 chroma rhizohaloes best represent pseudogley features that formed in root channels in CF floodplain soils.

Pipujol and Buurman (1994) established a 6 stage qualitative assessment of pseudogley in paleosols. CF rhizohaloes best conform to stage 2, based on strong depletion of iron and a 1–2 mm thick bleached rim and lack of neoferrans around the halo. We interpret carbonate accumulations in CF rhizohaloes to be the result of precipitation of pedogenic carbonate in soil macrochannels in a seasonally wet-dry climate.

The large diameter and highly penetrative nature of CF rhizohaloes suggests that they represent highly penetrative, primary tap roots of a large plant. Physiological water and oxygen preferences exert a strong control on root morphology and penetration depth (Cannon, 1949; Shultze et al., 1996; Shafroth et al., 2000; Shenk and Jackson, 2002). The deeply penetrative

nature of CF rhizohaloes suggests that they represent rooting deep in the vadose zone, or perhaps the top of the phreatic zone to allow for exploitation of deep water sources in dry soil conditions. Driese et al. (1997) suggested that deeply penetrative roots associated with CF stump casts at Trout Run represent the same behavior in response to dry soil conditions. Penetration of CF rhizohaloes to the intermediate vadose zone or phreatic zone is consistent with behavior of hygrophilic to hydrophilic organisms *sensu* Hasiotis (2002, 2007). The differential penetration depth of CF clay-filled, hematite-rich rhizoliths and rhizohaloes is significant, as it indicates that CF plants exhibited both terraphilic and hygrophilic to hydrophilic behavior.

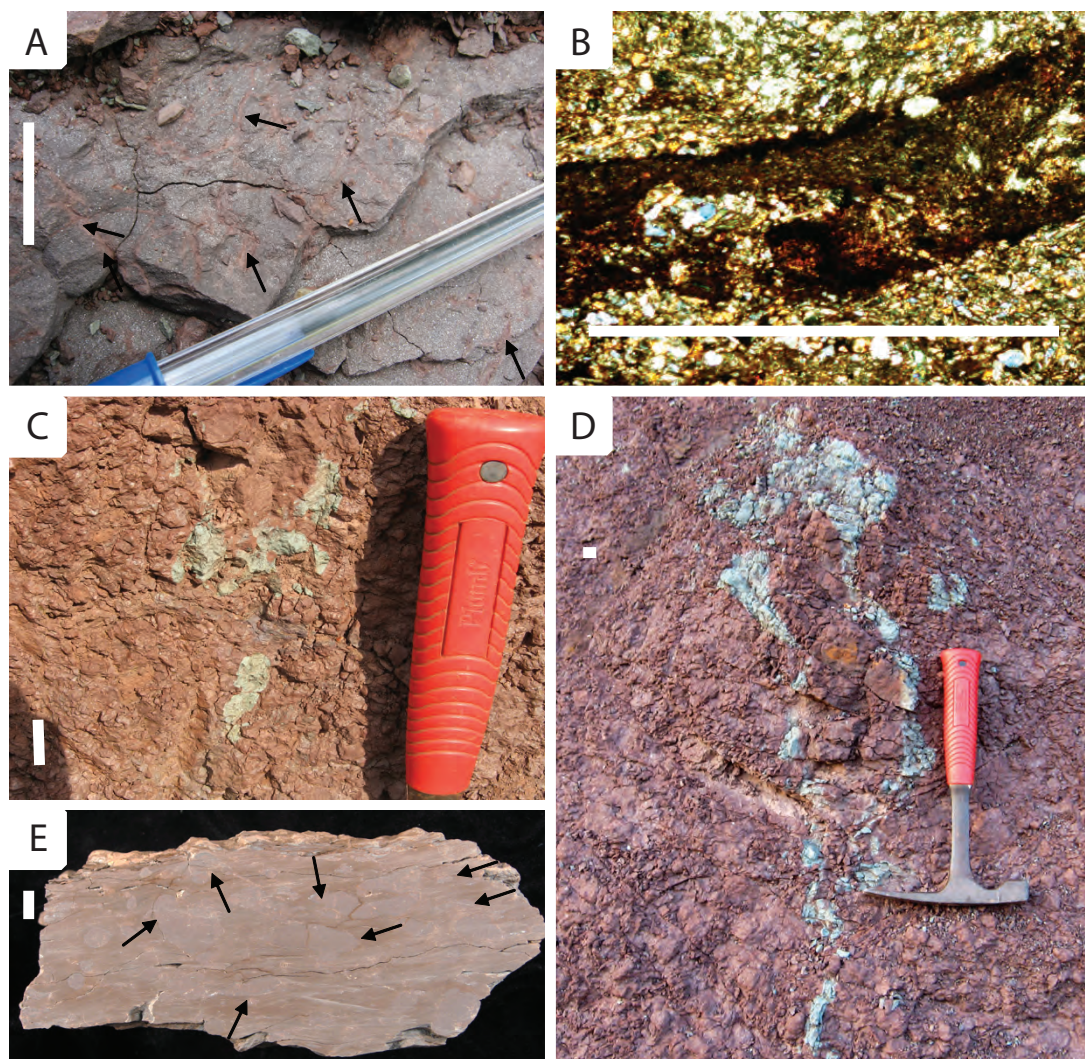


FIGURE 30—Rhizoliths; scale=10 mm. A) Clay-filled hematite-rich rhizoliths in finely laminated siltstone, Red Hill. B) Thin section of a clay-filled hematite-rich rhizolith cored with quartzose silt and pedogenic carbonate, Powys Curve. C) Rhizohalo in vertic claystone paleosol, Powys Curve. D) Rhizohaloes in vertic claystone, Red Hill, PA. E) Carbonate rhizocretions in platy claystone, Powys Curve.

Type 15—*In Situ* Progymnosperm Stump Casts Figure 22 A

Description.—Vertically oriented, cylindrical, sediment-filled structures; base of structures characterized by downward and laterally fractal-branching, sediment-filled rhizoliths; may exhibit a deeply penetrative, central tap root, or multiple deeply penetrative tap roots; fill material is similar to the host rock.

Interpretation.—We interpret these structures to be *in situ* progymnosperm stump casts based on their shape, orientation, and association with deeply penetrative rhizoliths. CF stump casts described here are similar in morphology to those described by Driese et al. (1997), and occur in paleosols interpreted to represent moderately well-drained to well-drained soils.

Inferred paleohydrologic relationships of deeply penetrative CF rhizohaloes are discussed in the previous section. CF *in situ* stump casts represent rooting in the lower vadose zone or upper phreatic zone by arborescent plants with hygrophilic to hydrophilic affinities.

In situ stump casts occur in all pedogenically modified CF facies, representative of well-drained soils, including thoroughly homogenized vertic claystone paleosols, which have been interpreted to represent vertisols (e.g. Driese et al., 1993). The deeply penetrative nature of rhizoliths associated with CF stump casts may represent deep roots that, in addition to allowing access to phreatic water sources, provided stability for aborescent plants growing in shrinking and swelling soils that were rich in expanding clay minerals.

ICHNOCOENOSES AND ICHNOPEDOLOGIC ASSOCIATIONS

Paleosol Ichnocoenoses

The Clay-filled, Hematite-Rich Rhizolith Ichnocoenosis

Description.—The Clay-filled, Hematite-rich Rhizolith Ichnocoenosis is characterized by bedding plane concentrations of tens to hundreds of 1–3 mm diameter, clay-filled hematite-rich rhizoliths and carbonate rhizoliths per dm² (Fig. 21 B, Fig. 31). *Beaconites antarcticus* and *B. barretti* also occur, generally in bedding plane concentrations of < 10 per dm² (Fig. 21 A, B; Fig. 31). In this ichnocoenosis < 1 percent of the host rock is disrupted by burrows and 5–30 percent of the host rock is disrupted by clay-filled, hematite-rich and carbonate rhizoliths. The dominance of clay-filled, hematite-rich rhizoliths in this ichnocoenosis indicates that plants were the dominant tracemaker.

Occurrence.—Finely laminated mudstone-sandstone interbeds, weakly pedogenically modified trough cross-stratified sandstone.

Interpretation.—The low concentration of burrows and rhizoliths in association with weakly developed paleosols indicates that this ichnocoenosis represents an early stage of colonization of CF soils. Rhizoliths represent rooting by plants, and *Beaconites antarcticus* and *B. barretti* represent burrowing by soil dwelling arthropods of unknown taxonomic affinity. Weak pedogenesis and low concentrations of traces resulted from disruption of pedogenesis by inundation and sedimentation of the proximal floodplain and natural levees (e.g. Kraus and Bown, 1986, 1988).

We interpret both clay-filled, hematite-rich rhizoliths and CF *Beaconites* isp. to represent behaviors of terraphilic to hygrophilic plants and animals, respectively. The Clay-filled, Hematite-rich Rhizolith Ichnocoenosis, as such, is interpreted to represent organismal behavior in the vadose zone.

The *Beaconites* Ichnocoenosis

Description.—The *Beaconites* Ichnocoenosis is characterized by bedding plane concentrations of tens to hundreds of backfilled burrows and 1–20 mm diameter rhizoliths per dm² (Fig. 24 B; Fig. 25; Fig. 31). In occurrences of the *Beaconites* Ichnocoenosis, 1–50 percent of the host rock is disrupted by burrows and 1–30 percent of the host rock is disrupted by clay-filled hematite-rich rhizoliths, carbonate rhizoliths, and rhizohaloes.

Occurrence.—Platy mudstone-sandstone interbeds, thoroughly homogenized vertic claystone, moderately to strongly pedogenically modified trough cross-stratified sandstone.

Interpretation.—The *Beaconites* Ichnocoenosis represents continued colonization of CF alluvial soils by plants and arthropods, when the floodplain was subaerially exposed. The transition from the Clay-filled Hematite-rich Rhizolith Ichnocoenosis to the *Beaconites* Ichnocoenosis represents a shift from colonization of soils dominantly by plants to colonization of soils dominantly by arthropods, based on the dominance of *Beaconites antarcticus* and *B. barretti*, rather than rhizoliths. We suggest that this change in the dominant trace fossil type reflects ecological succession in CF alluvial soils.

The high concentrations and crosscutting nature of burrows and rhizoliths in the *Beaconites* Ichnocoenosis indicates that it represents multiple episodes of burrowing and rooting, which may have been seasonal. This is corroborated by the occurrence of the *Beaconites* Ichnocoenosis in moderately well-developed paleosols. We interpret the *Beaconites* Ichnocoenosis to represent behavior of organisms in the vadose zone, as is true of the Clay-filled, Hematite-rich Rhizolith Ichnocoenosis.

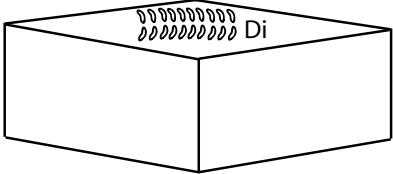
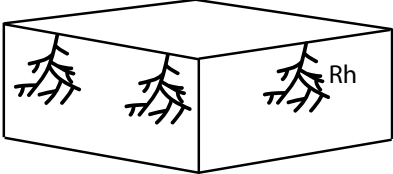
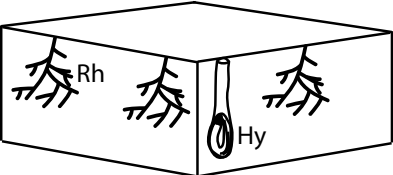
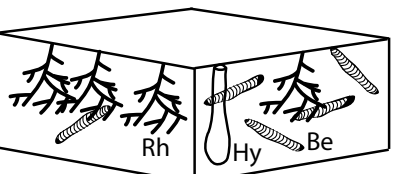
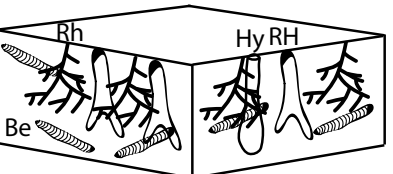
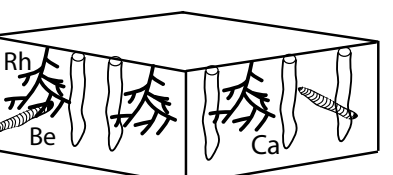
Ichnocoenoses	Trace fossil associations	Lithofacies associations	Environment
	<i>Diplichnites gouldi</i>	Finely laminated mudstone-sandstone interbeds, trough cross-stratified scour-based fine-grained sandstone (pedogenically modified)	Weakly developed soils; pedogenic features are likely an overprint
	Clay-filled, hematite-rich rhizoliths, carbonate rhizoliths, small rhizhaloes	Finely laminated mudstone-siltstone interbeds, weakly pedogenically modified scour-based fine-grained sandstone	Weakly developed soils
	Clay-filled, hematite-rich rhizoliths, carbonate rhizoliths, rhizhaloes, Beaconites antarcticus, Beaconites barretti, Hyperoethys teichonomos	All pedogenically modified facies	Weakly to well developed soils; burrows were constructed as seasonal floodwaters receded
	Clay-filled, hematite-rich rhizoliths, carbonate rhizoliths, rhizhaloes, Beaconites antarcticus, Beaconites barretti, Hyperoethys teichonomos	All pedogenically modified facies	Varbiably developed soils
	Clay-filled, hematite-rich rhizoliths, carbonate rhizoliths, rhizhaloes (>2 cm diameter), Beaconites antarcticus, Beaconites barretti, Hyperoethys teichonomos	Thoroughly homogenized vertic claystone paleosols	Mature soils
	Clay-filled, hematite-rich rhizoliths, carbonate rhizoliths, rhizhaloes (>2 cm diameter), Beaconites antarcticus, Camborygma eunekonomos	Thoroughly homogenized vertic claystone paleosols, weakly laminated to platy mudstone-sandstone interbeds	Weakly to well developed soils; burrows were constructed by hydrophilic organisms

FIGURE 31—Block diagrams of paleosol ichnocoenoses with facies occurrences and interpreted environments.

The *Camborygma* Ichnocoenosis

Description.—The *Camborygma* Ichnocoenosis is composed of *Camborygma litonomos* and *C. eumekonomos* (Fig. 22 B,C; Fig. 24 E; Fig. 31). *Camborygma litonomos*. and *C. eumekonomos* and are weakly overprinted by *Beaconites antarcticus* and clay-filled, hematite-rich rhizoliths.

Occurrence.—Platy mudstone-sandstone interbeds, thoroughly homogenized vertic claystones.

Interpretation.—The *Camborygma* Ichnocoenosis represents behavior of terraphilic to hydrophilic organisms, probably decapod-like arthropods that dwelled in the phreatic zone of CF soils, in the case of *C. eumekonomos*, and either terraphilic to hygrophilic burrowing arachnids, or hydrophilic decapod-like arthropods in the case of *C. litonomos*. The presence of *Beaconites antarcticus* and clay-filled, hematite-rich rhizoliths in *C. eumekonomos* burrow fills indicates that *Camborygma litonomos* and *C. eumekonomos* were modified by biotic pedoturbation, likely after the burrows were abandoned. Crosscutting relationships in the *Camborygma* Ichnocoenosis indicate that the *Camborygma* Ichnocoenosis was overprinted by the *Beaconites* Ichnocoenosis during pedogenesis.

The Lungfish Estivation Burrow Ichnocoenosis

Description.—The Lungfish Estivation Burrow Ichnocoenosis is characterized by lungfish estivation burrows, crosscut by 1–3 mm diameter rhizoliths and *Beaconites antarcticus* (Fig. 28; Fig. 31). CF lungfish burrows are typically solitary occurrences. They can, however, occur in bedding plain concentrations >5 burrows per m^2 .

Occurrence.—All pedogenically modified CF facies.

Interpretation.—The Lungfish Estivation Burrow Ichnocoenosis represents construction of estivation burrows by lungfish as floodwaters on the CF alluvial plain receded. These burrows were constructed by aquatic organisms to avoid desiccation. Lungfish burrows were likely superimposed on the dominant ichnologic and pedogenic fabric of the soils in which they were constructed. These burrows are normally crosscut and reworked by dense concentrations of rhizoliths and *Beaconites antarcticus*. Crosscutting ichnofabrics indicate that lungfish burrows were rooted and reburrowed by plants and soil arthropods during periods of subaerial exposure and after abandonment and fill of the open burrows.

The Rhizohalo Ichnocoenosis

Description.—The Rhizohalo Ichnocoenosis is characterized by prominent 1–50 mm diameter 5BG 8/4 chroma rhizohaloes, normally 10–30 mm in diameter, as well as bedding plane concentrations of hundreds of clay-filled hematite-rich rhizoliths, carbonate rhizoliths, *Beaconites antarcticus* and *B. barretti* per dm² (Fig. 25 A,D,F,G; Fig. 31). Rhizohaloes occur in discrete horizons, interpreted to represent soil A horizons (Retallack et al., 2009) (Fig. 25 F, G). Rhizohaloes in thoroughly homogenized vertic claystones occur in concentrations of 1 to 10's per m² of outcrop area. *Beaconites antarcticus* and *B. barretti* also occur in bedding plane concentrations of tens–hundreds per dm² (Fig. 25 B; Fig. 31). How much churning and disruption of the host rock was caused by bioturbation in occurrences of the rhizohalo ichnocoenosis is difficult to determine, because ichnopedofabrics in thoroughly homogenized vertic claystone paleosols are characterized by cross-cutting burrows, rhizoliths, and argilloturbation features.

Occurrence.—Thoroughly homogenized vertic claystones.

Interpretation.—Why 5BG 8/4 chroma rhizohaloes are so common in thoroughly homogenized vertic claystones is unclear. The high concentrations of rhizoliths and burrows, and high degree of paleosol maturity indicate that the Rhizohalo Ichnocoenosis represents the most advanced stage of ecological succession and pedogenesis in CF soils. Burrowing, rooting and other pedogenic processes must have continued uninterrupted or rarely interrupted by sedimentation for long periods of time, during which root channels were periodically waterlogged, resulting in surface water gleying. Biotic and abiotic pedoturbation features are equally abundant and crosscut one another, indicating that CF soils were strongly modified by both organism activity and abiotic pedoturbation (argilloturbation) processes.

We interpret the Rhizohalo Ichnocoenosis to represent hydrophilic behavior of large, arborescent plants, perhaps the prgoymnosperm *Archaeopteris*. This is evidenced by the large-diameter and deeply penetrative nature of CF rhizohaloes. Large-diameter, highly penetrative rhizohaloes likely represent tap roots whose purpose was to access water sources in the phreatic zone or deep in the vadose zone.

The *Diplichnites* Ichnocoenosis

Description.—The *Diplichnites* Ichnocoenosis is characterized by arthropod trackways attributable to *Diplichnites gouldi*. This ichnocoenosis occurs in weakly developed CF paleosols that retain remnant bedding (Fig. 27, Fig. 31).

Occurrence.—Finely laminated sandstone-mudstone interbeds, weakly pedogenically modified cross-stratified sandstones.

Interpretation.—*Diplichnites gouldi* represents locomotion of an apparently myriapod-like arthropod. Trackway production apparently did not contribute to pedogenesis. Beds containing trackways, however, can exhibit weak pedogenic features, that apparently postdate trackway production.

The *Diplichnites* Ichnocoenosis represents locomotion of a myriapod-like arthropod on newly deposited alluvial sediments. We suggest that the *Diplichnites* Ichnocoenosis further represents behavior of a subaerial, terraphilic organism. The occurrence of the *Diplichnites* Ichnocoenosis in weakly developed paleosols reflects the presence of remnant lamination in those paleosols. Weak pedogenesis and preservation of primary lamination are likely requisite to the occurrence of the *Diplichnites* Ichnocoenosis, because its preservation requires the preservation of the bedding plain on which the tracemaker walked.

The *Lockeia siliquaria* Ichnocoenosis

Description.—The *Lockeia siliquaria* Ichnocoenosis is characterized by one ichnotaxon: *Lockeia siliquaria* (Fig. 26 C; Fig. 32). *Lockeia siliquaria* that we identified did not co-occur with any other traces.

Occurrence.—We identified only one occurrence of this ichnocoenosis, at the bottom of a trough cross-stratified, fine-grained sandstone bed at Steam Valley.

Interpretation.—The *Lockeia siliquaria* Ichnocoenosis represents burrowing by shallow, siphonate, infaunal bivalves in actively accreting CF pointbars. The occurrence of bivalve burrows in pointbar deposits, without rhizoliths or other traces typical of CF paleosols indicates that these traces represent behavior of aquatic organisms and are unrelated to pedogenesis.

We assert that the predominance of bivalve resting traces and lack of bivalve escape traces and equilibria reflects a low energy environment with low to moderate rates of sedimentation during trace formation. Consistent with our assertion, high flow regime sedimentary structures (e.g. plane beds, antidunes, and ripup clasts) are absent from the interval in which *Lockeia siliquaria* occurs.

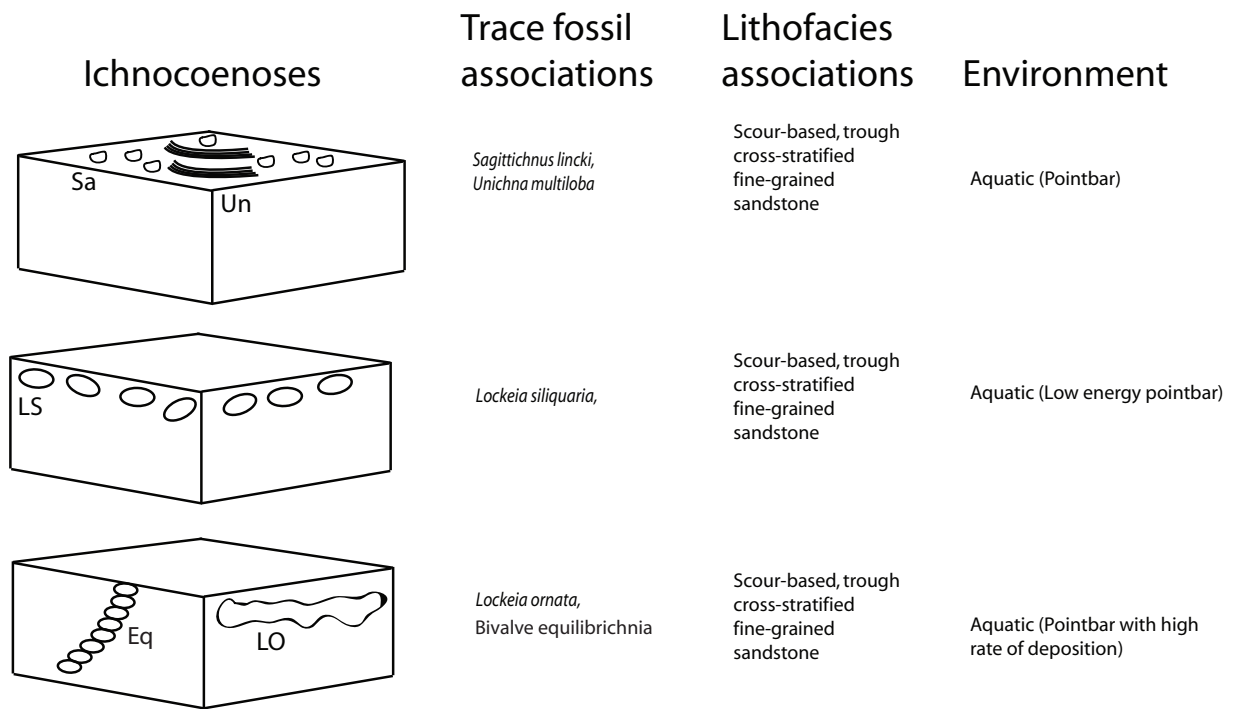


FIGURE 32—Block diagram of aquatic ichnocoenoses with facies occurrences and interpreted environments.

The *Lockeia ornata*, Bivalve Equilibrichnium Ichnocoenosis

Description.—The *Lockeia ornata*, Bivalve Equilibrichnium Ichnocoenosis is composed of *Lockeia ornata* and subvertical–inclined bivalve equilibrichnia (Fig. 26 A,B; Fig. 32).

Occurrence.—The *Lockeia ornata*, Bivalve Equilibrichnium Ichnocoenosis occurs at the bottoms of scour-based, very fine-grained sandstone beds at Trout Run and Powys Curve, PA.

Interpretation.—We interpret *Lockeia ornata* and bivalve equilibrichnia to represent readjustment of bivalves' position in the sediment column in response to sedimentation. *Lockeia ornata* represents horizontal movement by the bivalve, whereas subvertical to inclined equilibrichnia represent vertical readjustment in the sediment column. We assert that the *Lockeia ornata*, Bivalve Equilibrichnium Ichnocoenosis represents an environment with higher rates of sedimentation than the *Lockeia siliquaria* Ichnocoenosis, which placed stress on the bivalves, forcing them to move laterally and vertically to avoid burial.

The *Sagittichnus*, *Undichna* Ichnocoenosis

Description.—The *Sagittichnus*, *Undichna* Ichnocoenosis is characterized by *Sagittichnus lincki* and *Undichna multiloba*. *Sagittichnus lincki* occurs in high concentration and forms a characteristic ichnofabric that is crosscut by *Undichna multiloba* (Figs. 29, 32).

Occurrence.—We found only one occurrence of the *Sagittichnus*, *Undichna* Ichnocoenosis, 1.5 m from the base of a 3.6-m-thick channel filled with green and purple very fine, muscovite-rich, low angle trough cross-bedded sandstone.

Interpretation.—The lack of rhizoliths and pedogenic features in association with the *Sagittichnus*, *Undichna* Ichnocoenosis and the presence of *Undichna multiloba*, a fish swimming trace, indicate that the *Sagittichnus* ichnocoenosis represents behavior of aquatic organisms. We

found no indication that the depositional environment in which the *Sagittichnus* ichnocoenosis occurs differs from that in which the *Lockeia siliquaria* Ichnocoenosis occurs. Whether or not the difference in behavior from that of the *Lockeia siliquaria* Ichnocoenosis represented by the *Sagittichnus*, *Undichna* Ichnocoenosis indicates differing paleoenvironmental occurrences of the two ichnocoenoses is unclear. We interpret the *Sagittichnus*, *Undichna* Ichnocoenosis to represent a low energy environment, similar to the environment represented by the *Lockeia siliquaria* Ichnocoenosis.

DISCUSSION OF CF ICHNOCOENOSES

CF soil organisms as ecosystem engineers.—We interpret the transition from the Clay-filled, Hematite-rich Rhizolith, Ichnocoenosis to the *Beaconites* and Rhizohalo Ichnocoenoses to represent colonization and progressive modification of CF alluvial soils by soil-dwelling organisms, i.e., evidence of ecological succession. Modifications to CF soils by soil-dwelling organisms would have included: 1) probable addition of organics to the soil; 2) homogenization and destruction of sedimentary structure of parent material; 3) facilitation of clay translocation and precipitation of carbonate within the soil profile via creation of soil macrochannels; and 4) improvement of soil drainage conditions via production of macrochannels and pore space. These organismal modifications of CF soils worked in conjunction with argilloturbation, resulting from shrink-swell of expandable clays (e.g., Driese and Mora, 1993; Driese et al., 1993) to produce the characteristics observable in CF paleosols.

The increasing abundance of traces in increasingly mature CF paleosols suggests that organismal modifications were beneficial to CF soil-dwelling organisms. Behaviors that result in beneficial modification of an organism's environment are commonly observed in modern

continental ecosystems (e.g., Jones et al., 1994, 1997, 2006; Wright et al., 2002; Lill and Marquis, 2003; Jouquet et al., 2006) and have been termed ecosystem engineering by Jones et al. (1994). Jones et al. (1994) divided ecosystem engineers into 2 categories: 1) autogenic engineers, which modify their physicochemical environment, or create new environments by modifying themselves, e.g. reef-forming corals; and 2) allogenic engineers, which modify aspects of the surrounding environment in a way that benefits themselves, or other organisms by modulating resource flows within the environment, e.g., dam-building beavers. Evidence from the CF and from previous reports of Devonian continental ichnofossils (Bradshaw, 1981; Gordon, 1988; Driese and Mora, 1993; Morrissey and Braddy, 2004) indicates that Devonian soil organisms were primarily allogenic engineers.

Jones et al. (1994) additionally defined 6 cases that characterize possible ecosystem engineering by autogenic and allogenic ecosystem engineers. The inferred ecosystem engineering activities of CF soil organisms are consistent with cases 2, 4, and 6 of Jones et al. (1994) in which organisms: 1) directly modulate transformation of materials from one state to another; 2) modulate transformation of material from one state to another, thus modulating resource flows within an ecosystem; and 3) modulate transformation of material from one state to another, and thus modulate resource flows in an ecosystem that are additionally affected by one or more abiotic factors, respectively (Fig. 33).

Modern soil-dwelling organisms have been recognized as ecosystem engineers and are known to substantially modify soil aggregation, porosity, hydrology, aeration, organic content, and chemistry (Dauber et al., 2001; De De Deyn et al., 2003; Barros et al., 2004; Shipitalo and Le Bayon, 2004; Jones et al., 2006; Jouquet et al., 2006; Kuczak et al., 2006). No previous attempts have been made to recognize evidence of ecosystem engineering in early and middle

Paleozoic continental strata. Our recognition of ecosystem engineering by Late Devonian soil organisms is highly significant, as such.

CF plants as ecosystem engineers.—The direct provision of nutrient resources, e.g. production of leaf litter by higher plants, is not recognized as ecosystem engineering by Jones et al. (1994). The presence of autotrophs, however, is requisite to the development of trophic structure in a given ecosystem and does facilitate colonization of an area by primary consumers (Aber and Melillo, 2001). Our evidence suggests that CF plants contributed more to modifying CF soil ecosystems than providing nutrient resources. As such, they should be considered ecosystem engineers, because they modified their physical environment by producing soil macrochannels that improved soil drainage, and facilitated translocation of clay and precipitation of pedogenic carbonate in the soil profile. Improvement of soil porosity via root macrochannel production is recognized in modern soils (e.g., Kelly et al., 1998; Laio et al., 2001).

Direct physical evidence that CF plant roots served as channels for water drainage are: 1) the presence of illuvial clay in rhizoliths, which requires downward percolation of water, and 2) the presence of carbonate rhizoliths, whose production requires percolation and later drying of water in the soil profile (Cohen, 1982; Pipujol and Buurman, 1994; Kraus and Hasiotis, 2006). Rhizohaloes are surface water gley features that are produced because water in soil preferentially drains through root pores, producing localized reduced conditions (Pipujol and Buurman, 1994). The presence of rhizohaloes in nearly all mature CF paleosols is further evidence that roots served as channels for down-profile movement of water.

Percolation of water down-profile would also have accelerated rates of chemical mineral weathering in the soil profile. Water exerts a strong control on rates of chemical mineral weathering (e.g., Velbel, 1993). Mineral weathering, in addition to contributing to the

production of stable clay minerals (Retallack, 2001) releases mineral nutrients to be utilized by plants (White and Brantley, 1995; Kelly et al., 1998). Plants further accelerate mineral weathering rates via production of organic acids, biocycling of cations, and biogenic mineral production (Kelly et al., 1998). Evidence of these processes is likely impossible to find in ancient soils, however similar processes likely contributed to plant-mediated mineral weathering in CF alluvial soils. The release of mineral nutrients and contribution of organics to the soil would have supported additional plants which could then root, further increase weathering rates, and add organics to the soil. This is supported by the increase in abundance of rhizoliths in increasingly mature CF paleosols and suggests that colonization of CF soils initiated a positive feedback mechanism, resulting in an accelerated rate of ecological succession and pedogenesis.

Root macrochannels in soils further contribute to soil aeration, i.e. increased levels of soil-atmosphere interaction (Douglas et al., 1992; Jones et al., 2006). Aerobic soil organisms rely on oxygen trapped in soil pores and interstices for respiration (Villani et al., 1999). Soil aeration by root macrochannels would also have facilitated soil colonization by aerobic soil invertebrates, such as macroscopic and mesoscopic arthropods, as such.

Concentrations up to 30 percent of clay-filled hematite-rich rhizoliths and carbonate rhizoliths in CF paleosols indicate that plant root channels provided major pathways for illuviation of clay, subsoil precipitation of carbonate, and soil drainage and aeration. These pathways likely contributed greatly to the production of illuvial clay and pedogenic carbonate horizons, as well as facilitating further soil colonization by plants and invertebrates. Facilitation of pedogenic carbonate and illuvial clay deposition by root macrochannels is significant, because pedogenic carbonate horizons and illuvial clay horizons are characteristic of CF paleosols (Driese et al., 1993; Retallack et al., 2009). Driese and Mora (1993) have suggested that

fragmented carbonate rhizoliths provided nuclei around which CF subsoil carbonate nodules were precipitated, further supporting the idea that pedogenic carbonate facilitated by root channels substantially changed the physicochemical properties of CF soils. Substantial contributions to soil aeration and drainage in CF root macrochannels would have contributed greatly to ecological succession in CF soils.

Arborescent plants are known to produce shaded patches that both facilitate the growth of understory vegetation and shade their roots (Jones et al., 1997). Arborescent plants on the CF alluvial plain likely created similar patches, although this cannot be corroborated with physical evidence. CF arborescent plants may also have been autogenic engineers, as such.

CF burrowers as ecosystem engineers.—Backfilled burrow production contributed to pedogenesis by churning and homogenizing, as well as creating macropores and macrochannels in CF soils. Evidence for homogenization of weakly to moderately developed CF paleosols can be seen in slabbed sections, which contain zones of structureless sediment crosscut by dense concentrations of backfilled burrows. Where concentrations are dense, burrows crosscut one another, as well as crosscutting rhizoliths. Biotic pedoturbation by burrowers resulted in fragmentation of both clay-filled and carbonate rhizoliths, and homogenization of clay and organics into coarser host rock (Fig. 33).

In addition to homogenizing mineral soil components, backfilled burrows would have churned plant derived organics, and mineral nutrients derived from chemical weathering into the soil, facilitating further colonization of the soil by plants. This would have provided additional organic nutrients to be consumed by the arthropods that produced CF *Beaconites antarcticus* and *B. barretti*. Backfilled burrow production, thus, further contributed to the positive feedback mechanism driving CF ecological succession.

Results of neoichnologic experiments by Smith and Hasiotis (2008) and Counts and Hasiotis (2009) indicate that production of backfilled burrows by insect nymphs and larvae also contributes to soil porosity. Although backfilled burrows are not maintained as open tunnels to the soil surface, examination of neoichnologically produced backfilled burrows figured by Smith and Hasiotis (2008) and Counts and Hasiotis (2009) indicates that backfilled burrows exhibit substantially more pore space than the surrounding sediment. Pore space production by backfilled burrowers, as such, is likely to improve soil drainage conditions in modern soils, and also likely to have improved soil drainage in CF alluvial soils.

Churning of up to 50 percent of CF paleosols by *Beaconites isp.* indicates that the *Beaconites isp.* tracemakers substantially modified CF soils. Production of *Beaconites isp.*, as such, would have resulted in modification of aeration, pore space, and organic content of at least as much 50 percent of the sediment that formed CF alluvial soils. Production of *Beaconites isp.* could have resulted in greater modification of thoroughly homogenized vertic claystone paleosols, however, recognition of the extent of modification is made difficult by crosscutting rhizolith, burrow, and argilloturbation fabrics. We assert that modification of CF alluvial soils by the *Beaconites isp.* tracemakers contributed further to facilitating colonization of the soils by infaunal organisms and plants.

Open soil burrows produced by lungfish and arthropods (lungfish estivation burrows and *Camborygma isp.*) represent the behavior of transient and periodic soil organisms that were also likely ecosystem engineers. Lungfish estivation burrows and *Camborygma isp.* represent open, passively infilled burrows whose production would have made contributions of homogenization, pore space creation, and improved drainage of CF alluvial soils. Lungfish estivation burrows,

although constructed by aquatic organisms as seasonal floodwaters retreated, occurred locally in relatively high concentrations to have contributed to pedogenesis.

CF *Camborygma* isp., despite not contributing greatly to pedogenesis, has great evolutionary significance, because production of *Camborygma* in the Mesozoic and Cenozoic apparently contributed greatly to the pedogenic process, at times to such an extent that *Camborygma* is recognizable as the dominant pedogenic feature in some alluvial paleosols (e.g., Hasiotis et al., 2007; Smith et al., 2008b). The occurrence of *Camborygma* isp. in the CF, as such, represents the inception of a behavior that later became an integral contributor to pedogenesis in alluvial systems.

Distinction of aquatic ichnocoenoses.—We recognized aquatic ichnocoenoses based on the absence of pedogenic features in occurrences of these ichnocoenoses, as well as behavioral analyses of the traces that occur in those ichnocoenoses. As was previously mentioned, we assert that CF aquatic ichnocoenoses have important implications for recognizing paleoenvironmental differences in fluvial facies, e.g., sedimentation rate and depositional energy. We did not recognize evidence of ecosystem engineering in CF aquatic ichnocoenoses and, as such, consider that ecosystem engineering in Devonian continental organisms was restricted to infaunal soil organisms (plants and deposit-feeding arthropods).

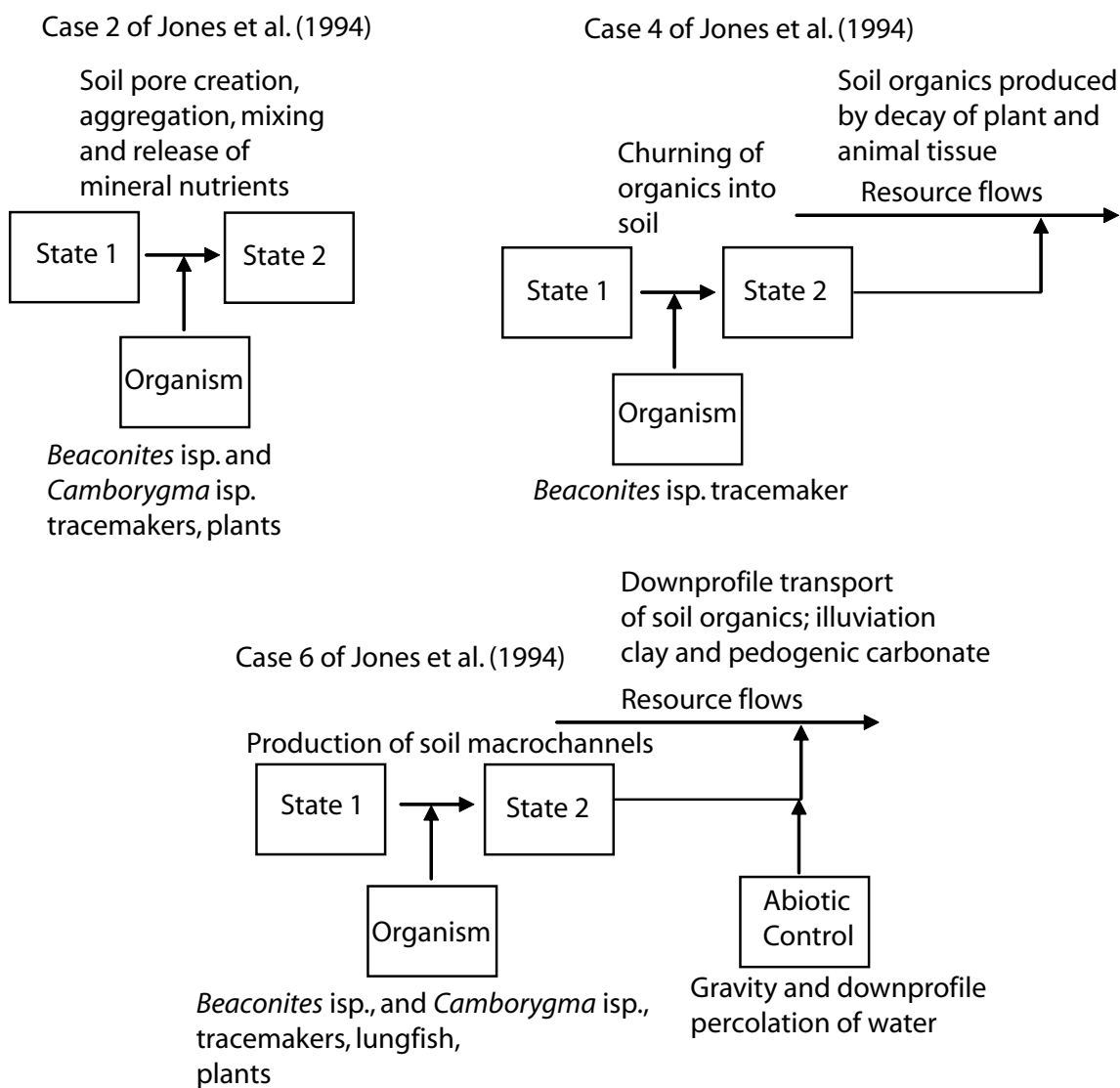


FIGURE 33—Diagram illustrating inferred ecosystem engineering activities of CF soil biota.

CONCLUSIONS

The CF trace fossil assemblage represents a moderately diverse suite of behaviors of soil-dwelling and aquatic organisms that inhabited the CF alluvial plain. The behaviors represented by these traces indicate that Devonian soil organisms already exhibited specialized behaviors characteristic of Mesozoic to recent soil organisms, and represent temporary, transient, and periodic soil biota *sensu* Wallwork (1970) and Hasiotis (2007). CF trace fossils further represent behavior of terraphilic to hygrophilic, and hydrophilic organisms, indicating that physiological responses of Devonian soil organisms to hydrology were complex.

Evidence from the CF indicates that Late Devonian soil organisms contributed greatly to the pedogenic process, as is considered of Mesozoic to recent soil organisms (e.g., Hasiotis, 2002, 2007; Jones et al., 2006; Jouquet et al., 2006). We further assert that pedogenesis by CF soil organisms contributed to a positive feedback that facilitated further colonization of CF alluvial soils by infaunal organisms. CF soil organisms, as such, should be considered ecosystem engineers, indicating that the inception of ecosystem engineering by soil organisms occurred in the Late Devonian, or earlier.

Although CF aquatic organisms were apparently not ecosystem engineers, CF aquatic ichnocoenoses have important paleoenvironmental implications. CF aquatic trace fossils, furthermore, represent important components of biodiversity in aquatic environments of the CF.

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**CHAPTER 4. LUNGFISH BURROWS OF THE UPPER DEVONIAN CATSKILL
FORMATION, NORTH-CENTRAL PENNSYLVANIA, USA: MORPHOLOGICAL
DISTINCTION AND EVOLUTIONARY IMPLICATIONS**

FORMATTED FOR PALAEONTOLOGY

ABSTRACT: Large-diameter, vertical, clavate burrows are common throughout the Frasnian to Famennian Catskill Formation, north-central Pennsylvania, USA, and can occur in bedding plane concentrations >5 per m^2 . A detailed comparison of the architectural and surficial burrow morphologies of the Catskill Formation burrows with fossil and modern lungfish aestivation burrows indicates that they are lungfish aestivation burrows. Furthermore, the Catskill Formation burrows are morphologically distinct from decapod burrows (*Camborygma* and *Psilonichnus* isp.), amphibian aestivation burrows (*Torridorefugium eskridgensis*), and *Macanopsis* isp. The morphological uniqueness of Catskill Formation large-diameter burrows merits the erection of a new ichnotaxon. *Hyperoeuthys teichonomos*, a new ichnogenus and ichnospecies for lungfish aestivation burrows is here described. Consistent with the presence of lungfish aestivation burrows in the Catskill Formation, lungfish cranial material and tooth plates occur at all stratigraphical levels, and in several different localities in the Catskill Formation. Lungfish skeletal material is rare, however. *Hyperoeuthys teichonomos* represents the oldest evidence of vertebrate aestivation, indicating that vertebrate aestivation evolved as early as the Late Devonian, rather than the Early Pennsylvanian, as previous ichnological evidence suggested.

THE purpose of this paper is to compare, subvertically to vertically oriented, clavate burrows of the Frasnian–Famennian Catskill Formation of north-central Pennsylvania with other vertical and

subvertical to vertical burrows that exhibit similar morphology in order to: 1) interpret the tracemaker, 2) interpret the behavior represented by the burrows, and 3) ichnotaxonomically evaluate the burrows. Catskill Formation vertical to subvertical, clavate burrows—herein referred to as Catskill Formation burrows with the understanding that numerous burrow morphotypes occur in the Catskill Formation—exhibit architectural and surficial morphology that suggests they represent behavior associated with lungfish (Dipnoi) aestivation, which is a state of dormancy in response to seasonal drought. Catskill Formation burrows, however, are not known to contain lungfish skeletal material, as is true of many lungfish aestivation burrows reported in the literature (e.g., Romer and Olson, 1954; Carlson, 1968; Olson and Bolles, 1975; Dalquest and Carpenter, 1977; Hasiotis, 2002).

Architectural and surficial morphological evidence that the Catskill Formation burrows are most likely lungfish aestivation burrows is provided. Catskill Formation burrows were compared to aestivation burrows of the Permian lungfish *Gnathorhiza*, many of which contain lungfish skeletal material, as well as to late Paleozoic burrows interpreted as lungfish burrows and to aestivation burrows of the modern lungfishes *Protopterus* and *Lepidosiren*. Catskill Formation burrows were also compared with decapod burrows (*Camborygma* isp., and *Psilonichnus* isp.), and *Macanopsis* isp., all of which exhibit morphological similarity to Catskill Formation burrows.

The morphological uniqueness of the Catskill Formation burrows indicates that they merit the erection of a new ichnogenus and ichnospecies (Hasiotis et al., 2002). If the Catskill Formation burrows represent lungfish aestivation, their presence in the Frasnian–Famennian Catskill

Formation is significant, as this trace fossil evidence extends the evolutionary timing of vertebrate aestivation from the early Pennsylvanian (late Pottsville age) (Carroll, 1965) to the late Frasnian (Sevon and Woodrow, 1985). More precise characterization of the range extension is made impossible by imprecise dating of both the previous oldest recorded lungfish aestivation burrows (Carroll, 1965) and the lower Catskill Formation in our field area.

Fragmental lungfish skeletal material in the form of tooth plates and cranial bone is known to occur rarely throughout the Catskill Formation, including at the sites investigated during this study (Daeschler and Mullison, 2004; Friedman and Daeschler, 2006). Catskill Formation burrows have long been recognized as probable lungfish aestivation burrows (Woodrow and Fletcher, 1969; Hasiotis et al., 1999). The lack absence of skeletal material from these burrows, however, has led researchers to doubt whether or not they are truly lungfish aestivation burrows (e.g., Daeschler and Mullison, 2004; Friedman and Daeschler, 2006).

GEOLOGICAL SETTING

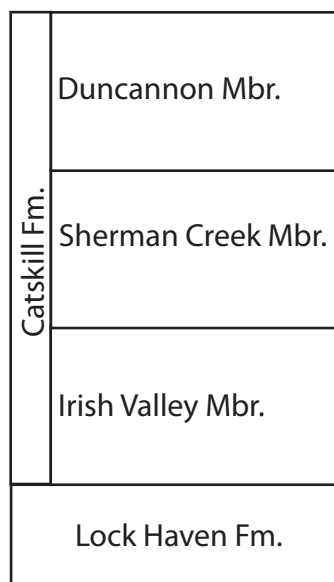
The Frasnian–Famennian Catskill Formation in Pennsylvania is a 300–1,500 m thick succession of alluvial pointbar deposits and overbank mudstones pedogenically modified to varying degrees, as evidenced by destruction of primary sedimentary structure, pedogenic slickensides, rubification, pedogenic carbonate horizons and the presence of rhizoliths (Diemer, 1992; Driese et al., 1993; Bridge, 2000). The Catskill Formation is divided into the Irish Valley, Sherman Creek, and Duncannon members in the study area (Sevon and Woodrow, 1985) (Text-fig. 34). Each member ranges from 300–600 m thick. Marine influence decreases up-section, whereas palaeosol maturity increases (Elick, 2006). Catskill Formation sediments were shed into the

Appalachian retroarc foreland basin from the Acadian orogenic center to the east (Kent and Opdyke, 1978; Ziegler et al., 1979; Ettensohn, 1985). Palaeogeographic reconstructions place the area now known as Pennsylvania at either $\sim 20^\circ$ (Kent and Opdyke, 1978; Ziegler et al., 1979) or $\sim 35^\circ$ south latitude (Joachimski et al., 2002) during the Famennian.

Catskill Formation pointbar deposits are 3–5 m thick and composed of trough cross-bedded, scour-based very fine- to fine-grained muscovite-rich sandstone, separated by low angle lateral accretion surfaces, and frequently topped by 5–20 cm of silty mudstone (Bridge, 2000). Pointbar deposits are green, purple or red, and vary in degree of pedogenic modification. Cross-bedding is retained in even the most strongly pedogenically modified pointbar deposits. Catskill Formation overbank deposits are composed of red, purple, and rarely green mudstones and claystones. Finely to weakly laminated mudstone and sandstone-mudstone interbeds are often current or oscillation ripple laminated, and rarely trough cross-bedded (e.g., Driese et al., 1993). Mudstones may also be platy, structureless, or dominated by angular blocky to prismatic peds and pseudoanticlines (Diemer, 1992; Driese et al., 1993; Bridge, 2000). Centimeter-scale pedogenic slickensides occur in weakly laminated to platy mudstones and along the boundaries of peds in thoroughly homogenized palaeosols. Pedogenic carbonate horizons occur in moderately mature to mature Catskill Formation palaeosols (Woodrow et al., 1973; Driese et al., 1993). The Catskill Formation alluvial plain experienced wet-dry seasonality as evidenced by the development of vertic palaeosols with variously well-developed pedogenic carbonate horizons, slickensides, and pseudoanticlines (Woodrow et al., 1973; Driese et al., 1993; Retallack et al., 2009). Seasonality of precipitation does not have to be extreme to produce these pedogenic features, however. The presence of pedogenic carbonate in soils generally indicates less than 760 mm mean annual

precipitation (Royer, 1999), indicating that the Catskill Formation alluvial plain experienced less than 760 mm mean annual precipitation. More precise paleoenvironmental inferences based on pedogenic features, such as estimating seasonality of precipitation based on depth of pedogenic carbonate (e.g., Retallack, 2009) have been shown to be ineffective (Royer, 1999). More precise precipitation estimates for the Catskill Formation alluvial plain are impossible at present, as such.

Trace fossils in pedogenically modified Catskill Formation deposits form a characteristic ichnofabric of crosscutting backfilled burrows (*Beaconites antarcticus* and *Beaconites barretti*) and 1–50 mm diameter rhizoliths. This ichnofabric is best developed in weakly laminated to thoroughly homogenized palaeosols, which contain dense concentrations of burrows and rhizoliths. Finely laminated, pedogenically modified Catskill Formation channel and overbank deposits often contain sparse concentrations of 1–3 mm diameter rhizoliths, as well as *Beaconites antarcticus* and *Beaconites barretti*. All Catskill Formation burrows examined in this study were found to be crosscut by this ichnofabric. Catskill Formation burrows also crosscut the dominant palaeosol ichnofabric.



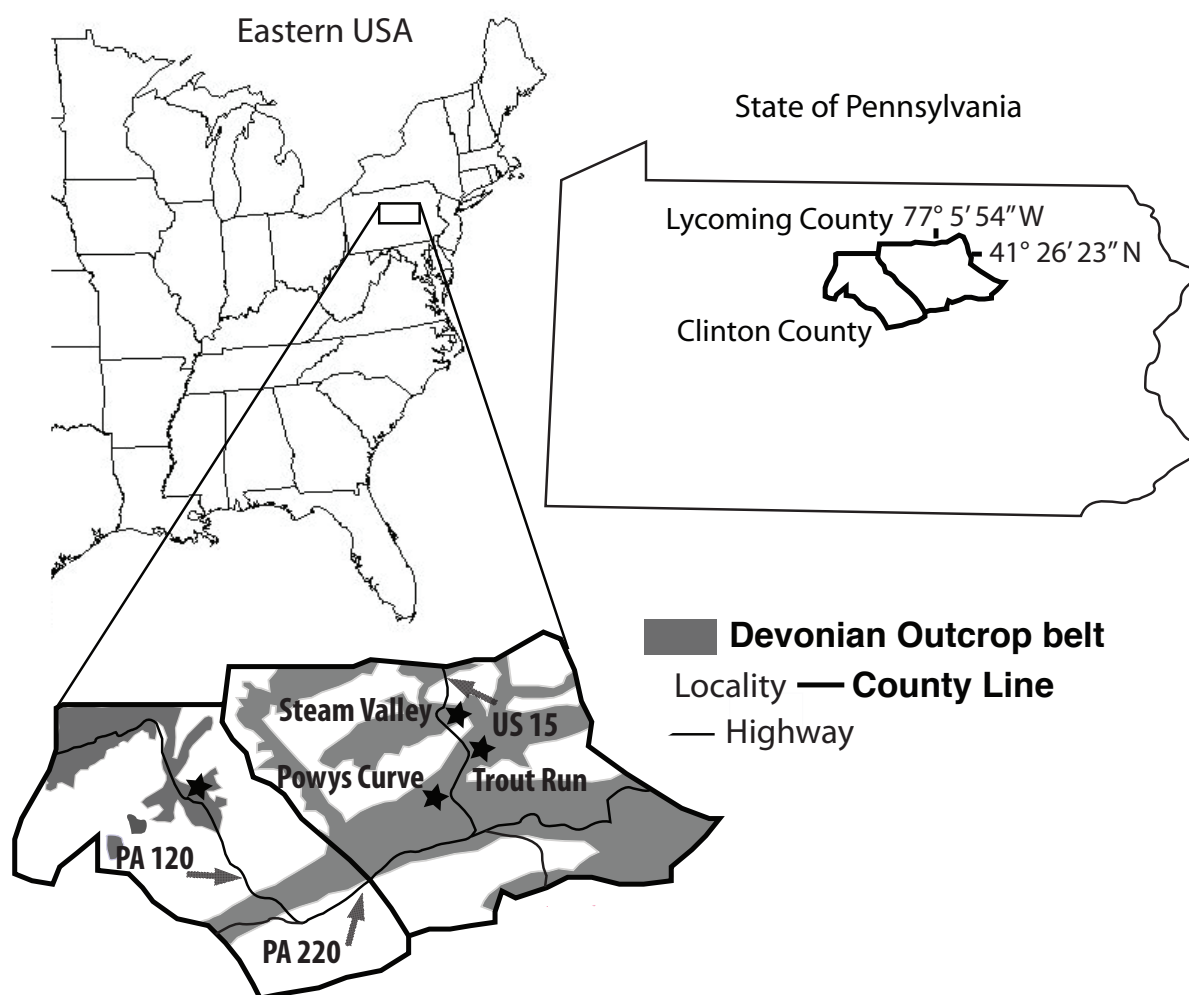
TEXT-FIG. 34—Generalized stratigraphy of our field area.

METHODS AND MATERIALS

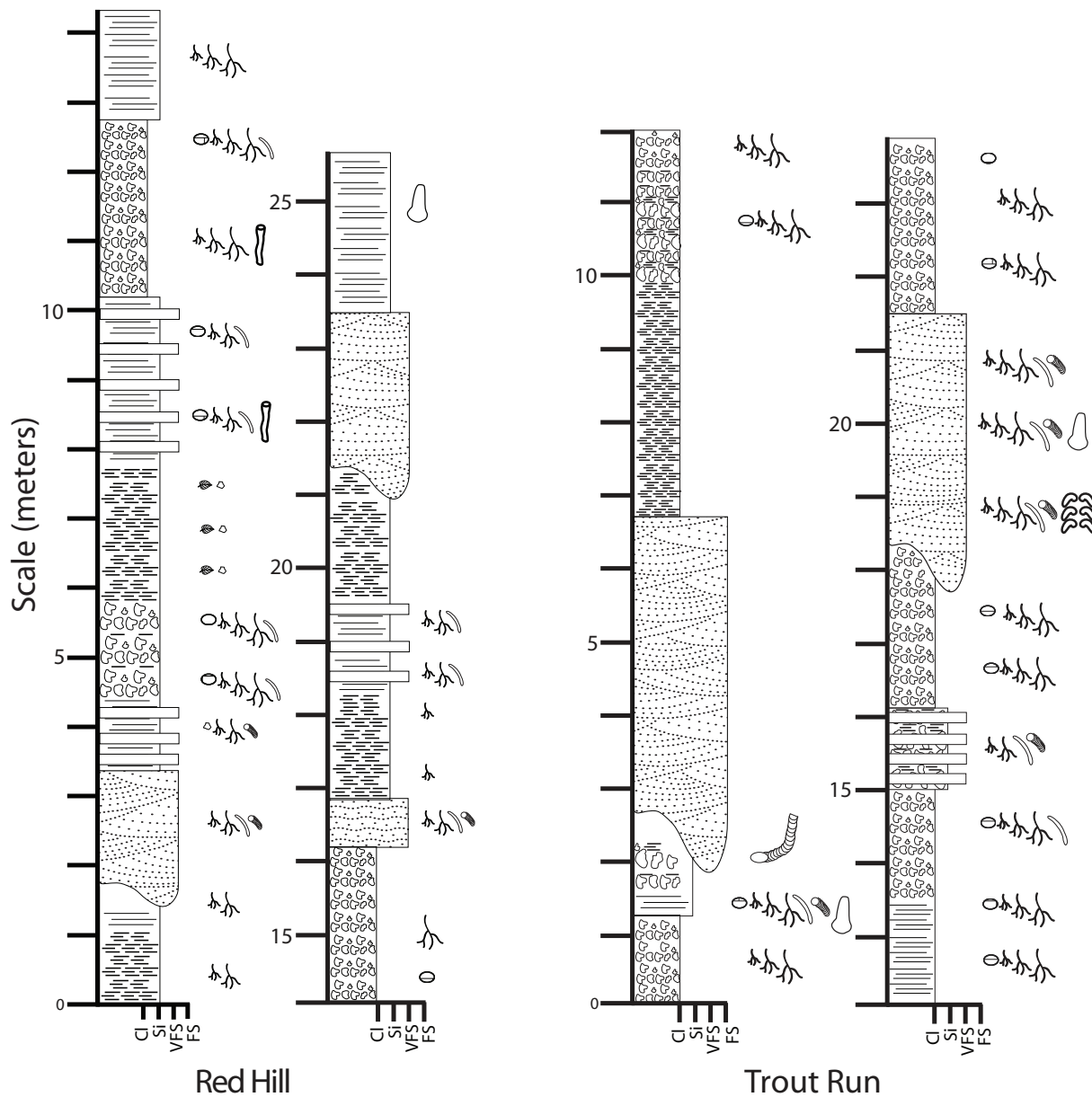
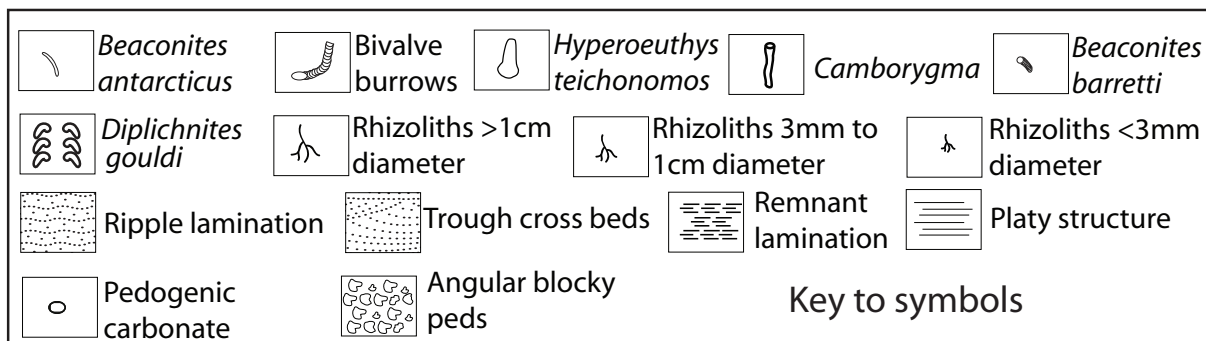
Fifty-six Catskill Formation burrows were collected, or measured and photographed at individual roadcut outcrops along US Route 15 in Southern Lycoming County, Pennsylvania, and at the Red Hill outcrop on PA Route 120 (Text-fig. 35). The stratigraphical position of burrows was recorded when they occurred in outcrop (Text-fig. 36). Associations of Catskill Formation burrows and other traces were also recorded.

Measurements included: long axes (D1) and short axes (D2) of burrow diameter (Text-fig. 37). Burrow length was measured when possible (Text-fig. 37). Measurements in the field were made with a metric ruler. Measurements in the laboratory were made with an analogue metric caliper. Burrows were described for their architectural (overall shape, orientation, and proportions) and surficial morphologies (characteristic morphology of the burrow surface) and fill material (the material that comprises the burrow) (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). Surficial morphologies were examined in hand sample and by using a Nikon model SMZ1000 binocular light microscope. Some burrows were cut and polished to study the internal morphology.

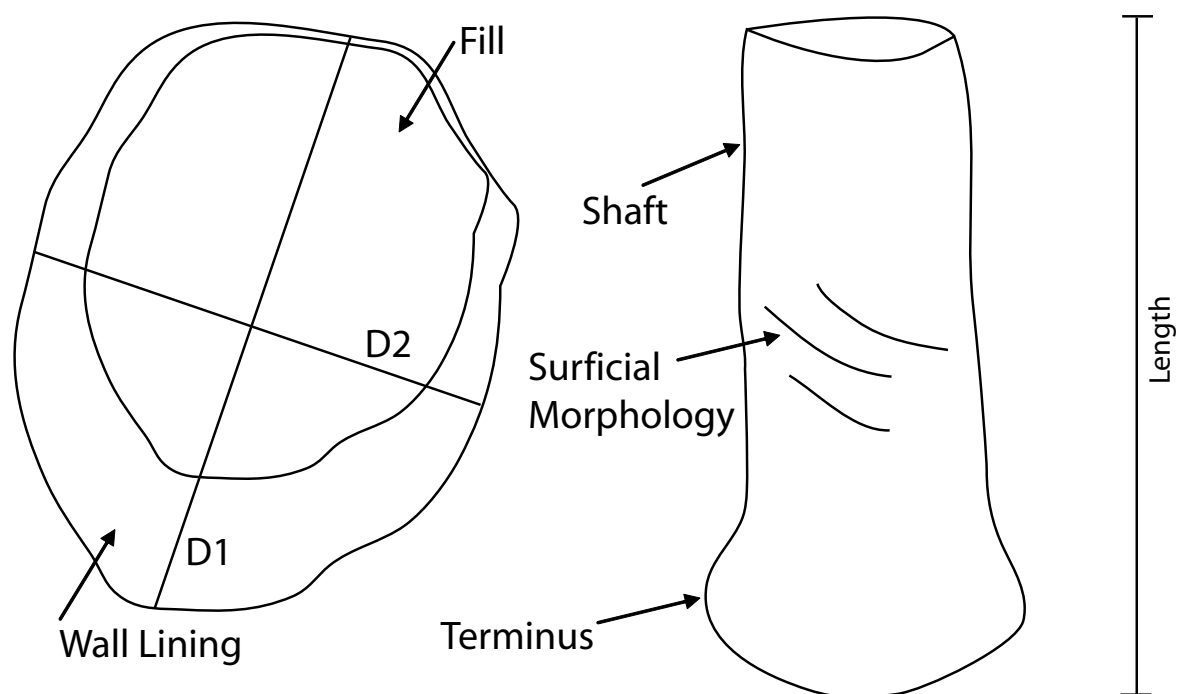
Catskill Formation burrows were compared to lungfish aestivation burrows widely accepted in the literature, including those containing skeletal material of the Permian lungfish *Gnathorhiza*. Catskill Formation burrows were also compared to burrows with similar morphology produced by other organisms, such as crayfish, crabs, and amphibians. The ichnotaxonomy of the Catskill Formation burrows is established based on the characteristics of the architectural and surficial morphologies and fill pattern.



TEXT-FIG. 35—Location of study outcrops.



TEXT-FIG. 36—Measured sections at Trout Run and Red Hill, Pennsylvania showing the occurrence of the Catskill Formation burrows and associated traces.



TEXT-FIG. 37—Explanatory drawing of burrow dimensions, and morphological features.

SYSTEMATIC ICHNOLOGY

There is currently no ichnotaxon that conforms to the architectural and surficial morphologies representative of the Catskill Formation burrows described here. The architectural and surficial morphological uniqueness of the Catskill Formation burrows indicates that they merit inclusion in a new ichnogenus and ichnospecies. The architectural and surficial morphology of the Catskill Formation burrows is compared to that of previously described, morphologically similar ichnotaxa, interpreted to represent amphibian aestivation burrows, and decapod crustacean dwelling burrows, as well as previously described burrows interpreted to be lungfish aestivation burrows later in the paper.

HYPEROEUTHYS new ichnogenus

Diagnosis. Vertically to subvertically oriented, clavate burrows possessing an elongated shaft and enlarged terminus; burrow shafts exhibit a discontinuous wall lining; surficial morphology characterized by regularly spaced transverse striations; wall lining thins toward the terminus and is absent from the terminus.

ETYMOLOGY—Greek, *Hyperos* pestle; Greek, *Euthys* upright.

Remarks. *Hyperoeuthys* is the only known ichnogenus for vertical to subvertical clavate burrows that exhibit a discontinuous wall lining and transversely striated surficial morphology.

Comparison with Pennsylvanian–Triassic lungfish aestivation burrows suggests that *Hyperoeuthys* represents lungfish aestivation, and that all previously described lungfish aestivation burrows should be included in this ichnogenus. *Hyperoeuthys* encompasses the

morphological variation of all previously described, well-documented fossil lungfish aestivation burrows (Romer and Olson, 1954; Vaughn, 1964; Carrol, 1965; Carlson, 1968; Olson and Bolles, 1975; Berman, 1976; Dalquest and Carpenter, 1977; Hasiotis et al., 1993; Hasiotis et al., 2002; Gobetz et al., 2006). Previously well-documented fossil lungfish aestivation burrows do, however, exhibit some morphological variability and likely merit multiple ichnospecies. Ichnospecific taxonomy of all previously well-documented fossil lungfish burrows is beyond the scope of this study, however.

Hyperoeuthys teichonomos new ichnospecies

Etymology. Greek, Teichos enclosed by walls; Greek, Nomos dwelling.

Diagnosis. Only known ichnospecies; same as for genotype.

Holotype. KUV152145

Paratypes. KUV152146 to KUV152191 and KUV152194

Type stratum. Upper Devonian Catskill Formation

Type locality. Lycoming and Clinton Counties, Pennsylvania, USA: West side of US Highway 15, Powys Township, Pennsylvania, ~10 km south of the village of Trout Run, Pennsylvania, USA, (41° 20' 26" N, 77° 05' 22" W); East side of US Highway 15, ~1 km north of Trout Run,

Pennsylvania, USA (41° 23' 31'' N, 77° 03' 31'' W); East side of US Highway 15, ~ 7 km north of Trout Run, Pennsylvania, USA (41° 26' 23'' N, 77° 5' 54'' W); ~1 km Southeast of North Bend, Pennsylvania, USA, between the villages of Hyner and Trout Run, Pennsylvania; PA Highway 120, NE side of the highway (41° 20' 49'' N, 77° 41' 18'' W).

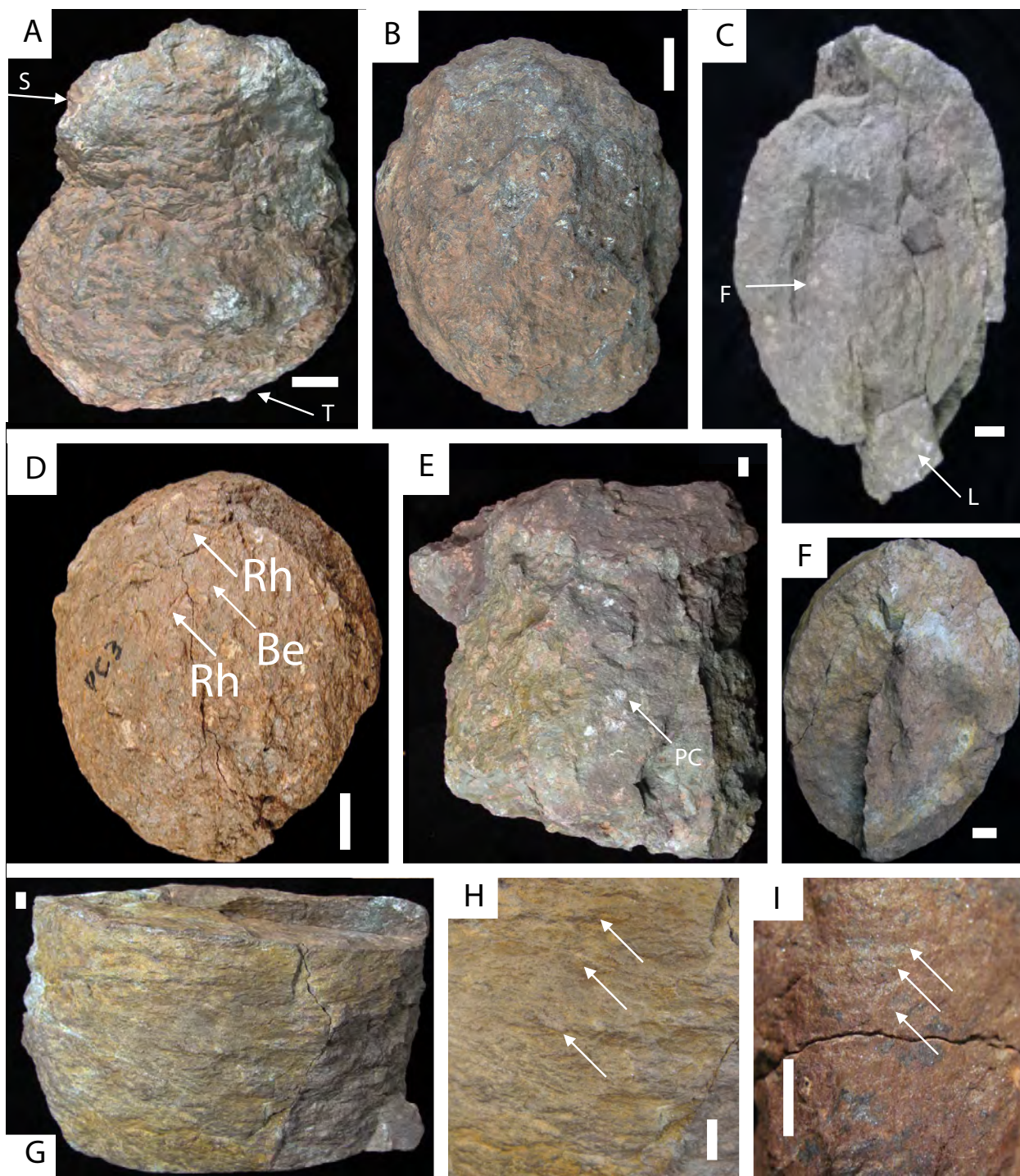
Repository. Division of Invertebrate Paleontology, Museum of Natural History and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA

Description. A single, vertical to subvertical, unbranched shaft with an enlarged terminus, resulting in overall clavate morphology (Text-figs. 38 A; 39 C, F); the shaft is inclined no greater than 10 degrees (Text-fig. 39 C, F); a variably thick wall lining or multiple wall linings are present around the periphery of the shaft (Text-figs. 38 C; 39 D, G); wall linings occur in 51.8 percent of specimens; the lining thins and eventually disappears around the terminus; the shaft and terminus are elliptical in cross section (26.4 to 145.4 mm minimum diameter and 21.2–121.6 mm maximum diameter) (Text-figs. 38 B, C, F; 39 A, D; 7); D1/D2 ratio 1.026 to 1.537; termini are 20–30 per cent greater in diameter than the shaft, but equally elliptical in outline (Text-figs. 38 A, B; 39 C, F; 40); termini comprise ~20 per cent of burrow height; burrows are up to 400 mm long (Text-fig. 39 C, F); surficial morphology is characterized by sets of evenly spaced, transverse striations (Text-fig. 38 H, I); striations are 1 to 5 mm wide and spaced 1 to 10 mm apart; striations are more prominent on the shaft than the terminus and more prominent on the surface of the burrow fill than the wall lining; the burrow fill is massive and identical in composition to the lining and host sediment, but can be identified, as it weathers separately from the burrow fill; the burrow fill is crosscut by 1–3 mm diameter rhizoliths and *Beaconites*

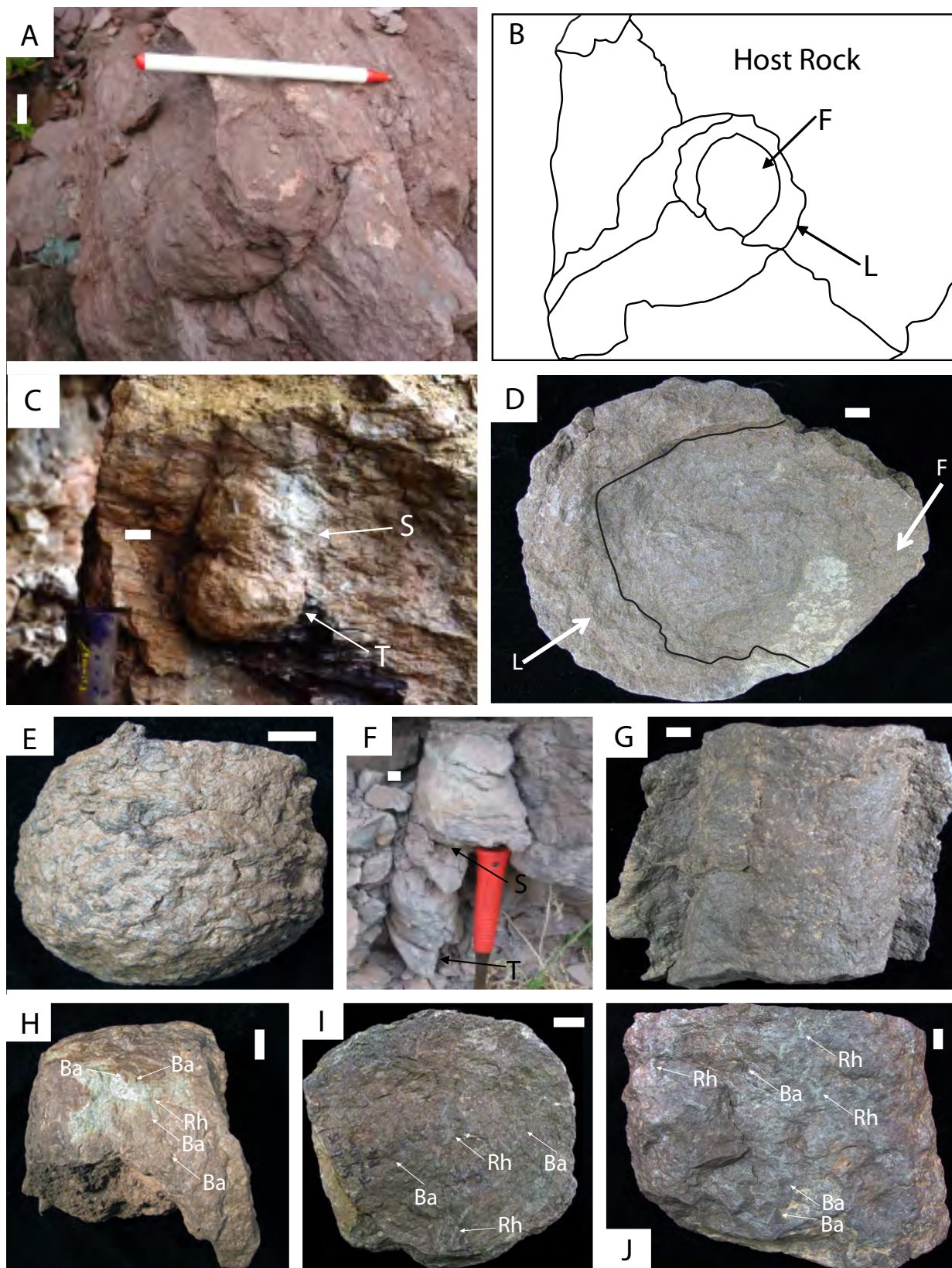
antarcticus, as well as pedogenic carbonate nodules (Text-fig. 38 E; 39 H–J).

Occurrence—*Hyperoeuthys teichonomos* occurs in all pedogenically modified facies of the Upper Devonian Catskill Formation in north-central Pennsylvania.

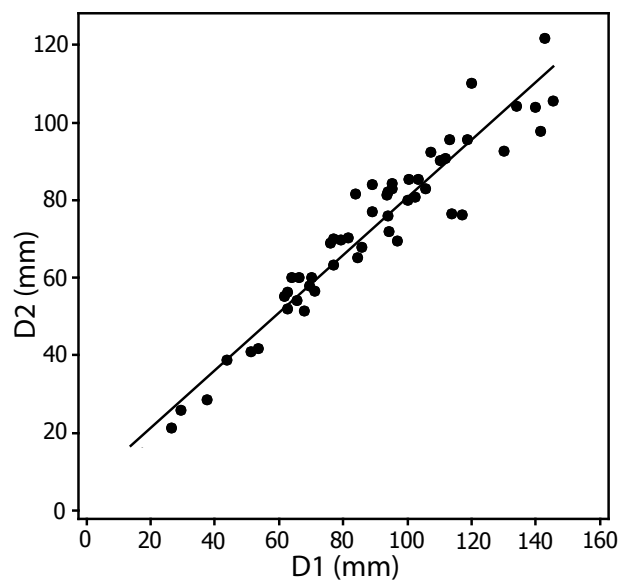
Remarks—*Hyperoeuthys teichonomos* is interpreted as a simple, passively infilled burrow that served as a temporary domichnium or refugium for lungfish aestivating in Catskill Formation alluvial soils. Lungfish constructed the burrows prior to seasonal periods of drought to avoid desiccation, and inhabited them in a state of torpor until the floodwaters brought on by the wet season returned. Burrows were abandoned during the wet season on the alluvial plain, during which time lungfish resumed life as aquatic organisms. *Hyperoeuthys teichonomos* was modified by pedogenesis after abandonment, as evidenced by cross-cutting rhizoliths, pedogenic carbonate nodules, and *Beaconites antarcticus*.



TEXT-FIG. 38—Catskill Formation burrow architectural and surficial morphologies; scale= 10 mm; A) The holotype, KUV152145; T= terminus; S= shaft; B) The terminal end of the Holotype in cross-section; C) A portion of shaft with multiple wall-linings in cross-section, KUV152157; F= fill; L= lining; D) A burrow terminus in cross-section, KUV152154; Rh= rhizolith; Ba= *Beaconites antarcticus*; E) A portion of burrow shaft cross-cut by pedogenic carbonate nodules, KUV152187; PC= pedogenic carbonate; F) A portion of burrow shaft in cross-section with an indistinct wall lining, KUV152183; G) Same burrow as F showing well-preserved surficial morphology; H) A close-up of G; arrows indicate surficial striations; I) A portion of burrow shaft with well-preserved surficial morphology; arrows indicate surficial striations, KUV152179.



TEXT-FIG. 39—CATSKILL FM. Large diameter burrow architectural and surficial morphologies; scale=10 mm; A) A large portion of burrow shaft with a distinct wall-lining, Trout Run; B) Interpretive drawing of B; C) The holotype in outcrop before collection, Powys Curve; T= terminus; S= shaft; D) A portion of burrow shaft in cross-section with a line-tracing of the lining-fill boundary, KUVVP152194; L= lining; F= fill; E) A burrow terminus, KUVVP152178; F) A complete burrow in outcrop, Steam Valley; T= terminus; S= shaft; G) A portion of burrow shaft with multiple distinct wall-linings in transverse section, KUVVP152157; H) A portion of burrow shaft cross-cut by *Beaconites antarcticus* and rhizoliths, KUVVP152166; Ba= *Beaconites antarcticus*; Rh= rhizolith; I) A portion of burrow shaft in cross-section crosscut by *Beaconites antarcticus* and rhizoliths, KUVVP152184; Ba= *Beaconites antarcticus*; Rh= rhizolith; J) A portion of burrow shaft cross-cut by *Beaconites antarcticus* and rhizoliths, KUVVP152194; Ba= *Beaconites antarcticus*; Rh= rhizolith.



TEXT-FIG. 40— Scatterplot of long and long and short diameter of the Catskill Formation burrows.

DISCUSSION OF LUNGFISH AESTIVATION BURROWS

Lungfish burrowing behavior. African and South American lungfish, *Protopterus* and *Lepidosiren*, respectively, construct aestivation burrows in alluvial floodplain and marginal lacustrine environments to avoid desiccation during the dry season (Kerr, 1898; Carter and Beadle, 1930; Johnels and Svennson, 1954; Bouillon, 1961; Greenwood, 1987; Hembree, 2010). Lungfish burrow by biting into the sediment, and forcing their way into the sediment by rotating and undulating, expelling sediment from the gills (Kerr, 1898; Carter and Beadle, 1930; Johnels and Svennson, 1954; Buillon, 1961; Greenwood, 1987; Hasiotis et al., 1993). The final burrow morphology is a vertical to subvertical shaft with a bulbous terminus (Kerr, 1898). The lungfish remain curled inside the burrow termini for months to years and secrete a mucous sac, which helps them avoid desiccation and apparently also prevents infection (Kerr, 1898; Smith, 1930; Fishman et al., 1992). The burrow shaft remains empty during occupation. Burrow entrances differ substantially between species, e.g. *Lepidosiren* burrows are plugged with clay from within (Kerr, 1898), whereas *Protopterus annectans* maintains an open shaft to facilitate air exchange (Bouillon, 1961). The similarity of modern and ancient lungfish burrow morphologies to Catskill Formation burrows indicates that the Catskill Formation burrows represent the same behavior and burrowing style as that of modern lungfish. Aestivating lungfish are able to breathe air from the surface, although their metabolism slows considerably during aestivation (Smith, 1930; Delaney et al., 1974; Fishman et al., 1992). When inundated once again during the wet season, lungfish emerge from their burrows and resume life as aquatic organisms (Johnels and Svennson, 1954; Greenwood, 1987). Aestivating lungfish represent transient soil biota in the sense of Wallwork (1970) and Hasiotis (2007), because of this behavior.

During the wet season, the modern African lungfish *Protopterus* spawns and deposits its eggs in U-shaped, club-shaped, or T-shaped breeding nests (Johnels and Svennson, 1954; Greenwood, 1987). Whether the male or female constructs the breeding nest is not known (Johnels and Svennson, 1954). After the eggs have been deposited, the male guards the nest until it has been vacated by the fry (Johnels and Svenson, 1954). Lungfish breeding nests have not been recognized in the fossil record (Hasiotis et al., 1993). Whether or not ancient lungfish constructed breeding nests is not known.

Australian lungfish (*Neoceratodus forsteri*) do not produce dry season aestivation burrows (Crigg, 1965). These lungfish inhabit the Burnett and Mary River basins of Queensland, Australia, and prefer shallow ponded areas of the alluvial plain with abundant vegetation (Arthington, 2009). *Neoceratodus forsteri* respire by air breathing and use of its gills, and apparently does not air breathe when optimum water oxygenation is maintained, only supplementing gill breathing when the lungfish is active (Crigg, 1965).

Occurrence of lungfish burrows and body fossils in the Catskill Formation. Fragmentary lungfish body fossils in the form of toothplates and cranial bone have been reported from several localities within the Catskill Formation, indicating that lungfish did live on the Catskill Formation floodplain (Daeschler and Mullison, 2004; Friedman and Daeschler, 2006). Lungfish burrows occur at every Catskill Formation outcrop investigated during this study. Two of these outcrops have yielded lungfish skeletal material. An additional outcrop, at the Tioga Welcome Center in Tioga, Pennsylvania, was not investigated in detail; however, a short excursion to the outcrop yielded a single example of a lungfish burrow in float. This outcrop has also yielded

lungfish skull roof material (Daeschler and Mullison, 2004). The rarity and fragmental nature of lungfish skeletal material in the Catskill Formation makes size comparisons between body fossils and burrows difficult. Skull roofs of the lungfish *Aptorhynchus opistheteretmus* and *Soederberghia groenlandica* described by Friedman and Daeschler (2006) from the Catskill Formation are ~80 mm and ~40 mm wide, respectively, fitting well within the range of diameters of Catskill Formation lungfish burrows.

The rarity and fragmental nature of Catskill Formation lungfish skeletal material indicates that it has a low preservational potential. Lungfish burrows, in contrast, are common in all pedogenically modified Catskill Formation facies—rarely in bedding plane concentrations > 5 burrows per m². These include facies interpreted as levee deposits, proximal floodplain deposits, and pedogenically modified pointbar deposits. High concentrations of burrows may represent multiple seasons of aestivation on areas of the floodplain that experienced repeated inundation and drying.

The occurrence of lungfish burrows in all pedogenically modified Catskill Formation facies suggests that lungfish inhabited a variety of settings on the Catskill Formation alluvial plain. They likely remained in areas, however, that were repeatedly inundated with floodwaters. Consistent with this, *Protopterus aethiopicus* ranges from shallow marginal lacustrine environments to water depths as great as 20 m (Greenwood, 1987). The absence of lungfish remains in Catskill Formation lungfish burrows (Daeschler and Mullison, 2004; Friedman and Daeschler, 2006) suggests that aestivating Catskill Formation lungfish experienced low rates of mortality during aestivation.

The greater abundance and frequency of occurrence of lungfish burrows than lungfish skeletal material indicates that lungfish were more abundant and widely distributed on the Catskill Formation alluvial plain than is indicated by the body fossil record. Crosscutting relations with rhizoliths and backfilled burrows indicate that Catskill Formation lungfish burrows were modified by pedogenesis after being abandoned. This is intuitive, as the lungfish burrowed in areas of repeated seasonal drought, which would have resulted in pedogenic modification of alluvial plain sediments during the dry season.

Palaeoenvironmental implications of lungfish burrows. The Catskill Formation burrows, as lungfish aestivation burrows, are indicators of pronounced wet-dry seasonality (e.g. Hembree, 2010). Palaeopedologic evidence—vertic structures and well-developed pedogenic carbonate horizons in Catskill Formation floodplain palaeosols—further indicates that the Catskill floodplain experienced a seasonally wet-dry climate (Woodrow et al., 1973; Driese et al., 1993). This evidence indicates that climatic conditions on the Catskill alluvial plain were consistent with the conditions that necessitate aestivation in modern lungfish. Lungfish aestivation burrows provide additional paleoenvironmental information in that they provide evidence of periodic inundation of the sediments in which they occur. Lungfish aestivation burrows, as such, can be used to estimate the magnitude of seasonal floods. The presence of lungfish aestivation burrows in pointbar deposits, proximal floodplain deposits and distal floodplain deposits indicates that even the distal-most Catskill Formation floodplain was periodically inundated, however, the frequency of inundation of distal floodplain environments cannot be estimated using lungfish aestivation burrows.

Evolutionary implications of lungfish aestivation burrows. The oldest known evidence of vertebrate aestivation prior to our interpretation of the Catskill Formation burrows as lungfish aestivation burrows were burrows described from the early Pennsylvanian of Michigan, USA (Carroll, 1965). Catskill Formation lungfish burrows are significant because they represent the oldest evidence of aestivation by vertebrates, setting the timing of evolution of this behavior back to the Frasnian. Catskill Formation lungfish burrows were originally described in an abstract by Woodrow and Fletcher (1969), who correctly identified them as lungfish aestivation burrows. The burrows, however, have never been properly figured or subjected to rigorous ichnotaxonomic and behavioral analysis. Doubt expressed about the true tracemaker of Catskill Formation lungfish burrows results from the lack of lungfish skeletal material in the burrows (Daeschler and Mullison, 2004; Friedman and Daeschler, 2006). Gordon (1988) suggested that lungfish aestivation burrows may be present in the Givetian–Frasnian Catskill Magnafacies of New York. If the burrows she described are lungfish burrows, the geological history of aestivation will be extended as far back as the Givetian, upon proper ichnotaxonomic and behavioral analysis. The significance of the evolutionary timing of vertebrate aestivation extends to groups other than lungfish. Modern amphibians and fish unrelated to lungfish, such as the aquatic salamander *Siren lacertina* and the marbled swamp eel (*Symbranchus marmoratus*), are also known to aestivate in response to seasonal drought (Carter and Beadle, 1930; Etheridge, 1990; Pinder et al., 1992; Zug et al., 2001). Amphibian aestivation burrows are known to occur in strata as old as Lower Permian (Hasiotis et al., 1993; Hembree et al., 2004; Hembree et al., 2005; Hembree, 2010). Aestivation has allowed amphibians and fish to inhabit a much wider geographical range than would otherwise be possible, because it provides organisms

with constant or nearly constant moisture needs the ability to inhabit areas where moisture availability is temporally variable (Hembree et al., 2004; Hasiotis, 2007; Hembree, 2010).

CARBONIFEROUS TO RECENT LUNGFISH AESTIVATION BURROWS

Mississippian burrows. Possible lungfish aestivation burrows were reported from the Mississippian of Kentucky by Garcia and Storrs (2006) (TABLE 3). These burrows, however, have not yet been well-documented. The tapering overall morphology of burrows from Garcia and Storrs (2006) is more morphologically consistent with lysorophid burrows (e.g., Hembree et al., 2005) than lungfish aestivation burrows.

Pennsylvanian burrows. Lungfish burrows were reported by Carroll (1965) from the Middle Pennsylvanian of Michigan, USA (TABLE 3). Figures therein indicate that burrows exhibit all of the architectural and surficial morphological criteria of Hasiotis et al. (1993). Whether or not these burrows include a wall lining of inconsistent thickness is unclear. Carroll (1965) reported burrow diameters of ~150 mm at the top of the burrow, and lengths up to 410 mm, although the burrows were suggested to be incomplete. This indicates that Pennsylvanian lungfish burrows were consistent in size with the Catskill Formation burrows. Burrow dimensions in cross-section (D1/D2) were not reported, precluding comparison with Catskill Formation large-diameter burrows.

Author	Age	Stratigraphic Unit	Year	Location
Woodrow and Fletcher	Devonian	Catskill Formation	1969	Pennsylvania, USA
Garcia and Storrs	Mississippian	Buffalo Wallow Formation	2006	Kentucky, USA
Carrol	Pennsylvanian	Saginaw Group	1965	Michigan, USA
Romer and Olson	Permian	Arroyo Formation	1954	Texas, USA
Vaughn	Permian	Sangre de Cristo Formation	1964	New Mexico, USA
Carlson	Permian	Wellington Formation	1968	Oklahoma, USA
Olson and Bolles	Permian	Arroyo, Vale, and Choza Formations	1975	Texas, USA
Berman	Permian	Abo Formation	1976	New Mexico, USA
Dalquest and Carpenter	Permian	Leuders or Arroyo Formation	1977	Texas, USA
Hasiotis et al.	Permian	Clear Fork Group, Vale Formation, Wellington Formation, Sangre de Cristo Formation	1993	Texas, Oklahoma, New Mexico, USA
Hasiotis et al.	Permian	Matfield Formation, Blue Springs Shale Member	2002	Kansas, U.S.A.
Gobetz et al.	Triassic	Redonda Formation	2006	New Mexico, USA
Orsulak	Cretaceous	Wahweap Formation	1997	Utah, USA
Surlyk et al.	Cretaceous	Rabekke Formation	2006	Denmark

TABLE 3—Previous studies of lungfish estivation burrows.

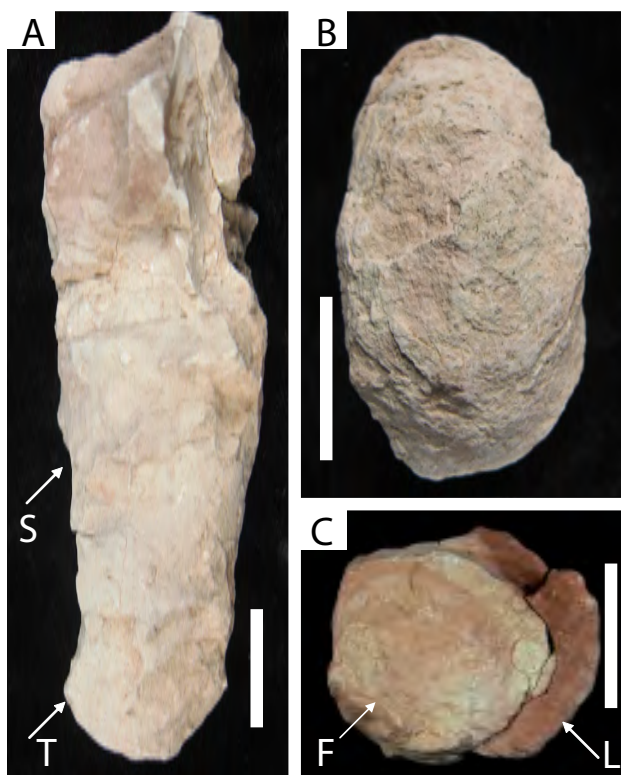
Permian burrows. Aestivation burrows of the Permian lungfish *Gnathorhiza* are known from Kansas, Oklahoma, New Mexico, and Texas, USA (Romer and Olson, 1954; Vaughn, 1964; Carlson, 1968; Olson and Bolles, 1975; Berman, 1976; Dalquest and Carpenter, 1977; Hasiotis et al., 1993; Hasiotis et al., 2002) (TABLE 3). These burrows exhibit all of the morphological criteria of Hasiotis et al. (1993), including being elliptical in cross-section and exhibiting a distinct, discontinuous wall lining (Carlson, 1968; Olson and Bolles, 1975) (Text-fig. 41 B, C). The wall lining of *Gnathorhiza* burrows sometimes contains fragments of bone and scales (Carlson, 1968). Shafts of individual *Gnathorhiza* burrows are uniform to highly inconsistent in diameter (Romer and Olson, 1954; Vaughn, 1964; Carlson, 1968; Olson and Bolles, 1975; Berman, 1976; Dalquest and Carpenter, 1977; Hasiotis et al., 1993; Hasiotis et al., 2002). The termini of *Gnathorhiza* burrows may be smaller, larger, or not differ in diameter from the thickest portion of the shaft (Romer and Olson, 1954; Vaughn, 1964; Carlson, 1968; Olson and Bolles, 1975; Berman, 1976; Dalquest and Carpenter, 1977; Hasiotis et al., 1993). The terminus is always wider than the adjoining portion of the shaft, however, resulting in a club-shaped overall morphology (Romer and Olson, 1954; Hasiotis et al., 1993) (Text-figs. 41 A, 42). The burrows are vertical to slightly subvertical in orientation (Romer and Olson, 1954; Vaughn, 1964; Carlson, 1968; Olson and Bolles, 1975; Dalquest and Carpenter, 1977; Hasiotis et al., 1993). *Gnathorhiza* burrows from the Blue Springs Shale Member of Manhattan, Kansas range in maximum diameter from 7–53 mm (Hasiotis et al., 2002). *Gnathorhiza* burrows figured in the literature rarely exceed 100 mm maximum diameter (Romer and Olson, 1954; Olson and Bolles, 1975; Hasiotis et al., 1993). *Gnathorhiza* burrows can be as much as 500 mm in length (Olson and Bolles, 1975).

Triassic burrows. Apparent lungfish aestivation burrows were described by Gobetz et al. (2006) from the Upper Triassic Redonda Member of the Chinle Formation in New Mexico (TABLE 3). These burrows are subvertical to subhorizontal in orientation. Additionally, burrows from Gobetz et al. (2006) are composed of an elongated shaft and bulbous terminus. The burrows of Gobetz et al. (2006) also exhibit a distinct wall lining and fill, and are reported to have transverse striations on the burrow surface. Although these burrows are substantially more inclined in orientation than previously reported fossil lungfish aestivation burrows, they exhibit all of the architectural and surficial morphological characteristics of lungfish aestivation burrows. Some modern burrows of *Lepidosiren* are known to be inclined in orientation (e.g., Kerr, 1898) and, as such, it is not improbable that some Mesozoic lungfish burrows were inclined as well. More detailed photographs of the burrow wall linings and surficial morphological features are necessary for definitive assessment, however.

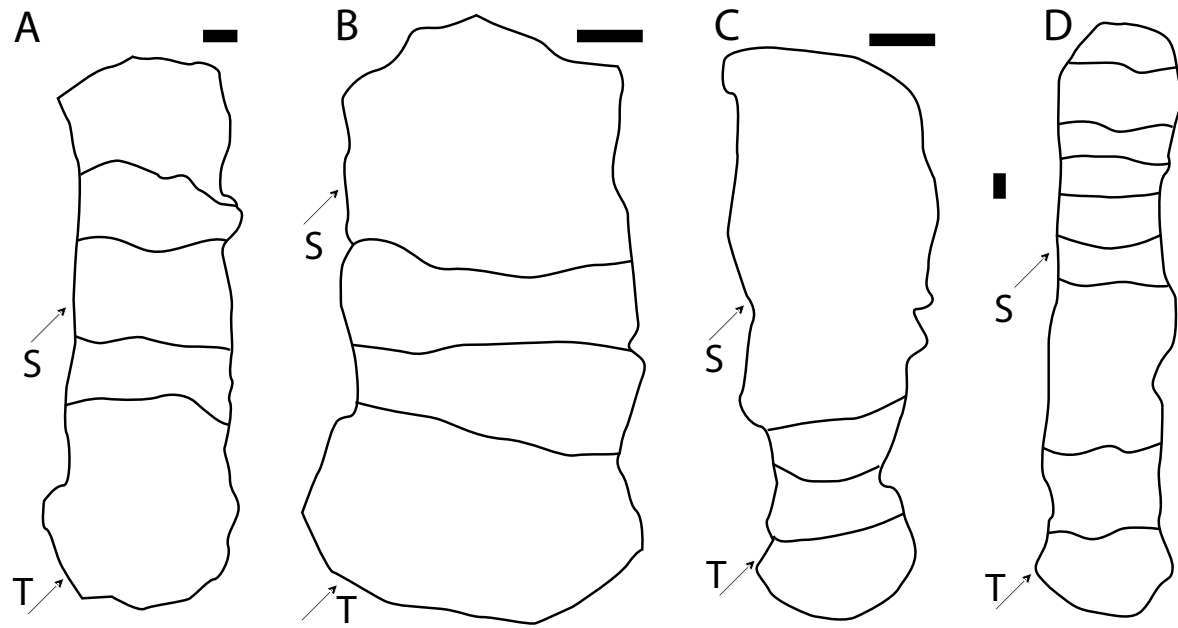
Cretaceous burrows. Lungfish aestivation burrows have been reported in an abstract by Orsulak (1997) from the Cretaceous of Utah, USA, and by Surlyk et al. (2008) from the Cretaceous of Denmark (TABLE 3). The descriptions of Orsulak (1997) are consistent with morphological criteria for identification of lungfish burrows, however, doubt must be expressed until the burrows are formally described and figured. The burrows of Surlyk et al. (2008) were not figured in great detail. These burrows appear to be highly sinuous, variable in orientation, and perhaps even branching. Doubt must be expressed as to their interpretation as lungfish burrows.

Recent burrows. Aestivation burrows of the modern lungfish *Protopterus* and *Lepidosiren* are composed of a vertical to inclined shaft and bulbous terminus (Kerr, 1898; Carter and Beadle,

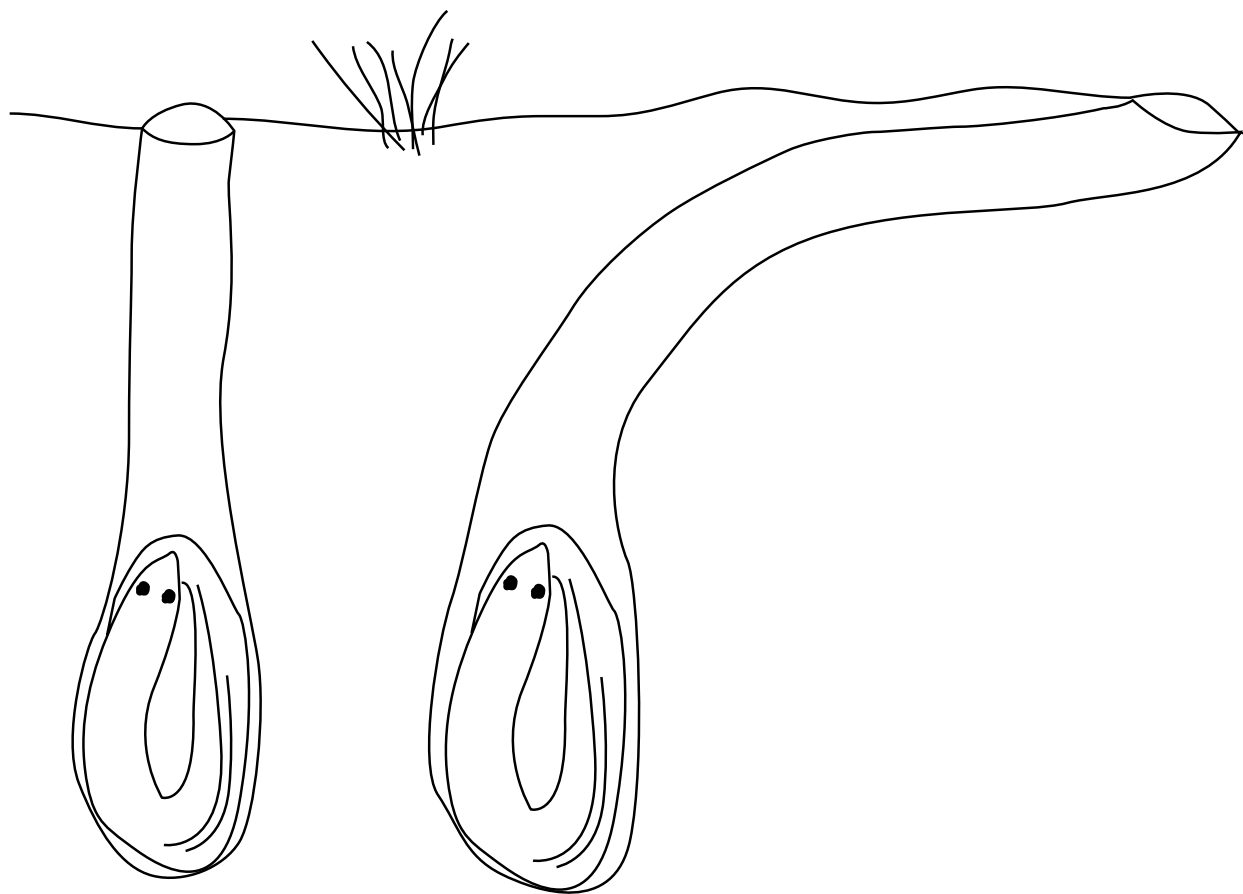
1930; Johnels and Svensson, 1954) (Text-fig. 43) (TABLE 3). These features are consistent with the architectural morphology of fossil lungfish aestivation burrows. Whether or not modern lungfish burrows exhibit a variably thick wall lining and surficial morphology characterized by transverse striations is unclear. Little recent work has been conducted on the architectural and surficial morphologies of modern lungfish aestivation burrows. Kerr (1898), and Johnels and Svensson (1954) discussed the architectural morphology of *Lepidosiren* and *Protopterus* aestivation burrows, respectively, however they included no description of the surficial morphology of the burrows that they described. Discussions of lungfish burrow architectural morphology in later publications (e.g., Greenwood, 1987; Hasiotis et al., 1993) cite the work of Kerr (1898), and Johnels and Svensson (1954), but do not contain new neiochnological data on lungfish aestivation burrows. Modern lungfish aestivation burrow morphologies, as such, need to be reevaluated with respect to surficial morphology and the presence or absence of a wall lining in order for a detailed morphological comparison of fossil and modern lungfish aestivation burrows to be conducted.



TEXT-FIG. 41—*Gnathorhiza* burrows from the Lower Permian Blue Springs Shale Member; scale=10 mm—A) Complete burrow; S=shaft; T=terminus; B) Terminus in cross section; C) Segment of shaft in cross section; F= fill; L=lining.



TEXT-FIG. 42—Lungfish burrows architectural morphologies; scale bar= 10 mm; A–C redrawn from Hasiotis et al. (1993); D redrawn from Romer and Olson (1954).



TEXT-FIG. 43—Modern lungfish burrow architectural morphologies, redrawn from Kerr (1898).

COMPARISON TO SIMILAR ICHNOTAXA

The Catskill Formation burrows exhibit similar architectural morphology to several known large-diameter burrows: *Torridorefugium eskridgensis*, *Camborygma* isp., *Psilonichnus* isp., *Macanopsis* isp., and lungfish aestivation burrows. Detailed analysis of architectural and surficial burrow morphology is necessary to interpret the tracemaker and behavior represented by the Catskill Formation large-diameter burrows, as well as previously existing ichnotaxa (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). The Catskill Formation burrows were compared to previously existing ichnotaxa to establish their morphological uniqueness.

Torridorefugium eskridgensis Hembree et al., 2005

The Catskill Formation burrows are distinguished from amphibian aestivation burrows (*Torridorefugium eskridgensis*) in possessing an outer wall lining, surficial morphology characterized by transverse striations, a bulbous terminus, and exhibiting greater uniformity in diameter (Hembree et al., 2004; Hembree et al., 2005). Termini of *T. eskridgensis* taper or are blunt rather than bulbous (Hembree et al., 2004; Hembree et al., 2005) (Text-fig. 44 D).

Torridorefugium eskridgensis lacks an outer sediment wall lining and exhibits surficial morphology characterized by the presence of irregularly spaced nodes, rather than transverse striations (Hembree et al., 2004; Hembree et al., 2005). *Torridorefugium eskridgensis* can also be slightly sinuous, and portions of the burrow sometimes deviate up to 40° from vertical. Catskill Formation large-diameter burrows are always vertical or nearly vertical. *Torridorefugium eskridgensis* can also exhibit a length to width ratio < 1, whereas Catskill Formation large-diameter burrows always exhibit a length to width ratio much greater than 1.

Camborygma Hasiotis and Mitchell, 1993

The Catskill Formation burrows are distinguished from *Camborygma* isp., interpreted as crayfish dwelling burrows, in exhibiting smooth surficial morphology marked by transverse striations, whereas the surficial morphology of *Camborygma* isp. exhibits transverse scrape marks, vertical scratch marks, knobby and hummocky surfaces, and triangular prod marks (Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). The wall lining of Catskill Formation burrows differs from the mud and lag liners of *Camborygma* isp. as described by Hasiotis and Mitchell (1989, 1993) in that its composition is identical to that of the host rock, and less robust than those of *Camborygma* isp. Catskill Formation burrows are simple in architecture and uniform in diameter until the beginning of the terminus. *Camborygma* isp. may be straight, but are often sinuous, and in many cases exhibit T and Y-shaped intersections (Hasiotis and Mitchell, 1993) (Text-fig. 44 A). Catskill Formation burrows are less elongated than *Camborygma* isp., which are up to 2,000 mm or more in length and vary in diameter from 5–125 mm in diameter (Hasiotis and Mitchell, 1989; 1993).

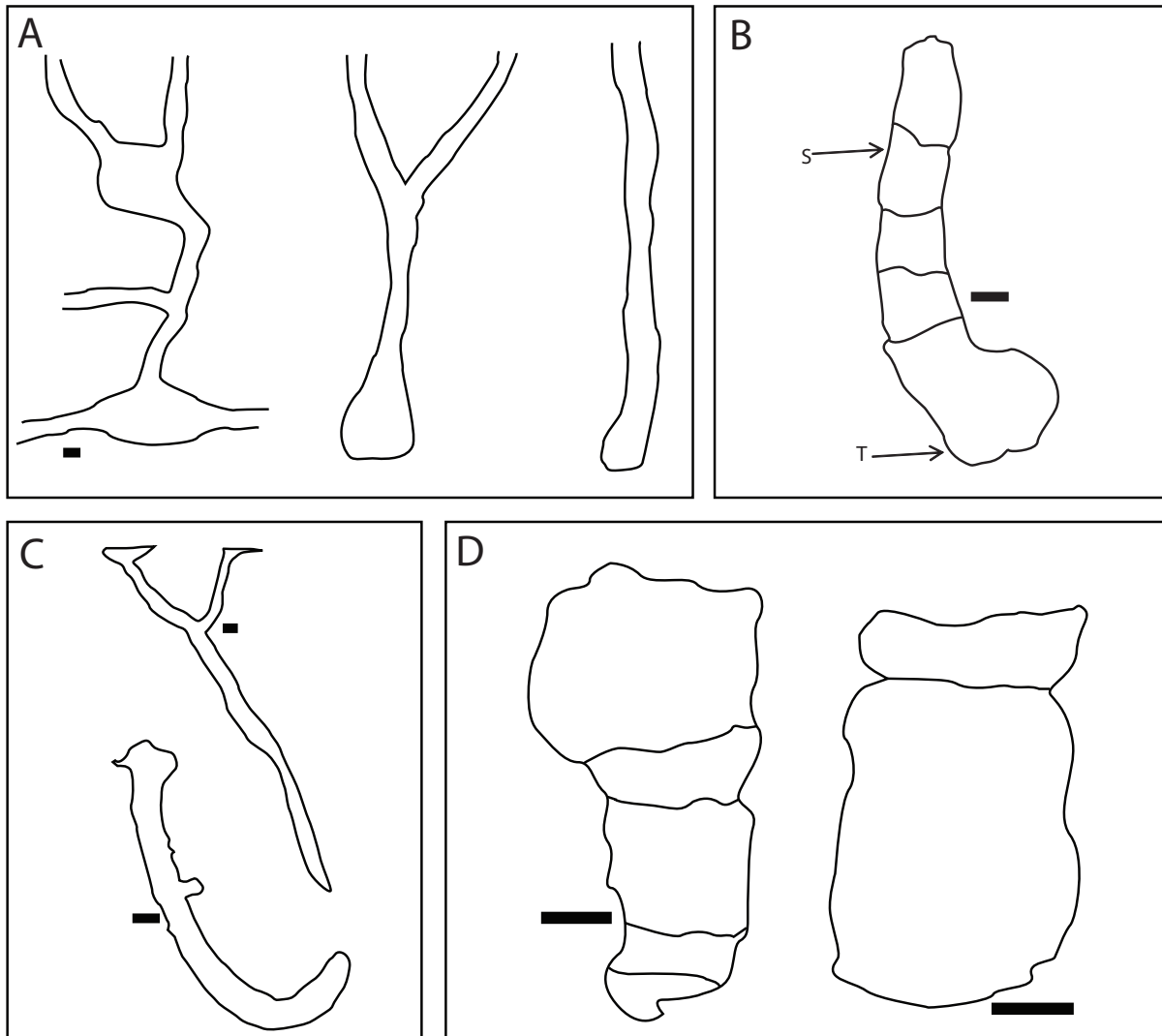
Psilonichnus Fürisch, 1981

Catskill Formation burrows are distinguished from *Psilonichnus* isp. in exhibiting single, straight, uniform-diameter shafts, whereas *Psilonichnus* isp. exhibit Y- or J-shaped branching, or U-shaped morphologies (Fürisch, 1981; Frey et al., 1984) (Text-fig. 44 C). Catskill Formation burrows are also more uniform in diameter than *Psilonichnus* isp., which often exhibit areas of wider diameters in the burrow shafts (Frey et al., 1984). *Psilonichnus* isp. are often sinuous (Fürisch, 1981; Frey, 1984), whereas Catskill Formation burrows possess straight shafts. *Psilonichnus* isp. are predominantly vertical, however, the emended diagnosis and figures of

Frey et al. (1984) indicate that they can be slightly inclined. Catskill Formation burrows are always roughly vertical. Surficial morphologies of Catskill Formation burrows and *Psilonichnus* isp. also differ in that *Psilonichnus* isp. is characterized by bulbous or stumpy cheliped marks (Frey et al., 1984), whereas Catskill Formation burrow surficial morphologies are characterized by straight to slightly sinuous transverse striations.

Macanopsis Macsotay, 1967

Macanopsis isp. are similar to Catskill Formation burrows in being oriented perpendicular to bedding, and exhibiting an elongated shaft and enlarged terminus (Macsotay, 1967) (Text-fig. 44 B). *Macanopsis* is also similar to Catskill Formation burrows in that its shaft is circular to oval in outline and it exhibits shaft diameters of 1–3 cm (Macsotay, 1967), which fall into the size range of Catskill Formation burrows. *Macanopsis*, however, differs from Catskill Formation burrows in that the terminus is ~2 times, rather than 1.2–1.3 times the diameter of the shaft, and it usually exhibits curvature in the shaft before enlarging into the terminus (Macsotay, 1967). *Macanopsis* can also be U-shaped (Macsotay, 1967). Catskill Formation burrows do not exhibit curvature in any portion of the shaft. Macsotay's (1967) description of *Macanopsis* also does not include a wall lining of any sort. The holotype and paratype of *Macanopsis* (as figured therein), furthermore appear not to exhibit any sort of wall lining.



TEXT-FIG. 44—Scale bar= 10 mm; A) Crayfish burrow architectural morphologies from the Upper Triassic Chinle Formation; after Hasiotis et al. (1993); B) Holotype of *Macanopsis pagueyi*, redrawn from Macsotay, 1967; C) *Psilonichnus* architectural morphologies, redrawn from Frey et al. (1984); D) Architectural morphology of lysorophid burrows, redrawn from Hembree et al. (2004).

CONCLUSIONS

Hypero euthys teichonomos from the Upper Devonian Catskill Formation of north-central Pennsylvania, USA, exhibits all of the architectural and surficial morphological criteria established for the identification of lungfish aestivation burrows. *Hypero euthys teichonomos* differs in surficial and architectural morphology from similar ichnotaxa, as has been demonstrated herein. Identification of lungfish burrows in the Catskill Formation is significant to paleobiological and paleoclimatic reconstructions of the Catskill Formation, because *H. teichonomos* is much more common and abundant in the Catskill Formation than lungfish skeletal material, and as an aestivation burrow, is evidence of pronounced wet-dry seasonality on the Catskill Formation alluvial plain. The interpretation of *H. teichonomos* as lungfish aestivation burrows has evolutionary significance, because they represent the oldest evidence of aestivation in the vertebrate lineage.

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CHAPTER 5. CONCLUSION

The CF trace fossil assemblage is similar in composition to previously reported Devonian continental ichnoassemblages (e.g., Gevers et al., 1971; Berg, 1972; Bradshaw, 1981; Walker, 1985; Thoms and Berg, 1986; Gordon, 1988; Driese and Mora, 1993; Driese et al. 1997; Morrissey and Braddy, 2004; Wisshak et al., 2004), which are composed of *Beaconites* isp., bivalve burrows (*Lockeia* isp., and *Pleurovurvus arenaorte*), arthropod trackways (e.g., *Diplichnites* isp.), fish swimming traces (*Undichna* isp.), and shallowly to deeply penetrative rhizoliths. The CF ichnoassemblage differs from other Devonian continental ichnoassemblages in that it contains probable lungfish estivation burrows (*Hypero euthys teichonomos*) and arthropod dwelling burrows (*Camborygma eunekonomos* and *C. litonomos*).

The traces that comprise the CF, as well as previously reported Devonian continental ichnoassemblages, represent the behavior of aquatic, subaerial, and soil-dwelling organisms with hygrophilic to terraphilic and hydrophilic affinities. The behavioral specialization of soil-dwelling organisms into terraphilic to hygrophilic, and hydrophilic organisms in the CF indicates that Devonian continental organisms exhibited tiering in response to paleohydrology, in a manner similar to that of Mesozoic to recent continental organisms (e.g. Hasiotis, 2002, 2007, 2008; Hasiotis et al., 2007).

The behavioral specialization of Devonian continental organisms, as evidenced by the CF ichnoassemblage, and previously described Devonian continental ichnoassemblies (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morrissey and Braddy, 2004; Davies et al., 2006) contrasts with previous assessments of behavioral complexity and ecospace utilization in Devonian continental ecosystems (e.g., Buatois et al., 1998). The results of our study and previous studies

of Siluro-Devonian continental ichnoassemblages indicate that the *Scoyenia* Ichnofacies, comprising behaviors assignable to the *Scoyenia* Ichnoguild of Buatois et al. (1998) occurs in Siluro-Devonian alluvial strata worldwide (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morissey and Braddy, 2004; Davies et al., 2006). Noteworthy, however, is that the use of the *Scoyenia* Ichnofacies and *Scoyenia* Ichnoguild concepts contribute little to our understanding of continental ichnology, as neither concept properly associates trace fossils with the paleohydrologic conditions under which they were constructed.

Our study and that of Gordon (1988) further demonstrate that deeply penetrative burrowing behavior had evolved by the Late, if not the Middle Devonian. Buatois et al. (1998) asserted that the evolution of deep burrowing behavior (and thus implicitly the evolution of hydrophilic, soil biota) in continental environments occurred in the Triassic. Buatois et al. (1998) cited the presence of deeply penetrative burrows from the upper Triassic Chinle Formation, interpreted to be freshwater decapod burrows by Hasiotis et al. (1993) and Hasiotis and Mitchell (1993) as the earliest evidence of deeply penetrative burrowing in the continental realm. Gordon (1988), however, described vertically oriented burrows from the Middle to Late Devonian CM of New York, USA that occur in alluvial deposits. The presence of Gordon's (1988) burrows in Givetian to Frasnian alluvial deposits indicates that deeply penetrative burrowing occurred in Middle to earliest Late Devonian alluvial deposits as well, and that the inception of deeply penetrative burrowing in alluvial environments began in the Middle to earliest Late Devonian, rather than the Triassic.

Previous analyses of the evolution of ecospace utilization and trace fossil distribution with respect to the development of Phanerozoic continental ecosystems (e.g., Buatois et al., 1998) have suggested that terrestrialization occurred gradually, culminating in the development

of complex ecosystems in the Mesozoic. Our results, and those of previous studies of Siluro-Devonian continental trace fossil assemblages (Gevers et al., 1971; Bradshaw, 1981; Gordon, 1988; Morissey and Braddy, 2004; Davies et al., 2006) indicate that organisms colonized land quickly, and that the spatial distribution and tiering of organisms in Paleozoic alluvial sediments was similar to that reported for Mesozoic to recent continental ecosystems (e.g., Bown and Kraus, 1983; Smith, 1993; Smith and Mason, 1998; Hasiotis, 1998, 2002, 2003, 2004, 2007, Hembree and Hasiotis, 2007, 2008; Hasiotis, 2008; Smith et al., 2008).

Early trace and body fossil evidence for life on land occurs in Middle to Late Ordovician paleosols and marginal marine environments (Retallack and Feakes, 1987; Johnson et al., 1994; Strother et al., 1996; Retallack, 2001). Ordovician continental trace fossil assemblages are characterized by rare, moderately penetrative subvertical structures (Retallack and Feakes, 1987; Retallack, 2001) and arthropod trackways (Johnson et al., 1994). Whether or not these traces truly represent behavior of continental organisms has been debated, however (e.g., Davies et al., 2010). Ordovician continental body fossil assemblages are characterized by plant spores, which are world-wide in distribution and may have been produced by liverwort-like plants (Strother et al., 1996; Kenrick and Crane, 1997).

The nature and timing of land colonization by plants and animals is still unresolved, however, the world-wide distribution of plant spores in Middle to Late Ordovician marginal marine strata, and the presence of trace fossils in Late Ordovician paleosols and subaerial, marginal marine strata suggests that plants and animals colonized land in the Middle to Late Ordovician. The presence of myriapod, arachnid, and plant body fossils (Selden and Edwards, 1989; Jeram et al., 1990; Edwards and Selden, 1993; Edwards et al., 1995; Shear and Selden, 1995; Shear et al., 1998), as well as abundant backfilled burrows and trackways in continental

settings by the Late Silurian (Morrissey and Braddy, 2004; Davies et al., 2006) indicates that continental ecosystems were well established by the Late Silurian and must have exhibited rapid evolution between the Late Ordovician and Late Silurian.

Evidence from the CF indicates that Late Devonian soil organisms contributed greatly to the pedogenic process, as is true of Mesozoic to recent soil organisms (e.g., Hasiotis, 2002, 2007; Jones et al., 2006; Jouquet et al., 2006). We further assert that pedogenesis by CF soil organisms contributed to a positive feedback that facilitated further colonization of CF alluvial soils by infaunal organisms. CF soil organisms, as such, should be considered ecosystem engineers, indicating that the inception of ecosystem engineering by soil biota occurred in the Late Devonian, or earlier. Although CF aquatic organisms were apparently not ecosystem engineers, CF aquatic ichnocoenoses have important paleoenvironmental implications, allowing for interpretation of sedimentation rates and depositional energy in CF channel deposits. CF aquatic trace fossils, furthermore, represent important components of biodiversity in aquatic environments of the CF.

Hyperoethys teichonomos from the CF exhibits all of the architectural and surficial morphological criteria established for the identification of lungfish estivation burrows. *H. teichonomos*, furthermore, differs in surficial and architectural morphology from similar ichnotaxa, indicating that these burrows do, indeed, merit the erection of a new ichnotaxon. Recognition of CF lungfish burrows is significant to paleobiological and paleoclimatic reconstructions of the CF, because *H. teichonomos* is much more common and abundant in the CF than lungfish skeletal material, and as an aestivation burrow, is evidence of pronounced wet-dry seasonality on the CF alluvial plain. *Hyperoethys teichonomos* has evolutionary significance, because it represents the oldest evidence of aestivation in the vertebrate lineage.

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