

Ichnotaxonomic Assessment of Mazon Creek Area Trace Fossils, Illinois, USA

by

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ABSTRACT

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The Francis Creek Shale Member (FCSM) of the Mid-Pennsylvanian Carbondale Formation along Mazon Creek in northern Illinois is known for soft-bodied organisms preserved within siderite concretions. Trace fossils, though less well known, also occur in concretions. Several hundred trace-fossil-bearing concretions were examined from collections at The Field Museum, Chicago, and The University of Kansas Natural History Museum, Lawrence. Identification was based on accepted diagnostic criteria and comparison with like specimens. Described were 24 ichnogenera and 28 ichnospecies, including a new ichnospecies of *Pennatulites* and a new ichnogenera of coprolite—*Funiculichnus spiralis*, unnamed trace fossils including a bivalve-locomotion trail, spiral and amorphous coprolites, and two possible galls, and several deformation structures and body fossils misidentified as trace fossils. Trace-fossil assemblages indicate a *Skolithos*–*Cruziana* ichnofacies transition from shallow, high-energy to deeper, lower-energy nearshore marine environments, which is consistent with previous interpretations that the FCSM was deposited in a nearshore, deltaic environment.

TABLE OF CONTENTS

	<i>Page</i>
Thesis Abstract	iii
Acknowledgments	v
Dedication	vii
Publication Abstract	1
Introduction	3
Abbreviations	4
Geologic Background	4
Materials and Methods	5
Lab Results	7
Systematic Ichnology	8
<i>Ichnotaxa</i>	8
<i>Bivalve trails</i>	42
<i>Coprolites</i>	42
<i>Galls</i>	47
Miscellanea	48
<i>Soft-sediment Deformation Structures</i>	49
<i>Wrinkled Textures (on Macroneuropteris)</i>	49
<i>Body Fossils</i>	50
Discussion	52
<i>Ichnotaxa</i>	52
<i>Behavior</i>	52
<i>Ichnofacies</i>	53
<i>Comparative Ichnotaxonomy</i>	55
Summary	64
Conclusions	67
Table 1	70
Figure Captions	74
Figures	79
References	104

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DEDICATION

This manuscript is dedicated to the memory of John M. Patterson for his unending support of my educational pursuits. Rest proudly in peace.

Abstract

The Francis Creek Shale Member of the Middle Pennsylvanian Carbondale Formation along Mazon Creek near Morris, Illinois, is a conservation Lagerstätte well known for the exquisite preservation of its diverse soft-bodied organisms within siderite concretions. Trace fossils, although less well known, also occur in siderite concretions. Examination of collections at the Field Museum of Natural History, Chicago, Illinois, and the University of Kansas Natural History Museum, Lawrence, Kansas, yielded 24 ichnogenera and 28 ichnospecies: *Arenicolites variabilis*, *Arenicolites* isp., *Arenituba verso*, *Aulichnites parkerensis*, *Bactryllium* isp., *Beaconites antarcticus*, *Bergaueria* cf. *perata*, *Bergaueria radiata*, cf. *Biformites* isp., *Chondrites intricatus*, *Chondrites targionii*, *Cochlichnus anguineus*, cf. *Cruziana* isp., *Cuniculonomus simplex*, *Diplichnites* isp., *Diplocraterion parallelum*, a new ichnotaxon of coprolite *Funiculichnus spiralis*, *Gyrophyllites* isp., *Monocraterion* isp., a new ichnospecies *Pennatulites nodosus*, *Phagophytichnus ekowskii*, *Planolites beverleyensis*, cf. *Planolites* isp., *Protovirgularia dichotoma*, *Rhizocorallium jenense*, *Skolithos* isp., *Taenidium satanassi*, and *Thalassinoides* isp. One specimen may contain the most common Mazon Creek worm, *Didontogaster cordylina*, preserved within the base of the most common trace, *Arenicolites*. Unnamed trace fossils include a locomotion trail associated with a bivalve, spiral and common or amorphous coprolites, and possibly the earliest galls known from the fossil record. Several specimens misidentified as trace fossils are actually soft-sediment deformation structures, wrinkled textures on *Macroneuropteris* pinnules, or body fossils including worms and worm-like animals, jellyfish and jellyfish tentacles, a *Calamites* stem, and a possible cololite. The inferred assemblage of *Arenicolites*,

Diplocraterion, *Monocraterion*, and *Skolithos* suggest a *Skolithos* ichnofacies, indicating a high-energy, shallow-marine environment with shifting media. This assemblage, along with *Bergaueria*, *Chondrites*, *Planolites*, *Rhizocorallium*, *Taenidium*, and *Thalassinoides* may also occur in the *Glossifungites* ichnofacies, indicating a shallow-marine, firmground environment. Scratch marks and coarse-grained burrow fill are lacking from all but three specimens; however, a firmground environment is possible but unlikely. The inferred assemblage of *Planolites*, *Cochlichnus*, and *Chondrites*, with *Arenicolites*, *Aulichnites*, and *Rhizocorallium*, suggest a *Cruziana* ichnofacies, representing a shallow-marine, subtidal environment within fair-weather to storm-wave base. The trace-fossil assemblages suggest a *Skolithos*–*Cruziana* ichnofacies transition from shallower to deeper water and higher to lower energy environments. This ichnofacies transition is consistent with previous interpretations that the Francis Creek Shale was deposited in a nearshore, shallow-marine, deltaic environment.

Introduction

The Mazon Creek area (MCA) is known primarily for its abundance of diverse soft-bodied organisms preserved in siderite concretions (Baird et al., 1986). Previous research has focused on the taxonomic description of the fauna (Richardson, 1956; Johnson and Richardson, 1966; Bardack, 1979; Schram, 1979; Baird et al., 1986; Bailey and Sroka, 1997; Fitzhugh and Sroka, 1997) and flora (Noé, 1925; Darrah, 1969; Pfefferkorn, 1979) found in the concretions. Trace fossils, although less well-known, are also found within concretions; however, little research has been conducted on Mazon Creek trace fossils (Shabica, 1970, 1997; Baird et al., 1986).

The objective of this study is to determine the ichnotaxonomy of trace fossils on or in concretions and in shales from the Francis Creek Shale Member (FCSM) of the Middle Pennsylvanian Carbondale Formation in northern Illinois. This study will also identify behavioral groupings of the ichnofauna, infer assemblages and assign them to ichnofacies, and compare the ichnofauna and ichnofacies to other deltaic, coal-bearing, or nearshore sequences. Collections studied are at the Field Museum of Natural History (FMNH), Chicago, Illinois, and the University of Kansas Natural History Museum and Biodiversity Research Center (KU), Lawrence, Kansas. These trace fossils are used to refine interpretations of the paleoenvironment from which the concretions and sediments formed (e.g., Shabica, 1970; Baird et al., 1986).

Trace fossils described previously from concretions from MCA include the *Rusophycus* and *Arenicolites*, spiral coprolites, and common coprolites—undifferentiated masses with no particular morphology (*sensu* Shabica, 1997)—as well as leaf margin damage represented by *Phagophytichnus ekowskii* (Scott and Taylor, 1983; Scott et al.,

1992) and *Cuniculonomus simplex* (Labandeira and Beall, 1990). Bivalves with associated trails and fugichnia (escape traces) have also been observed in concretions (Shabica, 1970; Bailey and Sroka, 1997; Shabica and Godfrey, 1997; Selden and Nudds, 2004).

Abbreviations

FCSM, Francis Creek Shale Member; FMNH, The Field Museum of Natural History; KU, The University of Kansas Natural History Museum and Biodiversity Research Center; KUMIP, University of Kansas Museum of Invertebrate Paleontology; MCA, The Mazon Creek Area.

Geologic background

Mazon Creek is a tributary of the Illinois River near Morris, Grundy County, Illinois (Fig. 1). The FCSM of the Middle Pennsylvanian Carbondale Formation along Mazon Creek is a conservation Lagerstätte well known for exhibiting exquisite preservation of its flora and fauna within siderite concretions. Deposition of the FCSM occurred during the Middle Pennsylvanian Westphalian D Stage (Moscovian—international stratigraphic age). The FCSM thin facies is overlain by the Mecca Quarry Member and the FCSM overlies the Colchester Coal Member (Fig. 2). Lithofacies in the FCSM along Mazon Creek include friable grey shale, siltstone, thin-bedded sheet sandstone, and cross-bedded sandstone (Bradley, 1870; Baird, 1979). The FCSM is described as a wedge-shaped detrital lobe interpreted as being deposited in a shallow-marine, tide-influenced, nearshore, deltaic environment (Shabica, 1970, 1979; Baird,

1979; Kuecher et al., 1990; Feldman et al., 1993). Sediment accumulation at MCA occurred during a marine transgressive event, inundating the coal swamp, indicated by the occurrence of a marine fauna in the basal beds of the FCSM (Baird et al., 1985a). Deposits within the FCSM suggestive of delta progradation followed the coal swamp inundation (Baird et al., 1985b).

MCA includes Mazon Creek, abandoned coal mines and their spoil-pile locations (Fig. 1), and the surrounding areas (Baird, 1979). Concretions are found among spoil piles in MCA, as well as within the basal 3–4 m of the dark gray shale lithofacies of the FCSM. Concretions may occur higher in the section and their distribution differs depending on the outcrop locality (Baird, 1979; Baird et al., 1986). Sedimentation was rapid and concretions formed early during diagenesis as indicated by the exceptional preservation of the fossils (Woodland and Stenstrom, 1979; Baird and Sroka, 1990; Kuecher et al., 1990). For detailed studies on lithology, paleoenvironment, and concretion formation see Shabica (1970, 1979), Smith (1970), Baird (1979), and Woodland and Stenstrom (1979).

Materials and Methods

Several hundred siderite concretions and several slabs of shale were examined from the paleobotany and invertebrate trace-fossil collections at FMNH and KU. Trace-fossil specimens were described and measured using a caliper accurate to 0.1 mm. Ichnotaxonomic identification was based on accepted diagnostic criteria and comparison with like specimens in the literature and in the KU Geology ichnology collection. Localities from where the concretions were collected are included in the individual

discussions. If a locality was not designated, then the trace fossil was considered from MCA. Detailed information on fossil localities was compiled on databases with FMNH and Northeastern Illinois University, DeKalb.

All specimens used for laboratory analyses were *Planolites*, as this trace fossil was very abundant and specimens could be sacrificed for study. Thin-sections were prepared by Texas Petrographic Services. A few samples were too small for thin-section slides, requiring blue-dye injection. X-ray diffraction was performed on several samples at the X-ray Crystallography laboratory at KU on a Bruker SMART APEX diffractometer equipped with a sealed tube x-ray source, a graphite monochromator, MonoCap collimator, and a charge-coupled device area detector.

Stable-carbon-isotope analysis was performed at the W. M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory at KU on specimens KUMIP 320211 and PE 47459. Stable-isotope samples were milled using a microscope-mounted dental drill with 3–500- μm -diameter tungsten-carbide burrs to produce samples ranging from 25 to 100 μg . Two concretions were sampled repetitively to evaluate their unique intrinsic variability, and to define diagenetic trends in carbon-oxygen isotope space that yielded information about the paleohydrologic processes that led to stabilization at the time of formation. Samples were vacuum roasted at 200 °C for 1 h to remove volatile contaminants and analyzed using phosphoric acid digestion at 75 °C on a ThermoFinnigan Kiel III single-sample acid-dosing system connected to a ThermoFinnigan MAT 253 isotope-ratio mass spectrometer. Precision was monitored by daily analysis of NBS-18 and NBS-19 and was better than 0.1‰ for both carbon and oxygen. All carbonate data were reported relative to Vienna Peedee belemnite. Siderite

oxygen isotopic values were corrected to account for the temperature-dependent fractionation factor between phosphoric acid and siderite utilizing data in Carothers et al. (1988). Mineral identification was done by visual inspection, X-ray diffraction, and use of hydrochloric acid (HCl used on one specimen).

Laboratory Results

Thin sections on several *Planolites* specimens yielded little additional information regarding the preservation and taphonomy of the trace fossils. Examination of trace fossils and the surrounding concretion material shows no change in mineral content, grain size, or roundness. The only visible difference was a slightly darker color of the sediment that comprised the trace fossil—identified by the area between the black lines in Figs. 3A and B. The injection of blue dye for thin sectioning revealed no porosity within the concretion. One specimen (KUMIP 320211), however, contains pellet-like structures within the trace (Fig. 3C and D).

Several samples contain visible pyrite. Several samples contain a soft, white, clayey mineral associated with the trace-fossil portion of the concretions. X-ray diffraction of the trace-fossil portion of PE 43127 indicates the soft, white, clayey mineral to be kaolinite (Fig. 4B). X-ray diffraction of the concretion portion of PE 51503 confirmed the presence of siderite and possibly quartz (Fig. 4A). The results for stable-carbon isotope analysis are in Figure 4C. Carbon-13 isotopes from KUMIP 320211 indicate a modified marine environment with little oxidation of methane, or that there is a small amount of organic oxidation of the pore fluids at the time of concretion formation. The results for PE 47459 indicate carbon dioxide reduction by methanogenesis,

suggesting anoxic pore waters at the time of concretion formation. Negative values for PE 47459 indicate the presence of calcite, suggesting later freshwater diagenesis (Luis Gonzalez, personal communication, 2010). The presence of calcite was confirmed by use of HCl.

The presence of siderite and kaolinite is consistent with X-ray diffraction results of Woodland and Stenstrom (1979), who also reported the presence of illite, chlorite, and quartz. The carbon isotope results confirmed previous findings by Woodland and Stenstrom (1979) of biogenic carbon dioxide production through the degradation of organic matter, and carbon dioxide reduction through methanogenesis. For a detailed study on concretions using X-ray diffraction and carbon-isotope analysis see Woodland and Stenstrom (1979).

Systematic Ichnology

***Arenicolites* Salter, 1857**

DIAGNOSIS—Vertical to slightly oblique U-shaped tube lacking spreiten with wide or narrowly spaced cylindrical openings (after Fürsich, 1974b).

Arenicolites variabilis Fürsich, 1974

Figures 5A–F, 13A, 18C

FMNH SPECIMENS—PE 25668, PE 29687, PE 30064, PE 30065, PE 30069, PE 30080, PE 30240, PE 31821, PE 31824–31826, PE 31828–31831, PE 31834–31841, PE 31843–31854, PE 31857, PE 31858, PE 31860, PE 31861, PE 31863, PE 31864, PE

31871, PE 44293, PE 44513, PE 46792–46794, PE 46797, PE 46800, PE 51576, PE 51580, PE 51586, PE 51593, PE 51618, PE 51626–51628, PE 51630–51633, PE 51635–51649, PE 51651

DESCRIPTION—Vertical, smooth-walled, U-shaped burrows lacking spreiten. Burrow symmetry variable. Burrow openings often observable on top surface of concretion in concave or convex epirelief. Diameter of openings ranges from 1.8–5.9 mm, averaging 3.37 mm, with the exception of one large form (PE 25668) with a burrow diameter of 11.5 mm. Distance between openings ranges from 4.1–45.9 mm, averaging 12.56 mm. Where measurable, the depth from opening to U-axis ranges from 1.5–3 cm. The large form is vertical at the top of the specimen, then curves to an angle of $\sim 45^\circ$. The base of the U is 25.6 mm from the top of the specimen, and the distance between openings is 13.4 mm.

DISCUSSION—Concretions PE 25668 through PE 46800 were collected at Pit 11. The remaining specimens are specified as collected from MCA. *Arenicolites* is interpreted as a dwelling burrow of a suspension feeder (Fürsich, 1974b). The specimens are preserved individually. They likely occurred as groups of individuals when formed, as is common with *Arenicolites*; however, there is no direct evidence from MCA specimens to confirm their occurrence in groups, as the concretions were not found *in situ*. Several concretions are well rounded or preserved as a U-shape and contain vertical to subvertical specimens of *A. variabilis* (Fig. 5A–B). Specimens, although lacking spreiten, are similar in preservation to *Diplocraterion parallelum* (Figs. 13A–B). *Arenicolites* was previously described from Mazon Creek (Shabica and Godfrey, 1997; fig. 21.5); however, the figured specimen has spreiten and, therefore, belongs to *Diplocraterion*.

Variability of burrow symmetry is observed within several concretions (Fig. 5A–B), and occasionally the base of the burrow U-shape can be seen on the bottom surface of the concretion in *Arenicolites*, as well as for *Diplocraterion* (Fig. 13D). The similarity in material, preservation, and morphology suggest these specimens are all of the same ichnospecies, although several specimens are incomplete or not entirely visible. PE 25668 is well preserved and in the same preservational fashion as the other specimens of *A. variabilis*, but has a considerably larger burrow diameter. There are no other specimens of this size for comparison. The size of this burrow suggests either a larger individual or a different organism produced it.

Arenicolites isp.

Figures 6A–E, 8B

FMNH SPECIMENS—PE 45091, PE 45749, PE 51654

KU SPECIMENS—KUMIP 320206 – KUMIP 320210

DESCRIPTION—Preserved as smooth-walled, U- or J-shaped burrows, or as two holes lacking visible spreiten between the openings within or on surface of concretion. Diameters range from 4–6.5 mm, averaging 4.7 mm; distance between openings ranges from 3–13.4 mm. Burrow dimensions: KUMIP 320206—burrow diameter 5.5 mm, distance between burrows 3 mm; KUMIP 320207, KUMIP 320208, and PE 51654 have a burrow diameter of 4 mm, with the distance between burrows at 9.7 mm, 10 mm, and 9 mm, respectively. PE 45091 has burrow diameter of 6.5 mm, with distance between openings of 13.3 mm. Specimen PE 45749 is a J-shaped burrow with the burrow opening

preserved on the top surface of the concretion, with a burrow diameter of 6.2 mm, and a surface opening diameter of ~ 29 mm.

DISCUSSION—KUMIP 320206 is preserved on the surface of the concretion. The concretion is split open, although the burrow is not observable within. The remaining KU specimens are preserved within concretions as two filled holes. KUMIP 320207 is preserved as a mold and cast of the two burrow openings. KUMIP 320208 is preserved within the concretion with one of the burrows also visible on one surface. The other two KU specimens are likely *Arenicolites*, although they are preserved poorly. Specimen PE 51654 (Fig. 6E) is preserved as two in-filled holes within the concretion with an individual *Planolites beverleyensis* (Fig. 6F). These four specimens were collected from MCA.

Specimens PE 45091 and PE 45749 were collected from Pit 11. PE 45091 is preserved as two holes on the surface of the concretion in association with *Chondrites intricatus* (Fig. 9A). PE 45749 is likely the complete burrow as the opening on the surface is presumed to be the funnel-shaped entrance and is considerably wider than the burrow (Fig. 6A–C). This specimen also has the animal that formed the burrow preserved within it (Fig. 6D). The animal was apparently trapped in its burrow and preserved in the concretion. The animal that formed this burrow is most likely the annelid worm *Didontogaster cordylina* Thompson, 1979. The jaws are not visible to make certain identification. The body morphology of this fossil, however, is most similar to *D. cordylina*, which is the most abundant polychaete species among the Mazon Creek fauna (Fitzhugh et al., 1997).

Didontogaster cordylina has been suggested to be a burrower (Thompson, 1979), as several specimens (e.g. PE 10334, PE 39289) are preserved oblique to bedding (Thompson, 1979; Baird et al., 1986; Baird and Sroka, 1990). Thompson (1979) also noted that some specimens of *D. cordylina* “have a light-colored trail-like area just anterior to the head,” most likely from the extension and retraction of the animal’s head or proboscis. This specimen, if *D. cordylina*, confirms the burrower hypothesis as the anterior portion of the annelid is preserved obliquely at the bottom of the burrow, and the narrower posterior end is preserved within the vertical portion of the burrow.

***Arenituba* (Chamberlain, 1971)**

DIAGNOSIS—Straight or slightly curving, occasionally branching, singly or bunched, irregularly arranged, sand-coated or sand-filled tubes radiating from a central gallery (after Chamberlain, 1971; Stanley and Pickerill, 1995).

Arenituba verso (Chamberlain, 1971)

Figure 7A

FMNH SPECIMEN—PE 51894

DESCRIPTION—Eight to ten lined, cylindrical tubes radiating outward and downward from a centralized area, preserved in convex epirelief on surface of concretion. Relief at highest point is ~ 6 mm. Tubes are 3–5 mm wide and ~ 10–15 mm of visible length.

DISCUSSION—A few tubes of this specimen appear to have a poorly preserved lining that is, although very fine grained, coarser than the material that comprises the

concretion. The tubes of this specimen are wider, more closely spaced, and not as long and curved as the Carboniferous specimens described by Chamberlain (1971) and Lockley et al. (1987). This specimen appears to have similar relief to the specimen described by Miller (1986). PE 51894 appears incomplete, however, as part of the concretion has broken away.

Chamberlain (1971) originally named this trace-fossil morphology *Micatuba*. Stanley and Pickerill (1995) renamed the ichnogenus *Arenituba*, noting that *Micatuba* was already assigned to a genus of foraminifer, and names applied to body fossils take precedence over ichnofossils. *Arenituba* is generally interpreted as a dwelling trace where the tubes are used as feeding structures where the organism extended itself in search of food (Chamberlain, 1971; Stanley and Pickerill, 1995).

***Aulichnites* Fenton and Fenton, 1937**

DIAGNOSIS—Straight to sinuous, unbranched, bilobate trail with narrow median furrow (after Howard and Frey, 1984).

Aulichnites parkerensis Fenton and Fenton, 1937

Figure 7D

FMNH SPECIMEN—PE 46360

DESCRIPTION—Straight to slightly curved, bilobate trail with a narrow median furrow, preserved horizontal to bedding in convex epirelief with respect to the concretion. Smooth surface with no apparent lining or ornamentation. Length 28.2 mm; width from 9–10 mm; median furrow width from 1.5–2 mm.

DISCUSSION—This single specimen, collected from the Chowder Flats strip mine area west of Morris, Illinois, is similar in morphology and size to specimens described by Fenton and Fenton (1937), Howard and Frey (1984), Eagar et al. (1985), and Buatois and Mángano (1993). This specimen is incomplete and reveals far less sinuosity than specimens typically preserved on bedding planes. *Aulichnites parkerensis* is a common occurrence in Carboniferous deposits (Hakes, 1977; Eagar et al., 1985; Buatois and Mángano, 1993). PE 46360 was preserved in a siderite concretion that formed within shale, whereas the other Carboniferous specimens are preserved in a fine-grained sandstone facies: cyclothem deposits (Hakes, 1977); deltaic inter-channel deposits (Eagar et al., 1985); turbiditic lake underflow current deposits (Buatois and Mángano, 1993).

***Beaconites* Vialov, 1962**

DIAGNOSIS—Horizontal, straight to sinuous, unornamented, tubular burrows of variable diameter, with strong or gently arching meniscate, or packets of sediment (after Bradshaw, 1981).

Beaconites antarcticus Vialov, 1962

Figure 7B–C, 7E

FMNH SPECIMENS—PE 36865, PE 36866, PE 40067–40070, PE 40071 – 2 specimens, PE 40074, PE 45085, PE 45094, PE 45095, PE 45097, PE 45748, PE 51523

DESCRIPTION—Straight to slightly sinuous, horizontal to subhorizontal, mostly unlined burrows with meniscate backfill structures. Backfills may be slightly offset from

one another and merge laterally to form a crenulate burrow wall. Generally preserved as concave epirelief, but occasionally preserved as convex epirelief. Lengths range from 30.5–92.8 mm of preserved specimens, averaging 49.3 mm. Diameters range from 6–11.8 mm averaging 9.2 mm. Specimens PE 36865 and PE 36866 preserved ~ 20° oblique to bedding. Menisci straight to arcuate. Sediment packets are thin and generally uniform in thickness.

DISCUSSION—*Beaconites antarcticus* specimens, collected from Pit 11, vary in preservational quality and visibility of menisci. *Beaconites* is recognized as a valid ichnotaxon, following the review of diagnostic criteria reviewed by Smith et al. (2008). The menisci in the horizontal specimens are generally straight, but rarely slightly arcuate (Figs. 7B–C). The menisci in the two oblique specimens are visibly more arcuate, and are concave down with respect to burrow orientation (Fig. 7E). *Beaconites antarcticus* specimens from MCA most closely resemble *B. antarcticus* specimens figured by Gevers et al. (1971; plate 18, fig. 2).

Bradshaw (1981) proposed the ichnospecies *B. barretti* and distinguishes it from *B. antarcticus* based on specimen width, burrow sinuosity, and thickness and curvature of menisci. *Beaconites barretti* is described as having diameters > 30 mm, thin menisci, and often sinuous in plan view (Bradshaw, 1981). *Beaconites antarcticus* is straight to slightly sinuous, generally < 30 mm diameter, and often has thick menisci (Bradshaw, 1981). Bradshaw (1981) also suggests different tracemakers produced the smaller and larger burrows; however, different tracemakers can produce the same type of trace fossil morphology. The figures of *Beaconites antarcticus* are too poor and descriptions of

menisci of the two ichnospecies of *Beaconites* are not sufficiently well defined in Bradshaw (1981), however, to fully differentiate the two ichnotaxa.

The differences in diameter and apparent lack of sinuosity described by Bradshaw (1981) do not necessarily indicate a difference in behavior, which is an accepted requirement for determining ichnotaxa. The differences in diameter represent differences in size of the tracemaker, and not differences in behavior. The lack of sinuosity in the smaller forms may be the result of the specimens being shorter; slight sinuosity still represents sinuosity. Keighley and Pickerill (1994; p. 311) stated that ichnogenera should not be differentiated based on variations in the style of backfill. The variations of the menisci, however, may represent different behaviors, as demonstrated by the research of Smith et al. (2008), Smith and Hasiotis (2008), and Counts and Hasiotis (2009). Keighley and Pickerill (1994) placed *B. barretti* under the ichnogenus *Taenidium* based on the lack of a wall or lining “actively constructed by the burrower” as redefined by them. They did not, however, take into account that the menisci observed in *Taenidium* form relatively thick, compartmentalized packets, whereas the menisci in *B. barretti* appear to be non-compartmentalized (Smith et al., 2008). The backfill morphology of *Beaconites*, as well as in other meniscate backfilled burrows, is distinctive and easily distinguishable from *Taenidium* such that the diagnosis and description of *Beaconites* is the most appropriate ichnotaxonomic designation (see Smith et al., 2008, for comparisons).

***Bergaueria* Prantl, 1946**

DIAGNOSIS—Hemispherical burrows with shallow central depression and possible radial ridges or lobes. Height \leq diameter; occur on soles of beds (after Alpert, 1973).

Bergaueria cf. perata Prantl, 1946

Figure 8A

FMNH SPECIMEN—PE 51561

DESCRIPTION—Smooth-walled, unornamented, hemispherical to conical burrow 16.6 mm in diameter with centrally located circular depression 5.5 mm diameter. Burrow 4.4 mm thick. Depression \sim 1 mm deep.

DISCUSSION—The ichnotaxonomy of *Bergaueria* has been discussed in detail by Pemberton et al. (1988). *Bergaueria* is interpreted as a permanent or semipermanent dwelling burrow (Alpert, 1973). *Bergaueria perata* is distinguished from *B. radiata* by the lack of ridges or lobes on the burrow walls. This specimen is preserved poorly and lacks structure with the exception of the central depression. The visible morphology and dimensions are consistent with the ichnogenus *Bergaueria*. *Bergaueria* has also been observed in Late Pennsylvanian cyclothems in Kansas (Hakes, 1977), and in mid-Carboniferous deltaic deposits in England (Eager et al., 1985).

Bergaueria radiata Alpert, 1973

Figure 8B–D

FMNH SPECIMENS—PE 51620 (a, b, c) – 3 specimens

DESCRIPTION—Circular to slightly ovate, protrusions with centrally located depressions. Specimens PE 51620a and PE 51620c have a 1-mm-diameter, cylindrical iron concretion (Fig. 8B) protruding from the central depression. Specimens have ridges, or more accurately lobes, up to ~ 2–4 mm long radiating from the central depression. Diameters of specimens are 25 mm, 27.5 x 28.5 mm, and 38.9 x 41.3 mm. The diameter of the depressions decreases the larger the specimen, from ~ 4 mm to 7.5 mm. The depressions are prominent and up to a few mm deep.

DISCUSSION—*Bergaueria radiata* is distinguished from *B. perata* by the presence of radial lobes. The depressions in *B. radiata* are more prominent than *B. perata*, and are relatively smaller in diameter with respect to the size of the trace. Specimens of *B. radiata* are relatively flat and slightly ovate, possibly due to compaction. The three specimens of PE 51620 closely resemble the type specimens described by Alpert (1973, fig. 3). An additional specimen—PE 51625—has similar dimensions and morphology as PE 51620, suggesting this specimen is possibly *B. radiata*. This specimen is preserved too poorly to accurately identify and lacks measurable structure, with the exception of a 4-mm-diameter depression. All five specimens assigned to the ichnogenus *Bergaueria* were collected from MCA.

***Biformites* Linck, 1949**

DIAGNOSIS—Horizontal, bimorphous burrow with narrow, tapered section continuing into uniformly wide ribbed section (after Boyer, 1979).

cf. *Biformites* isp.

Figure 8E

FMNH SPECIMEN—PE 51656

DESCRIPTION—Cylindrical, horizontal burrow preserved in full relief parallel to bedding. Burrow has a wider, segmented section and a smooth, conical section that tapers to a rounded point. Segmented portion is 8.5 mm in diameter. Segments are 1.5 mm thick, spaced evenly 1 mm apart.

DISCUSSION—*Biformites* has been interpreted as either a dwelling burrow (Seilacher, 1955a), or a resting trace linked to a crawling trace (Boyer, 1979). This specimen is weathered highly and preserved poorly. The visible morphological characteristics are closest to that of *Biformites*. The bedding plane is not evident but the trace appears to be parallel.

***Chondrites* Sternberg, 1833**

DIAGNOSIS—Smooth-walled, three-dimensionally branching, dendritic burrow systems that rarely interconnect (after Howard and Frey, 1984).

Chondrites intricatus Brongniart, 1823

Figure 9A–B, 9D

FMNH SPECIMENS—PE 40077, PE 40088, PE 40089, PE 40092, PE 40099, PE 40100, PE 45079, PE 45091, PE 51044, PE 51094, PE 51096, PE 51786

DESCRIPTION—Dendritic, unlined, smooth-walled, highly branching burrow system preserved as convex epirelief on surface of concretions. Some branches are

preserved poorly and are not continuous. Branches are cylindrical with a diameter of 1–2 mm. Singular segments are from 1–13 mm long.

DISCUSSION—*Chondrites* is generally accepted to be a feeding trace (Kennedy, 1970; Uchman, 2007). Bromley (1996), however, suggests *Chondrites* may be placed within agrichnia (gardening traces) based on its occurrence in dysoxic sediments and its chemosymbiotic nature. Uchman (1998) revised the systematics and diagnostic criteria of *Chondrites* to include four ichnospecies. *Chondrites intricatus* is distinguishable by its numerous downward radiating branches. The *C. intricatus* specimens, though varying in degree of preservation, show apparent numerous branches. The traces are generally preserved on the presumed top surface of concretion, but may also be present on the sides and bottom of the concretion. One broken specimen (PE 40077) revealed the trace within the concretion. PE 40099 and PE 40100 occur in association with *Funiculichnus* ichnogenus novum, and PE 45091 occurs in association with *Arenicolites* (Fig. 9A). Specimens PE 40077–51044 were collected at Pit 11. The remaining specimens are designated from MCA.

Chondrites targionii Brongniart, 1828

Figure 9C

FMNH SPECIMENS—PE 38318, PE 48568

DESCRIPTION—Dendritic, unlined, smooth-walled burrow system with few branches. Branches are long, slightly curved, and have uniform width ~ 1.5 mm.

Preserved in concave epirelief parallel to bedding on a single bedding plane.

DISCUSSION—*Chondrites targionii* is distinguished from *C. intricatus* by its slightly curving, well-defined, primary successive branching (Uchman, 1998). Specimen PE 48568 has only 7 total branches that are long, well defined, with sharp angles of branching ranging from a few degrees to almost 90°. In contrast, *C. intricatus* branches fairly regularly with relatively constant angles ranging from 45–65°, with 6–8 tunnels per cm². These specimens, collected from Pit 11, closely resemble those reproduced by Uchman (1998, figs. 19, 22). *Chondrites* has been described from several Carboniferous deposits including shallow marine shales of Kansas (Hakes, 1985), storm deposits in Poland (Gluszek, 1998), and flysch deposits of the Culm facies, Czech Republic (Mikulas et al., 2004).

***Cochlichnus* Hitchcock, 1858**

DIAGNOSIS—Horizontal, regularly sinusoidal burrow or trail (after Gluszek, 1995).

Cochlichnus anguineus Hitchcock, 1858

Figures 9E–F, 10A–C

FMNH SPECIMENS—P 30775, P 30779 – 3 specimens, P 31600, P 31253, P 31312, PE 38173 – 3 specimens, PE 38174 – 12 specimens, PE 38175 (a, b) – 9 specimens, PE 38176 – 9 specimens, PE 38177 (a, b) – 39 specimens, PE 51814 – 2 specimens, PE 51815, PE 51816, PE 51818, PE 51819 – 5 specimens, PE 51820, PE 51898 – 2 specimens, PE 52248, PP 4324, PP 4544, PP 16341, PP 26096

DESCRIPTION—Smooth, unlined, sinusoidal burrows preserved in concave or convex epirelief parallel to bedding. When multiple burrows are present, they may cross each other. Lengths range from ~ 12–100 mm; diameters range from 1–2.3 mm, averaging 1.6 mm; wavelength ranges from 5–16 mm, averaging 9.39 mm; amplitude ranges from 1–3 mm, averaging 1.58 mm.

DISCUSSION—*Cochlichnus* is interpreted as a surface or near-surface trace formed by the undulations of a worm or worm-like animal (Gluszek, 1995). Specimens are preserved either on a slab of gray shale (Figs. 10B–C), or associated with a pinnule of the pteridosperm *Macroneuropteris* (Figs. 9E–F, 10A). When associated with *Macroneuropteris*, the specimen may be in concave or convex epirelief depending on the preservation of the leaf, or how the leaf was revealed when the concretion was split. The specimens preserved as convex epirelief are the result of the organism moving over or underneath the leaf after it settled on the sediment surface. When preserved on slabs of shale, the specimens are preserved as convex epirelief on the top surface. Specimens may occasionally occur on the bottoms of the shale slabs, and are preserved in concave epirelief. No specimens occur within concretions without being associated with *Macroneuropteris*. The specimens within concretions were collected from Pit 11, and the shale slabs were collected from Pit 6. *Cochlichnus anguineus* has been described from several coal-bearing sequences throughout the Carboniferous including Union Chapel Mine, Alabama (Lucas and Lerner, 2005), Cumberland Basin, Nova Scotia (Archer et al., 1995), and Upper Silesia Coal Basin, Poland (Gluszek, 1995).

The specimens in this study were originally assigned to the ichnogenus *Belorhaphé*. These specimens are smoothly curved and sinusoidal, however, and lack the

sharper angled zigzag pattern of *Belorhaphe*. Several specimens in the FMNH collection cf. *Cochlichnus* or were not apparent: P 31151, P 31614, P 31667, P 31406, P 31594, P 31599, PE 51813, PE 51821, PE 52249, PE 51817, PP 1992, PP 26456 – 2 specimens, and PP 31386.

***Cruziana* d’Orbigny, 1842**

DIAGNOSIS—Elongated, bilobate trails with herringbone or transverse ridges (after Balistieri et al., 2002).

cf. *Cruziana* isp.

Figure 7F–G

FMNH SPECIMEN—PE 46784

DESCRIPTION—Two subparallel ridges horizontal to bedding. Distance between ridges narrows from ~ 17–13 mm. Median furrow not apparent.

DISCUSSION—This specimen, collected from Pit 11, is weathered highly and preserved poorly. The morphology resembles a bilobate trail, but the two subparallel ridges are the only structure preserved. The variation in the distance between the ridges is likely produced by the trace being shallowly impressed at one end of the concretion, and deeper at the other end of the trace.

***Cuniculonomus* Straus, 1977**

DIAGNOSIS—Simple or undular, U-shaped incision of constant width (after Müller, 1982).

Cuniculonomus simplex Müller, 1982

Figure 11A–D

FMNH SPECIMENS—P 18612, P 18619, P 18706, P 29934, P 31949, PE 52275, PP 11665, PP 16308, PP 31648, PP 31769, PP 36713, PP 52379

DESCRIPTION—Crescentic or U-shaped incisions with reaction rim, and possible fecal matter within the incision. Length greater than width. Two measured specimens: P 18619 – width at leaf margin 3 mm, total length 10 mm; P 18706 – width at leaf margin 3 mm, total length 28 mm. Venations within incised area are apparent, but not as prominent as the surrounding venations.

DISCUSSION—Specimens occur on *Macroneuropteris scheuchzeri* with the exception of PP 11665. PP 11665 occurs on the distal margins of the gymnosperm *Cyclopteris*, and was described by Labandeira and Beall (1990). The figure drawing by Labandeira and Beall (1990, Fig. 5a), however, does not clearly indicate if the venations are present within the incised area. The central area where the visibility of the venations is muted (i.e., less visible) is considered to be a necrotic zone, indicating surface feeding or abrasion (Labandeira, 1998, 2007). *Cuniculonomus* is interpreted to be a leaf mine (Müller, 1982; Labandeira and Beall, 1990; Labandeira, 1998). Labandeira (1998) discussed Paleozoic leaf mining in further detail and concluded that confirmation of the interpretation of leaf mines will require examination of permineralized foliage sectioned along with histological detail. An additional specimen (PP 5264) occurs on *Neuropteris ovata*. This specimen, however, is much smaller, has no reaction rim, and appears to be simple physical damage. *Cuniculonomus simplex* differs from *C. carpini*, *C. subtilis*, *C.*

tenuis, and *C. undulatus* based on its simple morphology and lack of undulations or sinuosity (Müller, 1982). One specimen described by Müller (1982) also occurs on a *Macroneuropteris* pinnule from the same time period (Westphalian D–Moscovian) as the Mazon Creek specimens.

***Diplichnites* Dawson, 1873**

DIAGNOSIS—Simple trackways of two parallel rows of blunt, circular, or elongate tracks of appendage imprints, closely and regularly spaced (after Buatois et al., 1998; Pollard et al., 2008).

Diplichnites isp.

Figure 12A–D

FMNH SPECIMEN—PE 52249 (a, b) – 3 specimens

DESCRIPTION—Three specimens preserved poorly in concave epirelief on the surface of gray shale. Two straight trackways, one curved. Widths ~ 2 mm, lengths 12.5, 26.5, and 30.5 mm. Parallel trackways with alternating circular imprints; imprints may include a slight furrow oblique to trackway orientation. Ridges of similar morphology preserved anterior to individual imprints. The two longer specimens are preserved on a separate piece of crossbedded shale (PE 52249b). The longest trackway is curved and is crossed over by the second longest trackway.

DISCUSSION—The shortest specimen of *Diplichnites* (PE 52249a) is associated with a *Skolithos* 2.1 mm in diameter, although the two are separated by ~ 10 mm (Fig. 12A). The curved specimen (PE 52249b) appears to also be associated with a *Skolithos*-

like structure connected at one end of the trail (Fig. 12C). The *Skolithos*-like structure is too poorly preserved, however, for accurate trace identification and determination of its association with *Diplichnites*. The widths of the specimens are, however, approximately the same as the diameters of the *Skolithos* specimens, suggesting that the two traces may be related to the same tracemaker.

Dawson (1873) interpreted *Diplichnites* as formed by worms or crustaceans. *Diplichnites* has since been interpreted as an arthropod trackway (Buatois et al., 1998; Smith et al., 2003; Pollard et al., 2008). Crimes (1970) and Gevers et al. (1971) interpreted the tracemakers to be trilobites based on associations with *Cruziana* from the Upper Cambrian. Gevers et al. (1971), however, adopted the ichnogenus *Arthropodichnus* for these types of trackways, which was later ascribed to *Diplichnites* by Bradshaw (1981) and endorsed by Buatois et al. (1998). Recent studies of Carboniferous specimens suggest the tracemakers to be myriapods (Briggs et al., 1984; Buatois et al., 1998; Pollard et al., 2008). Smith et al. (2003), additionally, interpreted the tracemakers to be myriapods from Early Devonian specimens. Morphologically, however, the same type of trackway can be produced by different tracemakers.

***Diplocraterion* Torell, 1870**

DIAGNOSIS—Vertical, U-shaped burrow with spreiten (after Fürsich, 1974b).

Diplocraterion parallelum Torell, 1870

Figure 13B–F

FMNH SPECIMENS—PE 29935, PE 30064, PE 30239, PE 30242, PE 31823, PE 31827, PE 31832, PE 31833, PE 31842, PE 31855, PE 31856, PE 31859, PE 31862, PE 31865, PE 42924, PE 44403, PE 46795, PE 46799, PE 51650

DESCRIPTION—Generally symmetrical, vertical, smooth-walled, U-shaped burrows with apparent spreiten, preserved entirely or, in part, within concretions. Burrow openings often observable on top surface of concretion in concave epirelief. Diameter of openings ranges from 2.8–4.7 mm, averaging 3.7 mm; the distance between openings ranges from 5.7–17 mm, averaging 9.56 mm; and spreite ~ 1 mm thick. One large form has elliptical burrow openings ~ 9.5 x 12 mm diameter and thicker spreite 4.5 mm wide. Where measurable, the burrow length from the opening to U-axis ranges from ~ 15–30 mm.

DISCUSSION—PE 29935–46799 were collected at Pit 11. PE 51650 is specified from MCA. Specimens of *Diplocraterion parallelum* are preserved in the same manner as *A. variabilis* (Figs. 13A–B), and have the same general size range with few exceptions. *Diplocraterion* is interpreted as dwelling burrows of suspension feeders (Fürsich, 1974b). The primary difference between the *Diplocraterion* and *Arenicolites* specimens is the presence of spreiten associated with *Diplocraterion*. The spreiten are apparent on the concretion surface and the classic dumb-bell shape is observable. The larger form (PE 42924; Fig. 13F) is incomplete as only the dumb-bell form is visible within the concretion. This specimen differs from the previous *Diplocraterion* specimens in that the burrows are more elliptical and the spreite is considerably thicker with respect to burrow thickness. PE 42924 also does not appear to be three-dimensionally preserved like the other specimens.

***Gyrophyllites* Glocker, 1841**

DIAGNOSIS—Several levels of short, lobate feeding tunnels radiating from central vertical shaft (after Fürsich, 1974b).

Gyrophyllites isp. Glocker, 1841

Figure 14E–F

FMNH SPECIMEN—PE 40093

DESCRIPTION—Star-like trace with lobate structures radiating from circular central structure 7 mm in diameter, preserved in convex epirelief on surface of concretion. Circular structure has smaller, centralized shaft ~ 3 mm in diameter preserved through the concretion. Preserved shaft length is 14.5 mm. Lobate structures radiate and widen outward from central shaft. Lobes measure from 3–10 mm long.

DISCUSSION—*Gyrophyllites* is interpreted as a three-dimensional feeding system (Fürsich, 1974b; Fürsich and Kennedy, 1975), with the lobate structures as the feeding tunnels (Fürsich, 1974b). This specimen collected from Pit 11 is incomplete with two larger lobes and a few smaller incomplete lobes. Fürsich and Kennedy (1975) describe *Gyrophyllites* as having several cycles or tiers of lobes. PE 40093 represents one tier preserved with the shaft that would presumably lead to the next tier. The shaft is visible on the bottom surface of the concretion, but lacking any feeding structures (Fig. 14F). *Gyrophyllites* is distinguished from *Asterosoma* by its apparent central plug or shaft (Fürsich, 1974).

***Monocraterion* Torell, 1870**

DIAGNOSIS—Funnel-shaped burrow with centrally located, straight or slightly curved plugged tube, vertical to bedding (after Torell, 1870).

Monocraterion isp.

Figure 14A–C

FMNH SPECIMEN—PE 42655

DESCRIPTION—Hollowed out, funnel-shaped burrow within an elliptical concretion preserved in full relief horizontal to bedding. Only the top portion of burrow is preserved with total thickness of 19.4 mm. Concretion diameters 39.5 x 46.2 mm, with a well-rounded base 26 mm in diameter. Funnel diameters at widest portion 21.5 x 26.5 mm; burrow diameter at bottom of concretion 5.0 x 6.8 mm. Burrow becomes more rounded with depth.

DISCUSSION—*Monocraterion* has been interpreted as a dwelling burrow, which was later filled in when no longer in use (Crimes et al., 1977). The fill that would normally plug the tube has been weathered out of this specimen. Only the top portion of a single, incomplete specimen is preserved, therefore, the length or depth of the burrow is not measurable. *Monocraterion* has been described as being commonly associated with *Skolithos* (Crimes et al., 1977; Pienkowski, 1985), and also within other Carboniferous deltaic deposits (Eager et al., 1985; Chakraborty and Bhattacharya, 2005).

***Pennatulites* De Stefani, 1885**

DIAGNOSIS—Compact, branching, tubular structure with straight to curved, subcylindrical nodose branches (after De Stefani, 1885; D’Alessandro, 1982).

Pennatulites nodosus ichnospecies novum

Figure 15A–F

FMNH SPECIMENS—PE 23477, PE 51092

HOLOTYPE— PE 23477

TYPE LOCALITY—Pit 11, Mazon Creek area, Francis Creek Shale Member, Carbondale Formation, Peabody Coal Company, Will County, north-central Illinois.

ETYMOLOGY—*Nodosus*, Latin for knotty; refers to knotty appearance and abundance of nodes on burrow surface.

DESCRIPTION—Straight to slightly curved, cylindrical to oval, lined, branched burrows with medial ridge preserved in full relief parallel to bedding. Burrows originate from a central region and subsequently branch outward in a Y-pattern. Burrows are generally adjacent but may cross under or over other branches. Diameters of individual burrows range from 10–15 mm. Lining is ~ 1 mm thick and its lining surface is covered with parallel rows of nodes, each ~ 0.1 mm diameter. Nodes are generally evenly spaced by ~ 0.1 mm. There are ~ 25 nodes per 2 mm². Nodes are preserved in biserially arranged packets ~ 2–3 mm thick along a median ridge.

DISCUSSION—Very little literature exists regarding the ichnogenus *Pennatulites*. *Pennatulites* is interpreted as a feeding trace (Seilacher, 1955b). The type ichnospecies is *Pennatulites longespicata* (Stefani, 1885). Specimen PE 23477, collected from Pit 11, is similar to *P. longespicata* in morphology and the presence of the nodes.

This specimen, however, has notable differences compared to *P. longespicata*. The nodes in *P. longespicata* are biserially arranged in single rows along the median furrow. The nodes of PE 23477 are smaller, more densely spaced, and are nonuniformly arranged in packets ~ 2–3 mm thick along a median ridge (Fig. 15B). A few of the nodes on this specimen may be up to three times larger. This specimen is preserved also with a cluster of *Bactryllium* isp. (Fig. 15C) and a small possible worm tube (Fig. 15D).

A second specimen collected from MCA—PE 51092—is much smaller, incomplete, and preserved poorly (Fig. 15E–F). The lining is evident, but the nodes have been completely weathered away, with the exception of one possible node preserved on the outer edge of the concretion—adjacent to a cross-sectional view of a burrow (Fig. 15F).

D’Alessandro (1982) proposed the new ichnospecies *P. corrugata* for specimens described from the Miocene of Italy. His figured specimens, however, are unbranched and appear to have more of a meniscate-type backfill, suggesting a different ichnogenus.

***Phagophytichnus* Van Amerom, 1966**

DIAGNOSIS—Semicircular excision cut into leaf edge that exhibits a thickened reaction rim (after Van Amerom, 1971).

***Phagophytichnus ekowskii* Van Amerom, 1966**

Figure 16A–F

FMNH SPECIMENS—P 18649, P 30741, P 31305, PE 52269, PE 52272, PE 52280, PE 52281, PE 52284, PE 52286, PP 1954, PP 4299, PP 11767, PP 20389, PP

20469, PP 24268, PP 24269, PP 26083, PP 26144, PP 26518, PP 28339, PP 30767, PP 31243, PP 31251, PP 31745, PP 35718, PP 36095, PP 36424, PP 38276, UP 47

KU SPECIMENS—P-1 25, P1143

DESCRIPTION—Crescentic to U-shaped excisions on pinnule margins.

Excisions rarely reach midrib. Widths of excisions on leaf margins range from 7.5–26 mm. Total lengths range from ~ 20–54 mm. Reaction rims, when apparent, are ~ 1 mm thick, kaolinitic, and follow the shape of the excision.

DISCUSSION—The holotype for *Phagophytichnus ekowskii* was first described occurring on *Neuropteris* leaves from the Permo-Carboniferous of Spain (Van Amerom, 1966). Van Amerom (1971) described specimens from the Permo-Carboniferous of South Africa that also occurred on pteridosperm leaves. The earliest evidence of *P. ekowskii* occurs on pteridosperms and has been dated to the Late Mississippian of Australia (Iannuzzi and Labandeira, 2008). The KU specimens and all FMNH specimens in this study except two occur on the pteridosperm *Macroneuropteris scheuchzeri*. FMNH specimen PP 28339 occurs on *M. macrophylla*, and FMNH specimen PP11767 occurs on *Neuropteris evenii*. *Phagophytichnus ekowskii* is attributed to insect feeding or bite marks (Scott and Taylor, 1983; Labandeira, 1998). Evidence from the fossil record indicates a dietary preference for pteridosperms.

Scott and Taylor (1983) and Scott et al. (1992) previously described specimens PP 4299, PP 11767, PP 24268, and PP 30767. Specimen PP 24268, as figured by Scott and Taylor (1983), Scott et al. (1992), and Stephenson and Scott (1992), shows the half of the concretion with the leaf impression. The impression and the figures show a large excision and a smaller excision just above the larger. The second half of the concretion

containing the internal mold shows that only the larger excision is real, as the smaller structure is an invaginated surface (Fig. 16C). This relationship causes the smaller structure to appear to be an excision when in fact it is a preservational artifact (Fig. 16B).

***Planolites* Nicholson, 1873**

DIAGNOSIS—Horizontal, straight to winding, smooth or ornamented, unlined, rarely branched, circular to elliptical burrow with structureless infill (after Gluszek, 1995).

Planolites beverleyensis Billings, 1862

Figure 6F, 17A–E

FMNH SPECIMENS—PE 13044, PE 21584, PE 21585, PE 21578, PE 23699, PE 24509, PE 30349, PE 36864, PE 36867, PE 36868, PE 36870, PE 36874, PE 36875, PE 39784, PE 39823 – 2 specimens, PE 39857, PE 43127, PE 43837, PE 44090, PE 44262, PE 44355, PE 44362, PE 44631, PE 46666, PE 47459, PE 49618, PE 50126–50128, PE 51033, PE 51042, PE 51495, PE 51496, PE 51503, PE 51506, PE 51508, PE 51520, PE 51524, PE 51528, PE 51561, PE 51578, PE 51654

KU SPECIMENS—KUMIP 320211–KUMIP 320222

DESCRIPTION—Straight to slightly curved, infilled, generally smooth, unlined burrows parallel to bedding. Generally preserved within concretions in full relief or convex epirelief, but also rarely preserved in concave epirelief within concretion or in convex epirelief on concretion surface. May also be preserved as compressed specimens with no apparent relief. Diameters range from 1–11 mm, averaging 5 mm, measured

along long axis if elliptical, with the exception of specimens occurring within concretions PE 49618 and PE 50126–50128 having diameter 0.5 mm. Lengths range from 14.5–63.1 mm, averaging 42.3 mm.

DISCUSSION—*Planolites* is interpreted as a worm feeding burrow, produced as a worm passes the sediment through its alimentary canal (Nicholson, 1873; Gluszek, 1995). *Planolites beverleyensis* differs from *P. annularis* by its lack of annulations, and from *P. montanus* by lacking sinuosity and an undulose nature (Pemberton and Frey, 1982). Specimens within concretions are preserved individually, and often in three dimensions; elliptical to circular in cross-section. Lengths of burrows were measured based on the visible portion within the concretion. The full length of few specimens were not measurable as a result of how the concretion split, leaving a portion of the burrow hidden (Fig. 17A), or the burrow may have been preserved partially during the formation of the concretion around only part of the trace (Figs. 17B and E). Specimens were collected from either Pit 11 or MCA.

PE 49618 and PE 50126–50128 were collected from Pit 11. The specimens within these four relatively thin concretions (< 15 mm thick) are poorly preserved, not visibly apparent, and reveal little detail. Close examination, however, reveals several small *Planolites*-like structures (Fig. 17D). PE 51033 is preserved with a specimen of *Skolithos*. Specimen PE 51578 was placed in with the *Arenicolites*–*Skolithos* specimens in the FMNH collection. The bedding planes are well preserved in the concretion showing a horizontal orientation of the trace. PE 51564 is preserved with an *Arenicolites*; *Arenicolites* is visible in plan view (Fig. 6E), whereas *Planolites* is visible in cross-

section (Fig. 6F). There are several additional compressed specimens in the FMNH and KU collections that were not included in this study.

cf. *Planolites* isp.

Figure 16G

FMNH SPECIMENS—P 30705, PP 2104, PP 4470, PP 4471, PP 4479, PP 8459, PP 26018, PP 26064, PP 26135, PP 31502, PP 31965, PP 31991

DESCRIPTION—Straight, structureless burrows preserved in convex epirelief parallel to bedding. Widths range from 0.5–2 mm and lengths vary from ~ 15–65 mm; measurements not made for all specimens. Specimens may overcross.

DISCUSSION—Specimens occur as one or more burrows in association with *Macroneuropteris* pinnules (Fig. 16G). The specimens are preserved as convex epirelief in the same manner as *Cochlichnus*, resulting from the organism moving underneath the leaf after it settled on the surface of the media. Several specimens may extend beyond the edge of the pinnule, where it loses most of its apparent relief. A few of these and other similar structures associated with *Macroneuropteris* pinnules may be physical deformation structures from being compressed onto other objects before preservation. Since the burrows are preserved as leaf compressions, no internal structure can be observed to make accurate identification of the traces.

***Protovirgularia* M’Coy, 1850**

DIAGNOSIS—Horizontal, straight to slightly curved, bilobate trail with biserial chevron-like ribs and narrow median ridge (after Han and Pickerill, 1994; Balistieri et al., 2002).

Protovirgularia dichotoma M'Coy, 1850

Figure 14D

FMNH SPECIMEN—PE 22022

DESCRIPTION—Straight to slightly curved, dichotomously branching, keel-like trail parallel to bedding. Trail resembles chevron pattern, or row of Vs. Width of trail ranges from 3.5 to 4.5 mm. Length is 84.7 mm. Single specimen preserved as part-counterpart within concretion. One half preserved as convex epirelief, the other concave epirelief.

DISCUSSION—Ichnotaxonomic determination was based on the reassessment of *Protovirgularia* by Han and Pickerill (1994). This specimen from Pit 11 closely follows one of the several patterns represented by Han and Pickerill (1994; fig. 2.5) as belonging to *Protovirgularia dichotoma*. *Protovirgularia* is suggested to be a bivalve locomotion trace produced by the anchoring of the cleft foot into the sediment to propel the animal (Seilacher and Seilacher, 1994; Uchman and Gaździcki, 2006). There are approximately two dozen bivalve species that have been identified from MCA that could have been the possible tracemaker. *Protovirgularia* has been described from several other Carboniferous deposits including Union Chapel Mine, Alabama (Lucas and Lerner, 2005), tidal-flat deposits of eastern Kansas (Mángano et al., 1998), and from rhythmites in Mafra, Brazil (Balistieri et al., 2002).

***Rhizocorallium* Zenker, 1836**

DIAGNOSIS—Straight, U-shaped burrow with spreite, preserved parallel or oblique to bedding (after Fürsich, 1974a).

Rhizocorallium jenense Zenker, 1836

Figure 19A–B

FMNH SPECIMEN—PE 50901

DESCRIPTION—Unlined, U-shaped burrow with spreiten structures, formed oblique to bedding. Preserved in full relief as a concretion with abundant organic debris. Tubes are slightly ovate measuring 10 x 14 mm diameter. The tubes are offset ~ 5–6 mm from the same bedding plane. Distance between limbs is 14 mm. Length from end of tubes to axis is 58.5 mm. Spreiten apparent but not prominent.

DISCUSSION—Ichnospecies determination is based on revision of *Rhizocorallium* by Fürsich (1974a). *Rhizocorallium jenense* differs from *R. irregulare* and *R. uliarensis* by its lack of sinuosity or spiral morphology. Specimens similar in appearance and dimension have been described from the Caseyville Formation (Early Pennsylvanian) of southern Illinois (Fraunfelter, 1986). PE 50901 has one tube that shallowed upward at a steeper angle (~ 25° from horizontal) than the other (~ 15°) as the burrow was lengthened. Organic debris is observable on bedding planes (Fig. 19B). *Rhizocorallium* is generally interpreted as a deposit-feeding trace of crustaceans (Fürsich, 1974a).

***Skolithos* Haldemann, 1840**

DIAGNOSIS—Straight to slightly curved, singular, cylindrical to subcylindrical, unbranched, lined or unlined, vertical to subvertical burrow (after Fürsich, 1974b; Alpert, 1974).

Skolithos isp. Type A

Figure 18A

FMNH SPECIMENS—PE 30064 – 3 specimens, PE 30066–30068, PE 31867, PE 31869, PE 31870, PE 31872, PE 31873, PE 44976, PE 44977, PE 46798, PE 51550–51575, PE 51577, PE 51579, PE 51581–51585, PE 51587–51590, PE 51592, PE 51594–51617, PE 51621–51624, PE 51629, PE 51634

DESCRIPTION—Vertical unlined burrows visible in plan view on surface of concretion in concave epirelief. Diameter ranges from 2.5–5.4 mm, averaging 3.6 mm. Preservation limits depth measurement.

DISCUSSION—PE 30064–46798 were collected from Pit 11. The remaining specimens were specified from MCA. These specimens are preserved individually (Fig. 18A), and may actually be one burrow opening of an *Arenicolites* (Fig. 18C). Since only one tube is preserved and only visible on the surface, they are placed under the ichnogenus *Skolithos*. One specimen of *Arenicolites* (PE 51586), for example, has only one hole preserved, although the second hole is apparent on the edge of the concretion. Specimens PE 51591, PE 51619, PE 51634 and PE 51652 are currently included in the FMNH collection, but have no visible traces.

Skolithos isp. Type B

Figure 18B, 18D–F

FMNH SPECIMENS—PE 42653, PE 47680, PE 51033, PE 51655, PE 52249

DESCRIPTION—Cylindrical, vertical unlined burrows preserved within concretions, except PE 52249 preserved in small slab of gray shale. Specimens are incomplete and lengths of burrows not fully preserved. Diameters vary among specimens: PE 42653 – 4.5–5.7 mm; PE 47680 – 5–6 mm; PE 51033 – 3.8–4.2 mm, PE 51655 – 9.6–11.3 mm, PE 52249 – 2.1 mm.

DISCUSSION—Ichnospecies determination is difficult due to the incompleteness of the specimens. Specimens are preserved individually. Specimen PE 51033, however, is associated with a *Planolites* specimen 2.7 mm in diameter preserved within the concretion. The burrow fill of specimens PE 47680 (Pit 11) and PE 51655 is visually coarser than surrounding concretion material (Figs. 18B and D). Specimens PE 42653, PE 51033, and PE 51655 were collected from the MCA. Specimen PE 52249 (Pit 6) is associated with the crawling trail *Diplichnites* (Fig. 12A).

***Taenidium* Heer, 1877**

DIAGNOSIS—Horizontal, straight to sinuous, unlined and unbranched, cylindrical burrow with meniscate or segmented infill (after D’Alessandro and Bromley, 1987).

Taenidium satanassi D’Alessandro and Bromley, 1987

Figure 19C–D

FMNH SPECIMEN—51093

DESCRIPTION—Horizontal burrows with weakly arcuate, pelleted meniscate of equal thickness ~ 1 mm. Diameter ~ 3.5 mm. Highly weathered incomplete specimen. Preserved in full relief on surface of concretion. May have radiating branching pattern.

DISCUSSION—*Taenidium satanassi* is distinguished from other *Taenidium* forms by its distinct pelleted meniscate packets. This specimen is highly weathered, but the pelleted characteristic is still evident. The sediment packets do not appear to alternate between two types of sediment, as part of the original diagnosis (D'Alessandro and Bromley, 1987). This may be a result of diagenesis or concretion formation. The burrows are generally incomplete, and few of the sediment packets appear disturbed. One burrow becomes narrow at the end, and the menisci become more angled with respect to the burrow margins. This could be a preservational relic, or perhaps where the organism left the burrow.

The burrows appear to radiate from a central location. Poor preservation, however, does not allow for observational certainty. Heer (1877) designated the radiating type as *T. fischeri*. After review of the ichnogenus *Taenidium*, D'Alessandro and Bromley (1987) removed branching meniscate burrows from *Taenidium* and proposed the new ichnogenus *Cladichnus* for this type of radiating meniscate burrow system.

***Thalassinoides* Ehrenberg, 1944**

DIAGNOSIS—Cylindrical to elliptical, three-dimensional, branching burrow network with T- or Y-shaped branch junctions (after Myrow, 1995).

Thalassinoides isp.

Figure 19E–F

FMNH SPECIMENS—PE 45083, PE 51095

DESCRIPTION—Unlined, incomplete burrows preserved in convex epirelief parallel to bedding on surface of concretions. Specimens may be branched in a T- or Y-shape, or preserved as individual segments. Widths range from 3–11.5 mm. Lengths range from 10–52.3 mm. The burrows are no longer cylindrical owing to compaction. A burrow wall or lining is not apparent. Bedding planes are, however, well preserved within concretions to determine orientation. The burrows may cross, and may appear enlarged at branch transitions.

DISCUSSION—The poor preservation and incompleteness of the specimens from Pit 11 makes a determination at the ichnospecies level difficult. The specimens being horizontal suggest they could be *T. suevicus*. A couple of the branches, however, appear to be of a different diameter than their main trunk suggesting it could be *T. paradoxicus* (Howard and Frey, 1984). *Thalassinoides* is produced commonly by crustaceans (e.g., Frey et al., 1984, Myrow, 1995). *Thalassinoides* is typically interpreted as dwelling or feeding burrows of shrimp and shrimp-like animals (Howard and Frey, 1984). Abundant fossil shrimp have been discovered at Mazon Creek that could possibly be the trace makers. Considering the abundance of shrimp collected at this locality and the rare occurrence of *Thalassinoides*, there may be more burrow systems in outcrop or in concretions that have yet to be discovered, or the burrow systems were destroyed upon compaction and diagenesis. PE 51095 is associated with the coprolites *Bactryllium* isp. and *Funiculichnus spiralis* nov. igen. nov. isp.

Bivalve trails

Figure 17F

FMNH SPECIMEN—PE 12302

DESCRIPTION—Bivalve at the end of *Planolites*-like trail or burrow preserved within a concretion. Slightly curving trail 6.5 mm wide x 71 mm long. The bivalve is elliptical, measuring ~ 9 x 13 mm. Elliptical portion of trace surrounding bivalve extends ~ 3 mm adjacent to the bivalve.

DISCUSSION—The trail is preserved similarly to the compressed specimens of *Planolites beverleyensis* in which some of the fill has been altered to kaolinite. The compressed *Planolites* specimens are, therefore, possibly an unnamed ichnotaxon of a bivalve trail. The extension of the trace around the bivalve indicates lateral movement, possibly upon burial. Poor preservation does not allow for accurate identification of the bivalve. This specimen, however, is most likely a solemyid bivalve as several specimens of solemyid bivalves have been preserved in the same manner as PE 12302 (Bailey and Sroka, 1997; Selden and Nudds, 2004).

Coprolites

***Bactryllium* Heer, 1853**

DIAGNOSIS—Small, subcylindrical or prismatic bodies with one to two longitudinal furrows, may be smooth or with striations, or transversely oblique ridges; internal cavity absent; 0.3–1.5 mm wide, 1–4 mm long (after Allasinaz, 1968).

Bactryllium isp.

Figures 15C, 20A–B

FMNH SPECIMENS—PE 23477, PE 40083, PE 51095

DESCRIPTION—Smooth cylindrical, aligned bodies with rounded ends preserved in convex epirelief that may display one or two longitudinal furrows. Three orders of size: 0.25 mm diameter x 0.5 mm long; 0.5 x 1 mm; 1 x 2 mm. Found in circular or linear clusters of similar-size specimens.

DISCUSSION—*Bactryllium* isp. specimens occur in association with *Funiculichnus spiralis* nov. igen. nov. isp., *Pennatulites nodosus* nov. isp., and *Thalassinoides* isp. The smallest specimens occur in association with the newly described coprolites *Funiculichnus spiralis* nov. isp. (PE 40083; Fig. 20A). The second-order specimens occur associated with the Y-branching form of *Thalassinoides* isp. (PE 51095; Fig. 20B). The largest specimens occur as a cluster crosscutting the surface of the main limb of *Pennatulites nodosus* nov. isp. (PE 23477; Fig. 15C). The longitudinal furrows are apparent on only the large forms. The large forms most closely resemble *B. canaliculatum* as it is distinguished from other forms by having an unornamented surface, and a principal medial furrow (Allasinaz, 1968). In all three size orders, the length is twice the diameter. The alignment of the *Bactryllium* specimens likely indicates a direction parallel to the locomotion of the tracemaker.

***Funiculichnus* ichnogenus novum**

ETYMOLOGY—*Funiculus*, Latin for string; more commonly used in reference to a spinal nerve cord composed of several nerve strands; *-ichnus*, latinized Greek term for trace – *iknos*.

DIAGNOSIS—Long, slender, sinuous string-like form that may crossover itself. Individual forms made up of several strands twisted together around the longitudinal axis. Three orders of diameter: up to 0.5 mm, 0.8–1.3 mm, 1.7–2.4 mm; lengths from 10–80 mm or more. Fecal in origin.

Funiculichnus spiralis ichnospecies novum

Figures 21–22

FMNH SPECIMENS—PE 29177, PE 40081, PE 40083, PE 40084, cf. PE 40087, PE 40091, PE 40098–40100, PE 45750, PE 51095

HOLOTYPE—PE 40083

TYPE LOCALITY—Pit 11, Mazon Creek area, Francis Creek Shale Member, Carbondale Formation, north-central Illinois.

ETYMOLOGY—*Spiralis*, Latin for spiral; refers to the spiraling nature of fecal strands twisted together.

DESCRIPTION—Specimens preserved in convex epirelief on surfaces of concretions. Three orders of size: First order—diameters up to 0.5 mm; lengths up to 10 mm; second order—diameter 0.8–1.3 mm; lengths up to 80 mm or more; third order—diameter 1.7–2.4 mm; lengths up to 40 mm or more. Lengths from 20–60x the diameter. First-order specimens are small, simple arcuate forms with no macrostructures. Second-order specimens show strands twisted together in rope-like fashion around longitudinal axis (Fig. 22E–F). Second-order specimens may crossover themselves (Fig. 22A), and portions may be hidden within the concretion (Fig. 22B). Third-order specimens have no apparent strands, but may have one or more longitudinal ridges.

DISCUSSION—The concretions were collected at Pit 11, with the exception of PE 45750 designated from MCA. Third-order specimens are the most common occurring on all concretions except PE 51095. Only second-order specimens occur on PE 51095, and are associated with the Y-branching form of *Thalassinoides* isp. and *Bacryllium* isp. Second-order specimens also occur on concretions PE 40083 and PE 40098, along with *Bacryllium* isp. as well as first-order specimens. First-order specimens may also occur on other concretions, but were not observed. Third-order specimens on concretions PE 40099–40100 occur associated with *Chondrites intricatus*.

First-order specimens are small and arcuate, and reveal no apparent structure (Fig. 21B). Observation with a microscope reveals possible fecal strand-like structures, but strands are not evident. Second-order specimens reveal apparent fecal strands. Several specimens appear to have uniformly arranged pellets, but are likely strands crosscut by weathering (Fig. 22C–D). Strands of the second-order specimens may be discontinuous. Second-order specimens are longest with respect to diameter. Third-order specimens lack any visible fecal strands, but generally have one or more longitudinal ridges that do not appear to twist around the specimen like the second-order fecal strands (Fig. 21C).

In comparison with other coprolites, the specimens described here are most similar to *Tomaculum problematicum*. Groom, 1902. *Tomaculum* are long, straight to slightly curving strands up to 2 cm wide, composed of clusters of fecal pellets. *Tomaculum* may bend at sharp angles (Eiserhardt, 2001). The fecal pellets may or may not show preferred orientation. The lengths of *Tomaculum* are approximately 5 to 10 times the diameter, approaching 100 mm. The Mazon Creek specimens are arcuate to highly sinuous, consisting of long fecal strands, twisted together in a rope- or twine-like

fashion (Fig. 22E–F). Pellets may be apparent, but the pellet-like nature is likely preservational crosscutting through the specimens (Fig. 22C–D). The observed maximum lengths of the Mazon Creek and *Tomaculum* specimens are similar for the longer specimens. The Mazon Creek specimens, however, are proportionately much longer with respect to their diameters. The length of the Mazon Creek specimens ranges from up to 20x the diameter or more in first and third order specimens, and up to 60x the diameter or more in second-order specimens.

The rope-like fecal strands of the second-order specimens indicate a different manner of fecal expulsion than is required for fecal pellet formation. For this reason, and the obvious morphological differences, the new ichnogenus and ichnospecies *Funiculichnus spiralis* is proposed. The lack of observable structure in the first-order specimens may indicate a different ichnospecies than second-order specimens. The lack of fecal strands and the presence of the ridge in the third-order specimens may likewise indicate a different ichnospecies. Thin sections may be necessary to determine the internal structure of the first and third order specimens to conclude if all three orders are the same ichnospecies.

COMMON COPROLITES—Common coprolites are defined as undifferentiated masses with no identifiable morphology, generally shaped as an oblate spheroid (Shabica and Godfrey, 1997). Specimen PE 36872, originally identified as a trail, is an irregularly shaped, amorphous mass with no apparent relief (Fig. 20C). The trace contains abundant kaolinite, and also pyrite or chalcopyrite in lesser quantities. The sediment that comprises the trace fossil appears to contain pellets and to be coarser than the surrounding

concretion material. The kaolinite occasionally appears to have a fenestral pattern (Fig. 20D); possibly the result of the infilling of the pore spaces within the pellets. The FMNH and KU collections contain abundant common coprolites, as well as spiral coprolites, which are not included in this study. Mazon Creek coprolites have been studied previously by Zangerl and Richardson (1963), Richardson and Johnson (1969), and Shabica and Godfrey (1997). An exhaustive study of Mazon Creek coprolites, however, has yet to be conducted.

Galls

Figure 23

FMNH SPECIMENS—PP 54655, PP 54656

DESCRIPTION—PP54655—centrally located depression ~ 3 mm in diameter on the internal leaf mold of *Macroneuropteris* pinnule. PP 54656—external structure: rust-colored, amorphous structure, centrally located on the internal leaf mold of *Macroneuropteris* pinnule, and ~ 1.75 mm diameter circular, reddish structure with dark gray halo on the opposite half. Gray halo extends from top-right portion of circular structure, following shape of amorphous structure on opposite concretion half. Halo is ~ 1 mm thick on left side of reddish structure, and ~ 0.3 mm thick on right. Structures obscure visibility of venations; midrib only slightly visible. Internal structure – two dark-red circular structures 0.15 mm diameter, with green halos 0.05 mm thick, within larger reddish structure. Small structures appear to have central nuclei. Second, poorly preserved, gall-like structure preserved near base of pinnule; no apparent internal structure.

DISCUSSION—The depression on PP 54655 is filled with kaolinite, although the venations are still visible. The depression may just be the result of physical deformation prior to preservation. Both specimens on PP 54656 have a reddish internal structure with a dark halo (Fig. 23D and G). The dark halos of the likely gall specimens are possibly a modified nutritive layer produced in response to an invasive parasite (Scott et al., 1992; Labandeira and Phillips, 1996). The internal circular structures (Fig. 23E) may be eggs lain within the host plant tissue by a female arthropod (Scott et al., 1992). Within the gall structure is also evidence of cuticle damage (Fig. 23E).

The earliest reported occurrence of fossil insect galls is ~ 302 Ma from the Late Pennsylvanian Early Kasimovian Stage (Labandeira and Phillips, 1996). If this specimen represents a gall, then it would push back the earliest gall evidence to the Moscovian Stage (Westphalian D) of the Middle Pennsylvanian at ~ 311 Ma. Although there is strong visible evidence, histological data (e.g. thin sections) is still needed for gall confirmation. Van Amerom (1973) described the ichnogenus *Acrobullillites* as a probable gall from Middle Pennsylvanian horsetails of Europe. Labandeira (1998) noted Van Amerom's research (1973) also requires histological confirmation.

Miscellania

Several specimens in the FMNH collections were misidentified as trace fossils. Specimens are reinterpreted as soft-sediment deformation structures, wrinkled textures on *Macroneuropteris* pinnules, *Calamites*, body fossils of jellyfish and worms, and a possible cololite.

Soft-Sediment Deformation Structures

Figure 24A–C

FMNH SPECIMENS—PE 44632, PE 50982, PE 51043, PE 51045, PE 51046

DISCUSSION—PE 44632, collected from Pit 11, has a dendritic or feather-like pattern resembling that of the pseudofossil *Dendrophycus* Lesquereux, 1884. The specimen is ~ 80 mm long and 20 mm wide and lacks the medial ridge present in specimens described by Lesquereux (1884) and Boyd (1963) (Fig. 24A). *Dendrophycus* has been interpreted as surge marks formed from a standing body of water being agitated by strong surging currents resulting from the temporary damming of a flash-flooding event (High, 1968). Specimen PE 50982 from Pit 11 has grooves running lengthwise along the specimen that typically branch distally (Fig. 24B). The specimen resembles the pseudofossil *Neantia* Lebesconte, 1887, which has been interpreted to be ripple or rill marks (Cloud, Jr., 1968). The remaining specimens from MCA are three clusters of oblong to amorphous masses oriented parallel or subparallel to bedding (Fig. 24C). The dimensions of the individual, structureless masses vary. All five specimens are preserved as concretions in a softer, lighter gray, finer grained material that differs from that of most concretions. Laminations can be seen within the bottom concretion layer of PE 44632 and PE 50982. The lighter color of these specimens suggests a more anoxic environment at the time of deposition.

Wrinkled Textures (on Macroneuropteris)

Figure 25B

FMNH SPECIMENS—P 30716, P 31167, P 31210, PP 2887, PP 4546

DISCUSSION—These four specimens of *Macroneuropteris* have a wrinkled texture with the appearance of a multiple crosscutting trails ~ 0.5 mm in diameter, preserved parallel to bedding in concave epirelief with respect to the pinnules. The structures do not resemble any known trace fossils, and are more than likely some type of physical deformation that occurred before or during preservation. These specimens had been prepared and have a shiny luster, eliminating some of the observable structural details.

Body Fossils

Figures 6D, 24D–F, 25A, 25C–D

FMNH SPECIMENS— PE 12450, PE 21580, PE 21581, PE 31046, PE 32749, PE 40071, PE 43654, PE 45754 PE 51534, PE 51653, PE 51657, PE 51785

CALAMITES—Specimen PE 43654 is a portion of a stem belonging to the genus *Calamites* Brongniart, 1828 (Fig. 25A). This stem is 83.5 mm long and ranges in width from 11.5–21.9 mm. This specimen was originally identified as a burrow when catalogued for the FMNH collection. Closer examination reveals nodes and longitudinal striations typical of *Calamites*. This specimen most closely resembles the species *C. cistii* Brongniart, 1828, as figured by Charbonnier et al. (2008; fig. 4A).

JELLYFISH—Specimen PE 45754 is the cnidarian *Essexella asherae* Foster, 1979. Specimens PE 21580 and PE 21581 (Fig. 24E) have several short, irregularly curved fossils that appear to be tentacles from the cnidarian *Anthracomédusa turnbulli* Johnson

and Richardson, 1968. These specimens are most comparable to that of a specimen figured by Selden and Nudds, 2004 (Fig. 24D). The preservation of these tentacles likely resulted from a predatory animal's feeding on the jellyfish but not consuming several of the tentacles, leaving them to settle onto the seafloor and subsequently being preserved.

WORMS—PE 51785 is poorly preserved, yet there is apparent segmentation. This specimen is preserved oblique to bedding suggesting this specimen is most likely the annelid worm *Didontogaster cordylina*. PE 31046, PE 32749, PE 51653 and PE 51657 are various forms of polychaete worms preserved too poorly for species identification. Specimen PE 40071 is a nonannelid worm as it is unsegmented and lacks any locomotory appendages (Fitzhugh et al., 1997). This specimen most closely resembles the chaetognath *Paucijaculum samamithion* Schram, 1973, or the nematode *Nemavermes mackeei* Schram, 1973. Specimen PE 51534 is the enteropneust, or acorn worm, *Mazoglossus ramsdelli* Bardack, 1997 (Fig. 24F). Body-fossil identification was conducted by observation and comparison with similar fossils and images within the literature.

COLOLITE—PE 12450 is a single specimen, preserved within a thin, light gray concretion, parallel to bedding with little or no apparent relief. The specimen bends three times at nearly right angles with rounded corners (Fig. 25C). The width ranges between 5 and 8 mm. Four segments are preserved and have lengths of 13.5, 15.5, 17, and 15 mm. The specimen contains a few pellet-like structures ~ 1 to 2 mm in diameter. The pellet-like structures are concentrated at, but not restricted to, the meanders (Fig. 25D). The

morphology of the specimen and the presence of the pellet-like structures suggest this is either a cololite or an intestinal cast.

Discussion

Ichnotaxa

Trace fossils from the MCA are represented by the following ichnotaxa:

Arenicolites variabilis, *Arenicolites* isp., *Arenituba verso*, *Aulichnites parkerensis*, *Bactryllium* isp., *Beaconites antarcticus*, *Bergaueria* cf. *perata*, *Bergaueria radiata*, cf. *Biformites* isp., *Chondrites intricatus*, *Chondrites targionii*, *Cochlichnus anguineus*, cf. *Cruziana* isp., *Cuniculonomus simplex*, *Diplichnites* isp., *Diplocraterion parallelum*, *Funiculichnus spiralis* nov. igen. nov. isp. *Gyrophyllites* isp., *Monocraterion* isp., *Pennatulites nodosus* nov. isp., *Phagophytichnus ekowskii*, *Planolites beverleyensis*, cf. *Planolites* isp., *Protovirgularia dichotoma*, *Rhizocorallium jenense*, *Skolithos* isp., *Taenidium satanassi*, and *Thalassinoides* isp. Additional traces include spiral and common coprolites, possible galls, and a bivalve at the end of a trail. These trace fossils were grouped into behavioral categories, and also used to infer ichnofossil assemblages and ichnofacies, and to compare with similar deposits of other Paleozoic and Mesozoic sequences.

Behavior

Behavioral categories are represented by cubichnia (resting traces), domichnia (dwelling traces)—including dwelling traces of deposit feeders, fodinichnia (feeding

traces), fugichnia (escape traces), and repichnia (locomotion traces). The majority of traces belong to either fodinichnia or repichnia. Fodinichnia is represented by the ichnogenera *Chondrites*, *Gyrophyllites*, *Pennatulites*, *Rhizocorallium*, and *Thalassinoides*. Additional feeding traces include *Cuniculonomus* and *Phagophytichnus*. Repichnia is represented by the ichnogenera *Aulichnites*, *Beaconites*, *Cochlichnus*, cf. *Cruziana*, *Diplichnites*, *Planolites*, *Protovirgularia*, *Taenidium*, and a *Planolites*-like trail associated with a bivalve. Domichnia is represented by the ichnogenera *Arenicolites*, *Arenituba*, *Diplocraterion*, *Monocraterion*, *Skolithos*, and cf. *Biformites*. Boyer (1979), however, includes *Biformites* within cubichnia. Cubichnia is represented by the sole ichnogenus *Bergaueria*. Fugichnia, although not present in the FMNH or KU collections, has been previously reported from the invertebrate paleontology collection at Northeastern Illinois University (Shabica and Godfrey, 1997; fig. 21.6).

Ichnofacies

The ichnocoenoses and ichnofacies represented by MCA trace fossils must be inferred because the concretions from MCA were previously collected with no detailed stratigraphic information. Ichnologic assemblages are difficult to infer because a single specimen or only a few specimens represent about half of the ichnotaxa. Additionally, several ichnotaxa can occur across ichnofacies—*Arenicolites*, *Chondrites*, *Planolites*, and *Rhizocorallium* (e.g., Ekdale et al., 1984). The high abundance and similarity in preservation of *Arenicolites*, *Diplocraterion*, and *Skolithos* Type A suggest these occur as an assemblage. This assemblage, along with one specimen of *Monocraterion*, suggests a *Skolithos* ichnofacies, which indicates a high-energy, shallow-marine environment with

shifting sediment, including tidal deltas (Ekdale et al., 1984; Pemberton et al., 2001). This assemblage, however, may also be observed in the *Glossifungites* ichnofacies, which indicates a marine firmground environment (Ekdale et al., 1984). Additional MCA trace fossils that may be included in the *Glossifungites* ichnofacies include *Bergaueria*, *Chondrites*, *Planolites*, *Rhizocorallium*, *Taenidium*, and *Thalassinoides*. Trace-fossil associations on or within the same concretion that support a *Glossifungites* ichnofacies include *Arenicolites–Chondrites*, *Arenicolites–Planolites*, and *Planolites–Skolithos*. The presence of these ichnogenera and assemblages, however, does not necessarily indicate a *Glossifungites* ichnofacies. Two specimens of *Skolithos* isp. Type B, containing coarser infill than the surrounding material and possible scratch marks associated with the specimen of *Rhizocorallium* may be indicators of a *Glossifungites* ichnofacies; however, there is not enough evidence to support this interpretation. The abundance and assemblage of *Chondrites*, *Cochlichnus*, and *Planolites*, along with *Arenicolites*, *Aulichnites*, cf. *Cruziana*, and *Rhizocorallium*, suggest a *Cruziana* ichnofacies, which represents a shallow-marine, subtidal environment within the fair-weather to storm-wave base (Ekdale et al., 1984). The trace-fossil assemblages suggest a *Skolithos–Cruziana* ichnofacies transition from shallower to deeper waters and lower to higher energy conditions. This ichnofacies transition is consistent with previous interpretations that the FCSM was deposited in a nearshore, shallow-marine, deltaic environment (Shabica, 1970, 1979; Baird, 1979; Kuecher et al., 1990; Feldman et al., 1993).

The assemblage of *Chondrites–Planolites–Thalassinoides* suggests a *Zoophycus* ichnofacies, which is indicative of an oxygen-limited environment, typically suggested to be on a deep shelf (Ekdale et al., 1984). The lack of additional deep-marine traces—

Cosmorhapse, *Paleodictyon*, and *Zoophycus*—and previous interpretation of the depositional environments of the FCSM, however, suggests the absence of a deep-water environment within the concretion-bearing portion of the FCSM.

Comparative ichnotaxonomy

The ichnodiversity of the MCA is comparable to the ichnodiversity of other Carboniferous coal-bearing marine, deltaic, and coastal-plain sequences (Pollard, 1988, and references therein; Table 1). The complete assemblage of ichnofossils from the MCA—24 ichnogenera—is most comparable to the assemblages found in the deltaic deposits of the Tweed and Pennine Basins of England. Eagar et al. (1985) and Pollard (1986) described ichnofossil assemblages from several stratigraphic sections: Late Mississippian Dinantian-Namurian (Serpukhovian—international stratigraphic age) Yoredale sheet deltas of the Tweed Basin (northern Pennines); Pendleian (Serpukhovian—international stratigraphic age) deep-water turbidite delta deposits in the Central Pennine Basin; Early Pennsylvanian Westphalian A (Bashkirian—international stratigraphic age) swamp-delta coal measures of the southern Pennines; and Marsdenian (Bashkirian—international stratigraphic age) shallow-water sheet deltas of the Central Pennine Basin. The Tweed basin assemblage is highly diversified (> 28 ichnogenera; Pollard, 1986) and includes *Arenicolites*, *Beaconites*, *Chondrites*, *Cochlichnus*, *Diplocraterion*, *Gyrophyllites*, *Monocraterion*, *Planolites*, *Rhizocorallium*, and *Skolithos*. The majority of Tweed Basin trace fossils occur in limestone or sandstone deposits associated with open marine to distal and proximal deltaic settings. The Pendleian deep-water delta deposits are divided into a turbidite, slope, and delta-top facies (Eagar et al.,

1985). The trace-fossil assemblage of *Bergaueria*, *Cochlichnus*, *Gyrophyllites*, *Planolites*, and *Rhizocorallium* occurs in the transition zone from the turbidite facies to the slope facies. The turbidite-slope assemblage is ascribed to the *Zoophycus* ichnofacies. The delta-top association includes *Aulichnites*, *Cochlichnus*, *Monocraterion*, and *Skolithos*, suggesting a *Cruziana-Skolithos* ichnofacies. The Westphalian A coal-measure assemblage includes *Arenicolites*, *Aulichnites*, *Beaconites*, *Cochlichnus*, *Planolites*, *Rhizocorallium*, and *Skolithos*. This assemblage occurs in muddy laminar deposits interbedded with fine-grained sandstone from crevasse-splay deposition associated with deltaic interdistributary bays and floodbasin lakes (Pollard, 1986; fig. 4). Trace fossils within the Marsdenian shallow-water, sheet-delta deposits occur in thin, muddy sandstone beds, and include *Cochlichnus*, *Gyrophyllites*, and *Planolites*.

MCA ichnotaxa and lithofacies relationships are variably comparable to several other Carboniferous deposits and ichnotaxa (Table 1). Prodelta shelf deposits composed of interbedded sandstone-siltstone-mudstone facies and dark mudstone facies in the Permo-Carboniferous Talchir Formation in the Saharjuri Basin, India (Chakraborty and Bhattacharya, 2005) contain a moderately diverse ichnofauna (13 ichnogenera). This ichnofossil assemblage—assigned to the *Cruziana* ichnofacies—has six ichnotaxa similar to MCA: *Diplocraterion parallelum*, *Monocraterion* isp., *Planolites beverleyensis*, *Rhizocorallium jenense*, *Skolithos* isp., and *Taenidium serpentinum*, as well as fugichnia.

Trace fossils have been described from two coal-bearing sequences of Alabama. The Upper Cliff coal interval of the Lower Pennsylvanian Pottsville Formation in northern Alabama (Gibson and Gastaldo, 1987) contains a medium to dark gray, shaley-siltstone lithofacies, with nodular siderite in the lower portion, interpreted as a

transgression of the interdistributary bay deposits. The presence of nodular siderite in the lower portion of the shaley lithofacies of the transgressive sequence is depositionally most similar to the FCSM. The Upper Cliff coal interval ichnofossil assemblage—assigned to the *Cruziana* ichnofacies—has four ichnogenera in common with the MCA: *Cochlichnus*, *Chondrites*, *Planolites*, and *Rhizocorallium*. The Upper Cliff coal interval *Cochlichnus*, however, are restricted to the lowermost deposits of the shaley-siltstone lithofacies, which were periodically influenced by freshwater from inland flooding (Gibson and Gastaldo, 1987). Trace fossils were also described from the Union Chapel Mine sequence of the Pottsville Formation, Alabama (Lucas and Lerner, 2005). Trace fossils present include *Cochlichnus* isp., *Diplichnites gouldi*, and *Protovirgularia* isp. These traces, however, are found within tidal rhythmites deposited on an estuarine tidal flat (Lucas and Lerner, 2005).

Miller and Knox (1985) described trace fossils from three lithofacies from a coal-bearing sequence of the Pennsylvanian Fentress Formation, Tennessee. A sandstone-siltstone facies of a subtidal lagoon, occurring just above a coal shale, includes *Planolites* and *Skolithos*. A thinly bedded sandstone facies representing tidal flat deposits include *Biformites*, *Planolites*, *Skolithos*, and *Thalassinoides*. A rippled sandstone facies attributed to tidal-delta deposits include *Bergaueria*, *Planolites*, *Rhizocorallium*, and *Skolithos*. Although the Fentress Formation deposits contain only six ichnogenera similar to MCA, the trace fossils of this formation are highly diverse (20 ichnogenera).

Hakes (1985) described a highly diverse trace-fossil assemblage (20 ichnogenera) from the brackish-marine Upper Pennsylvanian Missourian (Kasimovian—international stratigraphic age) Rock Lake Shale and Timberhill Siltstone Members of the Stanton

Limestone Formation, and the Virgilian (Gzhelian-Kasimovian—international stratigraphic age) upper portion of the Lawrence Formation, Kansas—referred to by Hakes (1985) as the Lawrence Shale Member. Trace fossils similar to MCA present in the medium-gray clayey shale of the Rock Lake Shale Formation include *Bergaueria*, *Chondrites*, *Cochlichnus*, *Cruziana*, *Planolites*, and cf. *Taenidium*. *Chondrites* and *Planolites* occur in the light-gray siltstone of the Timberhill Siltstone Member. *Chondrites*, *Cruziana*, and *Planolites* occur in the medium-gray, friable shale of the Lawrence Shale Member. Trace fossils are generally preserved on siltstone and fine-grained sandstone lenses within the predominantly shale units (Hakes, 1985).

The Morrowan (Bashkirian—international stratigraphic age) Dugger Formation in southwestern Indiana (Archer and Maples, 1984) contains fluvio-deltaic deposits that include a calcareous gray shale facies with nodular siderite. The moderate to highly diverse ichnofossil assemblage (16 ichnogenera) of the Dugger Formation includes a gray shale facies containing *Chondrites*, *Planolites*, looping traces, and *Rhizocorallium* (Archer and Maples, 1984). *Diplocraterion* is also found in the Dugger Formation, but occurs in the flaser-bedded sandstone facies interpreted as a tidal flat. An ichnofacies was not assigned to these deposits, however, as many of the ichnotaxa are ichnofacies-crossing types (e.g. *Chondrites*; Bromley, 1996). Archer and Maples (1984) also described *Cochlichnus* from the Mansfield Formation, occurring in sandstone fluvial-channel and proximal flood-plain deposits.

The majority of ichnofossils from coal-bearing sequences in coastal plain deposits of the Middle Pennsylvanian Kanawha Formation, West Virginia, occur within a thin-bedded, sandstone-siltstone facies attributed to a lower-middle tidal flat environment

(Martino, 1989). The West Virginia assemblage—assigned to the *Cruziana* ichnofacies—is moderate to highly diverse (17 ichnogenera), but contains only two ichnogenera similar to MCA: *Aulichnites* and *Planolites*. *Planolites* also occurs in a dark gray shale-mudstone facies with nodular siderite, attributed to upper tidal flats.

Trace fossils from the Upper Silesian (Pennsylvanian) Coal Basin, Poland, occur in three continental lithofacies: Cracow sandstone series, mudstone series, and Upper Silesia sandstone series (Gluszek, 1995). *Cochlichnus anguineus* occurs in all three lithofacies. *Planolites montanus* occurs in the mudstone series and Upper Silesia sandstone series. *Fugichnia* is present in the two sandstone series. The most abundant and best preserved traces occur in the mudstone series within crevasse-splay, flood-basin, and meandering-fluvial deposits (Gluszek, 1995).

Trace fossils reported from Carboniferous sequences are of moderate to high diversity and occur in continental-fluvial, tidal-flat, lagoon, channel, and deltaic deposits, with MCA traces most similar to traces found in deltaic deposits. Trace fossils common to deltaic environments are *Chondrites*, *Cochlichnus*, *Monocraterion*, *Planolites*, *Rhizocorallium*, and *Skolithos*. These ichnotaxa represent a *Cruziana* ichnofacies or a *Skolithos*–*Cruziana* ichnofacies transition similar to that of MCA. Trace fossils common to the fluvial and channel deposits are *Cochlichnus*, *Planolites*, and *fugichnia*. Trace fossils reported from tidal-flat deposits vary between locations, but include *Aulichnites*, *Biformites*, *Diplichnites*, *Diplocraterion*, *Planolites*, *Skolithos*, and *Thalassinoides*. Trace fossils occurring in the lagoon deposits are *Planolites* and *Skolithos*.

Middle Paleozoic marginal-marine deposits also have ichnotaxa similar to the MCA. Gouramanis et al. (2003) described two trace-fossil-bearing facies from the

Middle Silurian Major Mitchell Sandstone of the Grampians Group, western Victoria, Australia. The sandstone-siltstone facies deposited in a shallow-marine, low-energy delta front with minor tidal influences contains *Rhizocorallium* and *Thalassinoides*, indicating a *Cruziana* ichnofacies. The massive sandstone facies deposited on a high-energy marine shoreface with shifting sediment contains *Cruziana problematica* and *Skolithos linearis*, indicating a *Skolithos* ichnofacies. Unlike its occurrence in the MCA, *Beaconites* (*Taenidium*) *barretti* is found in fluviially deposited, trough cross-bedded sandstones assigned to the *Scoyenia* ichnofacies.

Metz (1998) described four trace-fossil-bearing lithofacies from the Lizard Creek Member of the Upper Silurian Shawangunk Formation, New Jersey. Medium-light to dark gray fine-grained sandstones and siltstones contain *Arenicolites* isp. and *S. verticalis*. Lagoonal-tidal channel deposits of dark gray silty shales and shaley silts contain *Arenicolites* isp., *Planolites beverleyensis*, *Protovirgularia* isp., and *S. verticalis*. Medium-light gray limonitic sandstones contain *Arenicolites* isp. and *S. verticalis*, as well as *Chondrites* cf. *arbuscula*, indicating depleted oxygen. Intertidal to shallow-subtidal deposits of silty sandstone interbedded with silty shale and shaley siltstone contain *Monocraterion tentaculatum* and *S. verticalis*.

Trace fossils reported from Silurian sequences occur in intertidal, tidal-channel, shoreface, and delta-front deposits, with MCA traces most similar to traces found in deltaic deposits. Silurian trace fossils are low to moderately diverse—9 ichnogenera at both locations. The lower diversity is likely the result of lower faunal diversity. Silurian ichnofacies similar to MCA deposits are *Skolithos* and *Cruziana*. Trace fossils of the *Cruziana* ichnofacies occur in delta-front deposits and include *Rhizocorallium* and

Thalassinoides. Although there are few similarities in the ichnogenera present, the presence of a *Cruziana* ichnofacies within deltaic deposits is equivalent to the Carboniferous deltaic deposits, including MCA. Trace fossils of the *Skolithos* ichnofacies occur in intertidal or shoreface deposits and include *Cruziana*, *Monocraterion*, and *Skolithos*. Tidal-channel deposits contain trace fossils associated with both the *Skolithos* and *Cruziana* ichnofacies, including *Arenicolites*, *Chondrites*, *Planolites*, *Protovirgularia*, and *Skolithos*.

The ichnodiversity and lithofacies occurrence of MCA is also similar to that found in deltaic and coal sequences of Mesozoic rocks. McIlroy (2004) described a trace-fossil assemblage of high diversity (22 ichnogenera) from Middle Jurassic tide-dominated delta deposits from the Ile Formation, Norway. Ichnotaxa similar to MCA include *Arenicolites* isp., *Chondrites* isp., *Planolites beverleyensis*, and *Taenidium* isp. described from medium- to coarse-grained sandstones of proximal mouth-bar deposits. Mud-rich siltstone and fine-grained sandstones of proximal prodelta deposits contain *Planolites beverleyensis*, *Rhizocorallium irregularis*, *Taenidium* isp., *Taenidium serpentinum*, and *Thalassinoides suevicus*. Interbedded sandstones with silt- and mudstones of distal mouth-bar deposits contain *Diplocraterion parallelum* and *Skolithos verticalis*. Medium- to fine-grained sandstones of central mouth-bar deposits contain *Chondrites* isp., *Diplocraterion parallelum*, *Planolites beverleyensis*, and *Skolithos verticalis*. The distal prodelta deposits (lithology not given) contain *Planolites* and *Rhizocorallium*. Sandstone and mudstone deposits of tidal flats contain *Planolites beverleyensis*, with *Bergaueria* cf. *perata* and *Thalassinoides suevicus* occurring with *P. beverleyensis* in the subtidal portions of the tidal flats.

McIlroy (2007) also described the ichnology from four facies associations in a tide-dominated delta system of the Middle Jurassic Lajas Formation, Argentina. The Lajas Formation is highly diverse (24 ichnogenera) and includes nine ichnogenera similar to those found in the FMNH and KU collections: *Arenicolites*, *Diplocraterion*, *Chondrites*, *Cruziana*, *Planolites*, *Protovirgularia*, *Rhizocorallium*, *Taenidium*, and *Thalassinoides*. Of the four facies associations, Facies Association 1, interpreted as offshore shelf to tide-dominated delta front deposits, contains the most similar ichnofossil assemblage to MCA. *Chondrites* and *Rhizocorallium* occur in shelf mudstones, *Protovirgularia* occur in shelf-sand turbidites, and *Diplocraterion*, *Planolites*, and *Thalassinoides* occur within sand-rich mouth-bar deposits.

Hovikoski et al. (2008) described moderately to highly diverse (15 ichnogenera), mud-dominated deltaic coast deposits in the Campanian (Late Cretaceous) Alderson Member of the Lea Park Formation, western Canada, with four of seven lithofacies containing ichnotaxa similar to MCA. Facies 1 is a bioturbated dark to light-gray silty shale divided into two subfacies: subfacies 1A is *Chondrites*-dominated with common *Planolites*; and subfacies 1B is *Planolites*-dominated with common *Chondrites*. Facies 2 is a bioturbated sandy shale divided into three subfacies. Subfacies 2A and 2B contain *Chondrites* and *Planolites* representing the *Cruziana* ichnofacies of the proximal offshore to lower shoreface. Subfacies 2B is muddier than 2A, and also contains *Arenicolites*, *Thalassinoides*, and fugichnia. Subfacies 2C is light to dark gray, burrow-mottled sandy shale with *Diplocraterion*, *Planolites*, *Rhizocorallium*, cf. *Taenidium*, and *Thalassinoides* formed in an episodic shoreline alternating between low and high energy deposition. Facies 3 is muddy heterolithic bedding indicating periods of rapid deposition on a wave-

or tide-agitated coastal mud wedge, containing *Arenicolites*, *Chondrites*, *Planolites*, and *Thalassinoides*. Facies 7 is a *Glossifungites* ichnofacies-bearing sandy shale with palimpsest *Thalassinoides*.

Nearshore to offshore sequences of the Upper Cretaceous Blackhawk Formation, east-central Utah, described by Kamola (1984; limited to the Spring Canyon Member) and Howard and Frey (1984) also contain ichnotaxa similar to MCA. Kamola (1984) described *Skolithos* and *Thalassinoides* from channel-fill sandstones, *Arenicolites*, *Planolites montanus*, and *Thalassinoides* from delta sandstones, and *P. montanus* and *Thalassinoides* from lagoon silt- and sandstones. Howard and Frey (1984) described trace fossils based on their stratigraphic position within deposits of the lower, middle, and upper offshore, and lower, middle, and upper shoreface of the Blackhawk Formation. Lower offshore dark mudstone deposits contain *Planolites beverleyensis*. Middle offshore silt- and mudstone deposits contain *P. beverleyensis* and *Thalassinoides suevicus*. Upper offshore siltstone deposits contain *P. beverleyensis*, *Skolithos linearis*, and *T. suevicus*. Lower shoreface muddy fine- to medium-grained sandstone deposits contain *Chondrites* isp., *P. beverleyensis*, *S. linearis*, and *T. suevicus*. Middle and upper shoreface fine-grained sandstone deposits contain *Aulichnites parkerensis* and *S. linearis*, as well as *Chondrites* isp., *P. beverleyensis*, *P. montanus*, and *Thalassinoides paradoxicus*, and *Arenicolites* isp. and *A. variabilis*, respectively. Trace fossils within the Blackhawk Formation are highly diverse (20 ichnogenera); however the majority of ichnotaxa similar to MCA occur in the offshore to shoreface deposits.

Trace fossils reported from Mesozoic depositional sequences primarily occur in deltaic, tidal-flat, channel, and offshore to shoreface deposits, with MCA traces most

similar to traces found in deltaic deposits. Trace fossils typical of the deltaic deposits include *Arenicolites*, *Chondrites*, *Diplocraterion*, *Planolites*, *Rhizocorallium*, and *Thalassinoides*. These ichnogenera are common components of the *Cruziana* ichnofacies (Ekdale et al., 1984). The presence of *Arenicolites* and *Diplocraterion*, however, may suggest a *Skolithos*–*Cruziana* ichnofacies transition. The presence of a *Cruziana* ichnofacies or a *Skolithos*–*Cruziana* ichnofacies transition in the Mesozoic deltaic deposits is equivalent to the Paleozoic deltaic deposits, including MCA. *Planolites* is the only common trace found in the tidal-flat deposits. The differences in ichnogenera present—e.g., *Bergaueria* and *Thalassinoides* (Norway), and *Arenicolites*, *Cruziana*, *Skolithos*, and *Taenidium* (Argentina)—may suggest a difference in fauna present, or that the traces were produced at different times of deposition—e.g., low or high tide. Trace fossils typical of the channel deposits are *Planolites*, *Skolithos*, and *Thalassinoides*. These trace fossils are common components of the *Cruziana* ichnofacies, suggesting these traces were produced in the subtidal portion of the channel (Ekdale et al., 1984). The presence of *Arenicolites* and *Monocraterion* in the Norway channel deposits, suggests a *Skolithos*–*Cruziana* ichnofacies transition from a shallower to deeper section of the channel. Trace fossils from the offshore to shoreface deposits have been assigned to the *Cruziana* ichnofacies, and include *Chondrites*, *Planolites*, and *Thalassinoides*, as well as ichnogenera specific to certain deposits.

Summary

The ichnodiversity and lithofacies of the FCSM in MCA is comparable to Middle to Late Paleozoic and Mesozoic deltaic deposits, coal-bearing successions, coal-bearing

deltaic sequences, and nondeltaic nearshore sequences (Table 1). The deltaic coal-bearing systems are the Carboniferous Upper Cliff coal interval (Alabama, USA), the Fentress Formation (Tennessee, USA), the Kanawha Formation (West Virginia, USA), the Mansfield and Dugger Formations (Indiana, USA), and deposits of the Pennines (England), and the Cretaceous Blackhawk Formation, (Utah, USA). Deltaic systems lacking coal deposits include the Permo-Carboniferous Talchir Formation (India), the Silurian Major Mitchell Sandstone (Victoria, Australia), the Jurassic Ile Formation (Norway) and the Lajas Formation (Argentina), and the Cretaceous Lea Park Formation (western Canada). Nondeltaic nearshore systems include the Carboniferous Rock Lake Shale, Timberhill Siltstone, and Lawrence Shale (Kansas, USA), and the Silurian Shawangunk Formation (New Jersey, USA). Nondeltaic, coal-bearing sequences include the Carboniferous Pottsville Formation (Alabama, USA), and the Upper Silesia Coal Basin (Poland). These sequences contain two to eleven ichnogenera also found at MCA: Ile Formation–11; Lajas Formation and Pennine sequences–10; Lea Park Formation and Mansfield and Dugger Formations–8; Talchir Formation–7; Fentress Formation, Blackhawk Formation, and Kansas sequences–6; Shawangunk Formation–5; Upper Cliff coal interval, Upper Silesia Coal Basin, and Major Mitchell Sandstone–4; Pottsville Formation–3; Kanawha Formation–2.

The Jurassic sequences contain the most similar ichnogenera to those in the FCSM; however, several of the ichnogenera are distributed over several different lithofacies compared to MCA. Trace fossils within the Cretaceous sequences generally occur within sandstones, with the highest number of similar ichnogenera (8) representing a *Cruziana* ichnofacies and occurring within the sandy shale lithofacies of the Lea Park

Formation. Trace fossils of the Silurian sequences occur in sandstones, shaley siltstones, and silty shales of the Shawangunk Formation, and in sandstones of the Major Mitchell Sandstone. Trace fossils occur within two lithofacies of the Major Mitchell Sandstone, and represent a *Skolithos* ichnofacies within the massive sandstone, and a *Cruziana* ichnofacies within the sandstone-siltstone facies.

The Carboniferous deltaic coal-bearing deposits of the Pennines are most similar to MCA in its high ichnodiversity and similar ichnogenera (10). The trace fossils of the Pennines, however, generally occur in limestone and sandstone. Trace-fossil associations of the Pennines represent a *Skolithos*–*Cruziana*–*Zoophycus* ichnofacies transition. Trace fossils of the Mansfield and Dugger Formations occur within limestone, sandstone, and shale, with the highest diversity and most similar ichnogenera (4) occurring within the gray shale lithofacies. The tidal-flat and tidal-delta sandstones of the Fentress Formation contain the most similar ichnogenera (6) compared to MCA. Trace fossils of the Fentress Formation also occur in a lagoonal sandstone-siltstone lithofacies. The lithofacies of the Upper Cliff coal interval is similar to MCA in that nodular siderite is present within a shaley siltstone lithofacies. Ichnodiversity is low, however, with only four ichnogenera in common with MCA.

Trace fossils within the glaciodeltaic deposits of the Talchir Formation occur within a sandstone-siltstone-mudstone lithofacies, containing seven similar ichnogenera. The distribution of trace fossils in the sandstone, siltstone, or mudstone is unclear, however. Trace fossils within the nearshore cyclic marine deposits of Kansas occur within the Timberhill Siltstone and on siltstone lenses of the Rock Lake and Lawrence Shales. Trace fossils of the Upper Silesia Coal Basin occur within sandstones and

mudstones, with the most abundant and best-preserved traces occurring in mudstones. Trace fossils of the Pottsville Formation occur within tidal rhythmites, and are of low diversity. The Kanawha Formation contains the least ichnodiversity and similar ichnogenera (2). Trace fossils occur within a thinly bedded siltstone-sandstone lithofacies, and also a dark gray shale lithofacies with nodular siderite similar to that of the FCSM.

Conclusions

The ichnodiversity of MCA comprises 24 ichnogenera and 28 ichnospecies. Unnamed ichnotaxa include spiral and common coprolites, a bivalve at the end of its *Planolites*-like trail, and two possible galls. Several specimens originally identified as trace fossils are actually soft-sediment deformation structures and wrinkled textures on *Macroneuropteris* pinnules. Several body fossils also were originally identified as trace fossils including worms and worm-like animals, jellyfish and jellyfish tentacles, a *Calamites* stem, and a possible cololite. Thin sections of several *Planolites* burrows yielded little additional information, with the exception of a few possible peloids. X-ray diffraction confirmed the presence of siderite and kaolinite. Stable carbon-isotope analysis of one specimen indicated a modified marine environment with little oxidation of methane, or that there is a small amount of organic oxidation of the concretion pore fluids. Stable carbon-isotope analysis of a second specimen indicated carbon dioxide reduction by methanogenesis, suggesting anoxic pore waters at the time of concretion formation.

Ichnofossils of MCA primarily occur within siderite concretions formed in a dark gray to black shale, and are represented by the behavioral categories of cubichnia, domichnia, fodinichnia, fugichnia, and repichnia, with the majority of traces belonging to repichnia. Inferred ichnoassemblages include *Arenicolites-Diplocraterion-Skolithos* representing a *Skolithos* ichnofacies, and *Chondrites-Cochlichnus-Planolites* representing a *Cruziana* ichnofacies. Two specimens of *Skolithos* with coarser infill than the surrounding material, and one specimen of *Rhizocorallium* with possible scratch marks may indicate a *Glossifungites* ichnofacies.

The most common trace-fossil association among Paleozoic and Mesozoic nearshore marine, deltaic, or coal-bearing sequences is *Chondrites-Planolites-Rhizocorallium*, or a variation of, described from several studies. The most common ichnofacies are *Skolithos* and *Cruziana*. The Paleozoic and Mesozoic deltaic environments are invariably represented by the *Cruziana* ichnofacies or a *Skolithos-Cruziana* ichnofacies transition. The ichnofossil assemblages and paleoenvironments of the comparable localities, like those of the FCSM, indicate that deltaic or nearshore-marine systems have a transition of softground ichnofacies from shallower to deeper water and from higher to lower energy represented by the transition between the *Skolithos* and *Cruziana* ichnofacies. Ichnofossil assemblages with evidence of tide-influenced paleoenvironments suggest periods of non-deposition, allowing the media (=substrate) to become more firm and able to sustain a fauna capable of producing a *Glossifungites* ichnofacies. This ichnofacies represents subaqueous compaction followed by erosion and colonization of the newly exposed subaqueous surfaces, which could also

have formed in deltaic environments. A *Glossifungites* ichnofacies may be present within the FCSM; however, additional evidence is needed to confirm this hypothesis.

Trace fossils from deltaic or coal-bearing sequences range from low to high diversity, with higher diversity occurring in deltaic settings dominated by marine conditions. Although these environments share similar ichnogenera, several ichnogenera are specific to certain deposits; for example, *Pennatulites* is only present in MCA deposits. Differences in ichnogenera in Paleozoic and Mesozoic sequences compared to MCA are likely the result of differences in the fauna present. The presence of such marine trace fossils as *Chondrites* and *Diplocraterion* supports previous interpretations that the FCSM was deposited in a marine environment. Carbon-isotope results indicate a freshwater influence of the marine sediments after burial, which is typical of deltaic environments.

Table 1—Ichnotaxonomic comparison of various-aged deltaic, coal-bearing, and near-shore depositional sequences. Ichnofossils listed are similar to or present at MCA.

Age	Location	Stratigraphic Unit	Depositional Environment	Ichnofossils	Reference
Middle Silurian	Victoria, Australia	Major Mitchell Sandstone	Delta front	<i>Rhizocorallium</i> , <i>Thalassinoides</i>	Gouramanis et al., 2003
			Shoreface	<i>Cruziana</i> , <i>Skolithos</i>	
Upper Silurian	New Jersey	Shawangunk Formation	Lagoon-Tidal Channel	<i>Arenicolites</i> , <i>Chondrites</i> , <i>Planolites</i> , <i>Protovirgularia</i> , <i>Skolithos</i>	Metz, 1998
			Inter- to subtidal	<i>Monocraterion</i> , <i>Skolithos</i>	
Early Pennsylvanian	Poland	Upper Silesia Coal Basin	Fluvial	<i>Cochlichnus</i> , <i>Planolites</i> , fugichnia	Gluszek, 1995
	Alabama	Pottsville Formation	Estuarine tidal flat	<i>Cochlichnus</i> , <i>Diplichnites</i> , <i>Protovirgularia</i>	Lucas and Lerner, 2005
			Deltaic	<i>Chondrites</i> , <i>Cochlichnus</i> , <i>Planolites</i> , <i>Rhizocorallium</i>	Gibson and Gastaldo, 1987
	Tennessee	Fentress Formation	Subtidal lagoon	<i>Planolites</i> , <i>Skolithos</i>	Miller and Knox, 1985
Tidal flat			<i>Biformites</i> , <i>Planolites</i> , <i>Skolithos</i> , <i>Thalassinoides</i>		
			Tidal delta	<i>Bergaueria</i> , <i>Planolites</i> , <i>Rhizocorallium</i> , <i>Skolithos</i>	

Age	Location	Stratigraphic Unit	Depositional Environment	Ichnofossils	Reference
Early Pennsylvanian	England	Pennine Basin	Deltaic	<i>Arenicolites</i> , <i>Aulichnites</i> , <i>Beaconites</i> , <i>Bergaueria</i> , <i>Cochlichnus</i> , <i>Gyrophyllites</i> , <i>Monocraterion</i> , <i>Planolites</i> , <i>Rhizocorallium</i> , <i>Skolithos</i>	Eagar et al., 1985; Pollard, 1986
	Indiana	Dugger Formation	Delta	<i>Chondrites</i> , <i>Planolites</i> , <i>Rhizocorallium</i> , looping trails	Archer and Maples, 1984
Middle Pennsylvanian			Tidal flat	<i>Diplocraterion</i>	
		Mansfield Formation	Channel	<i>Cochlichnus</i> , <i>Rhizocorallium</i> , bilobed trails, fugichnia	
	West Virginia	Kanawha Formation	Tidal flat	<i>Aulichnites</i> , <i>Planolites</i>	Martino, 1989
Late Pennsylvanian	Kansas	Stanton Limestone Formation	Cyclothem	<i>Bergaueria</i> , <i>Chondrites</i> , <i>Cochlichnus</i> , <i>Cruziana</i> , <i>Planolites</i> , <i>Taenidium</i>	Hakes, 1985
		Lawrence Formation		<i>Chondrites</i> , <i>Cruziana</i> , <i>Planolites</i>	
Pennsylvanian-Permian	India	Talchir Formation	Glacio-deltaic	<i>Diplocraterion</i> , <i>Monocraterion</i> , <i>Planolites</i> , <i>Rhizocorallium</i> , <i>Skolithos</i> , <i>Taenidium</i>	Chakraborty and Bhattacharya, 2005

Age	Location	Stratigraphic Unit	Depositional Environment	Ichnofossils	Reference
Middle Jurassic	Norway	Ile Formation	Delta	<i>Arenicolites,</i> <i>Chondrites,</i> <i>Diplocraterion,</i> <i>Planolites,</i> <i>Rhizocorallium,</i> <i>Skolithos,</i> <i>Taenidium,</i> <i>Thalassinoides</i>	McIlroy, 2004
			Tidal flat	<i>Bergaueria,</i> <i>Planolites,</i> <i>Thalassinoides</i>	
			Channel	<i>Arenicolites,</i> <i>Chondrites,</i> <i>Monocraterion,</i> <i>Planolites,</i> <i>Skolithos,</i> <i>Thalassinoides</i>	
	Argentina	Lajas Formation	Shelf	<i>Chondrites,</i> <i>Protovirgularia,</i> <i>Rhizocorallium</i>	McIlroy, 2007
			Delta	<i>Chondrites,</i> <i>Diplocraterion,</i> <i>Planolites,</i> <i>Rhizocorallium,</i> <i>Thalassinoides</i>	
			Tidal flat	<i>Arenicolites,</i> <i>Cruziana,</i> <i>Planolites,</i> <i>Skolithos,</i> <i>Taenidium</i>	
			Channel	<i>Planolites,</i> <i>Skolithos,</i> <i>Thalassinoides</i>	

Age	Location	Stratigraphic Unit	Depositional Environment	Ichnofossils	Reference
Late Cretaceous	western Canada	Lea Park Formation	Delta	<i>Chondrites, Planolites</i>	Hovikoski et al., 2008
			Offshore to shoreface	<i>Chondrites, Diplocraterion, Planolites, Rhizocorallium, Thalassinoides</i>	
			Mud wedge and firmground	<i>Arenicolites, Chondrites, Planolites, Thalassinoides</i>	
	Utah	Blackhawk Formation	Offshore	<i>Planolites, Skolithos, Thalassinoides</i>	Howard and Frey, 1984
			Shoreface	<i>Arenicolites, Aulichnites, Chondrites, Planolites, Skolithos, Thalassinoides</i>	
			Delta	<i>Arenicolites, Planolites, Thalassinoides</i>	Kamola, 1984
			Channel	<i>Skolithos, Thalassinoides</i>	
Lagoon	<i>Planolites, Thalassinoides</i>				

Figure Captions

FIGURE 1—Mazon Creek locality with stars indicating labeled nearby towns; numbered areas represent Pit localities from previous mining operations (modified from Baird et al., 1985).

FIGURE 2—Stratigraphic column showing relationship of the Francis Creek Shale Member thin facies of the Carbondale Formation (modified from Baird et al., 1985).

FIGURE 3—Thin-section images. **(A)** KUMIP 320211 – trace fossil occurs between black lines. **(B)** Line drawing of Fig. 3A – burrow occurs between lines. **(C)** Pellet-like structures within the trace-fossil portion of KUMIP 320211. **(D)** Line drawing of pellet-like structures from Fig. 3C.

FIGURE 4—X-ray diffraction and stable-carbon isotope C13 graph results. **(A)** Resulting siderite and quartz peaks from the concretion portion of PE 51503. **(B)** Resulting kaolinite peaks from the trace-fossil portion of PE 43127. **(C)** Carbon-isotope results for KUMIP 320211 and PE 47459.

FIGURE 5—*Arenicolites variabilis*. **(A)** Symmetrical form—PE 31866. **(B)** Asymmetrical form—PE 46793. **(C)** PE 31847 with surficial pyrite. **(D)** PE 31841. **(E)** Cross section of large form—PE 25668. **(F)** Top view of large form—PE 25668.

FIGURE 6—*Arenicolites* isp. and *Planolites beverleyensis*. **(A–D)** PE 45749: **(A)** Top view. **(B)** Bottom view. **(C)** Cross-sectional view. **(D)** Close up of cf. *Didontogaster cordylina*. **(E–F)** PE 51654: **(E)** *Arenicolites* isp. **(F)** *Planolites beverleyensis* associated with *Arenicolites* isp.

FIGURE 7—*Arenituba verso*, *Aulichnites parkerensis*, *Beaconites antarcticus*, and cf. *Cruziana* isp. (A) *Arenituba verso*—PE 51894. (B) *Beaconites antarcticus*—PE 51523. (C) *Beaconites antarcticus*—PE 45094. (D) *Aulichnites parkerensis*—PE 46360. (E) *Beaconites antarcticus*—PE 36866. (F–G) cf. *Cruziana* isp.—PE 46784.

FIGURE 8—*Bergaueria* and cf. *Biformites* isp. (A) *Bergaueria* cf. *perata*—PE 51561. (B–D) *Bergaueria radiata*: (B) PE 51620a with centrally located cylindrical iron concretion. (C) PE 51620b. (D) PE 51620c. (E) cf. *Biformites* isp.—PE 51656.

FIGURE 9—*Chondrites* and *Cochlichnus anguineus*. (A) *Chondrites intricatus* with arrows pointing to associated *Arenicolites* isp.—PE 45091. (B) Inset of Fig. 8A—close up of *C. intricatus*—PE 45091. (C) *C. targionii*—PE 48568. (D) *Chondrites intricatus*—PE 51786. (E–F) *Cochlichnus anguineus* on *Macroneuropteris* pinnules: (E) PE 52203. (F) PE 30779.

FIGURE 10—*Cochlichnus anguineus*. (A) PE 51898 on *Macroneuropteris* pinnule. (B) PE 38177b on gray shale. (C) PE 38173 on gray shale.

FIGURE 11—*Cuniculonomus simplex*. (A) P 18706. (B) P 18619. (C) Inset of Fig. 11A—close up of P 18706. (D) Inset of Fig. 11B—close up of P 18619.

FIGURE 12—*Diplichnites* isp.—PE 52249 (A) *Diplichnites* isp. associated with *Skolithos* isp. (B) Close up of Fig. 12A. (C) Second specimen on separate piece of shale. (D) Close up of second specimen.

FIGURE 13—*Diplocraterion parallelum* and *Arenicolites variabilis*. (A) *Arenicolites variabilis* for comparison with *Diplocraterion parallelum*. (B) *Diplocraterion parallelum*—PE 31833. (C) *D. parallelum*—PE 31827. (D) Bottom view of PE 31827

showing U-turn on concretion surface. **(E)** *D. parallelum*—PE 31842. **(F)** *D. parallelum* large form—PE 42924.

FIGURE 14—*Monocraterion* isp., *Protovirgularia dichotoma*, and *Gyrophyllites* isp. **(A–C)** *Monocraterion* isp.—PE 42655: **(A)** Top view. **(B)** Bottom view. **(C)** Side view. **(D)** *Protovirgularia dichotoma*—PE 22022. **(E–F)** *Gyrophyllites* isp.—PE 40093: **(E)** Top view. **(F)** Bottom view close up of shaft. **(D–E)** Grayscale modified for trace visibility.

FIGURE 15—*Pennatulites nodosus* nov. isp. **(A–D)** PE 23477: **(A)** Full view. **(B)** Rightmost inset of Fig. 15A—close up of nodes on left side of medial ridge. **(C)** Lowermost inset of Fig. 15A—*Bactryllium* isp. crosscutting main shaft. **(D)** Upper-left inset of Fig. 15A—associated worm tube. **(E–F)** PE 51092: **(E)** Full view. **(F)** Side view of burrow within concretion with arrow pointing to possible node.

FIGURE 16—*Phagophytichnus ekowskii* and cf. *Planolites* isp. **(A–F)** *Phagophytichnus ekowskii*: **(A)** KU specimen P 1143. **(B)** Mold of PP 24268—arrow pointing to misinterpreted bite mark. **(C)** Cast of PP 24268—arrow pointing to invaginated surface. **(D)** Inset of 16A—close up of P 1143, rotated 90° counterclockwise. **(E)** Close up of 16D. **(F)** KU specimen P-1 25. **(G)** cf. *Planolites* isp. associated with *Macroneuropteris* pinnule.

FIGURE 17—*Planolites beverleyensis* and bivalve trail. **(A–E)** *Planolites beverleyensis*: **(A)** PE 36864. **(B)** KUMIP 320211. **(C)** PE 51561. **(D)** PE 49618. **(E)** PE 47459. **(F)** Bivalve at the end of a *Planolites*-like trail—PE 12302.

FIGURE 18—*Skolithos* isp. and *Arenicolites variabilis*. **(A)** *Skolithos* isp. Type A—PE 31873. **(B)** *Skolithos* isp. Type B—PE 51655—top view. **(C)** *Arenicolites variabilis* for

comparison—PE 31835. **(D–F)** *Skolithos* isp. Type B **(D)** PE 51655—side view. **(E)** PE 42653. **(F)** PE 47680.

FIGURE 19—*Rhizocorallium jenense*, *Taenidium satanassi*, and *Thalassinoides* isp. **(A)** *Rhizocorallium jenense*—PE 50901. **(B)** Organic material following bedding planes of *Rhizocorallium jenense*—PE 50901. **(C)** *Taenidium satanassi*—PE 51093. **(D)** Inset of Fig. 19C—close up of *Taenidium satanassi*, rotated counterclockwise 90°. **(E)** *Thalassinoides* isp.—PE 45083. **(F)** *Thalassinoides* isp.—PE 51095.

FIGURE 20—Coprolites. **(A)** *Bactryllium* isp. associated with *Funiculichnus spiralis* nov. igen. nov. isp.—PE 40083. **(B)** Lower-left inset of Fig. 19F—*Bactryllium* isp. associated with *Thalassinoides* isp.—PE 51095. **(C)** Common coprolite—PE 36872. **(D)** Close up of fenestral pattern of replacement mineral on PE 36872.

FIGURE 21—*Funiculichnus spiralis* nov. igen. nov. isp.—PE 40083. **(A)** Full concretion view. **(B)** Close up of upper-left inset of Fig. 21A—first-order specimen below portion of second-order specimen. **(C)** Rightmost inset of Fig. 21A—third-order specimens with longitudinal ridges.

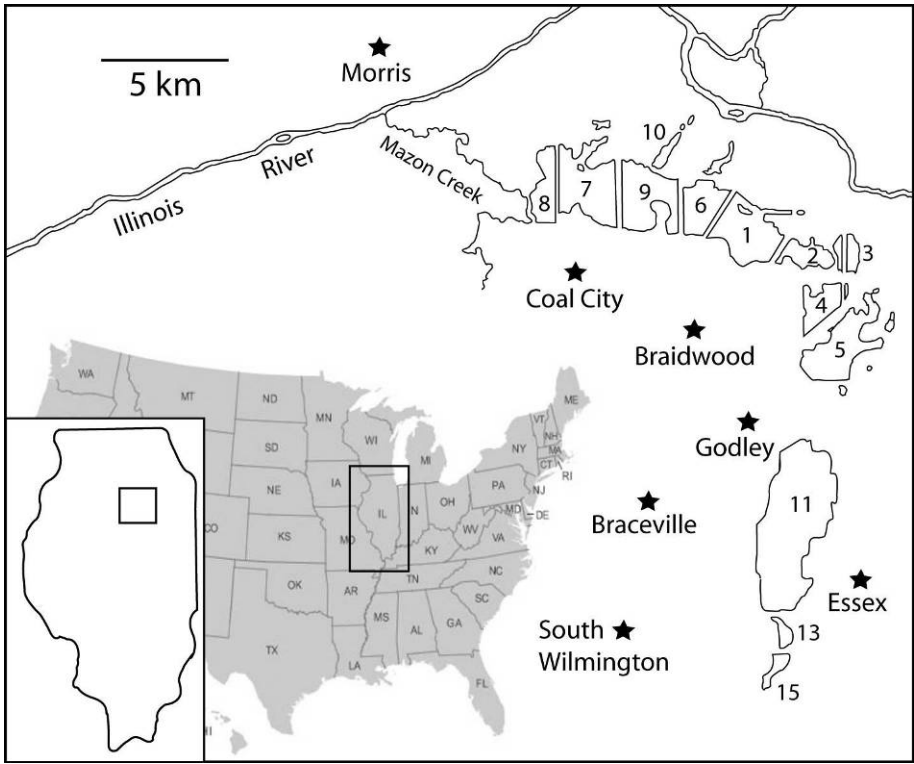
FIGURE 22—*Funiculichnus spiralis* nov. igen. nov. isp. **(A–D)** PE 40083: **(A)** Large inset of Fig. 21A—second-order specimen crossing over itself. **(B)** Close up of Fig. 22A. **(C)** Close up of Fig. 22B showing fecal strands. **(D)** Upper-left inset of Fig. 21A rotated 180°. **(E–F)** Second-order specimens showing rope-like strands twisting around longitudinal axis, associated with *Thalassinoides* isp.—PE 51095. **(E)** Right inset of Fig. 19F. **(F)** Upper-left inset of Fig. 19F.

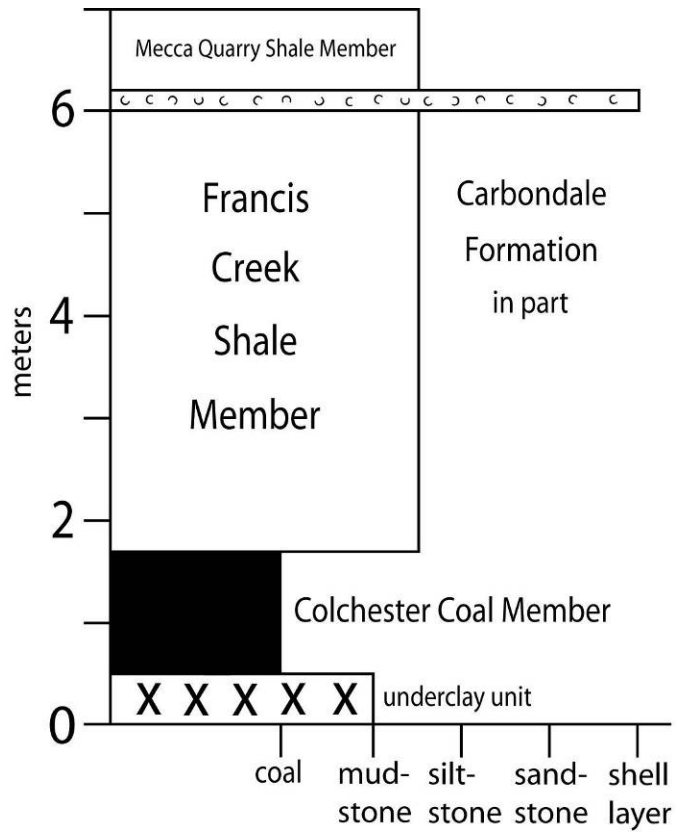
FIGURE 23—Galls—PE 54656. **(A)** Cast. **(B)** Mold. **(C)** Inset of Fig. 23A. **(D)** Small inset of Fig. 23B. **(E)** Close up of Fig. 23B—leftmost arrow pointing to cuticle damage,

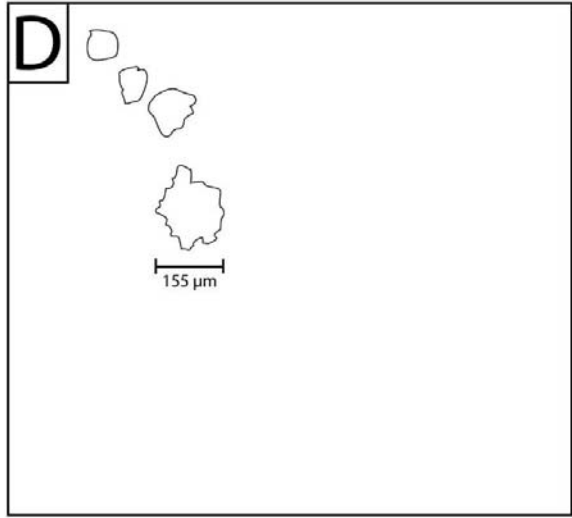
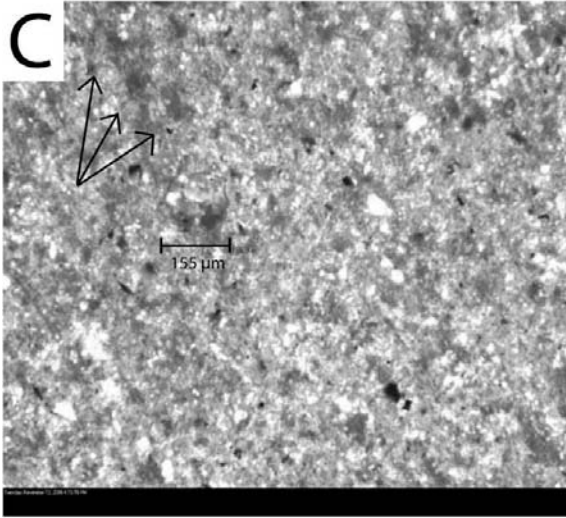
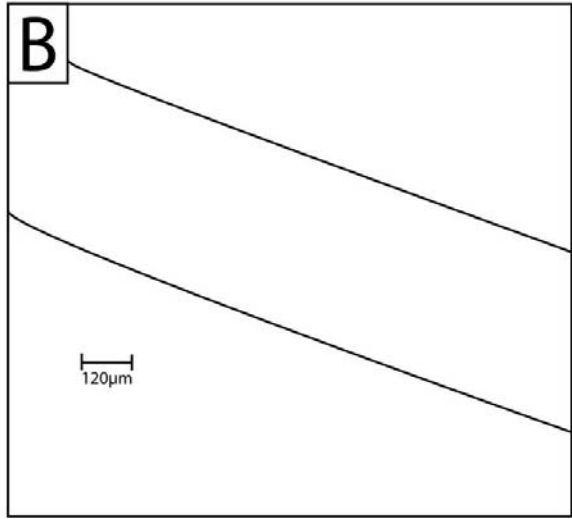
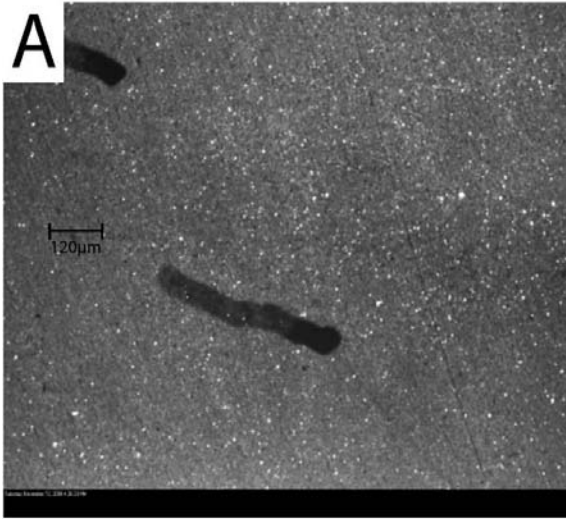
additional arrows pointing to internal circular structures. **(F)** Large inset of Fig. 23B. **(G)** Close up of Fig. 23F.

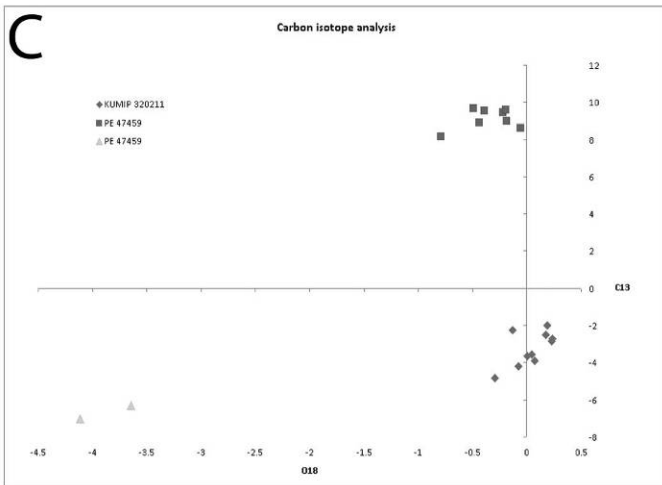
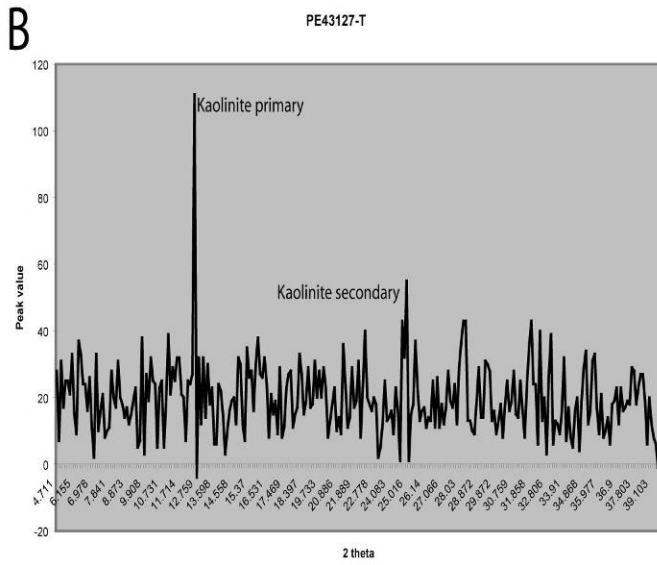
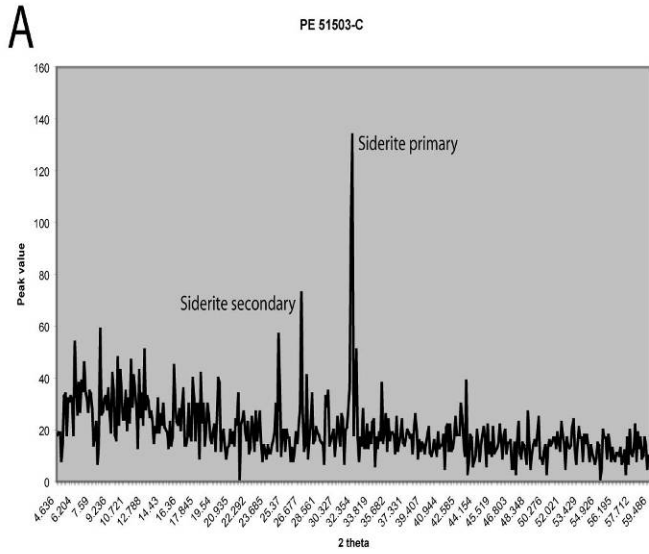
FIGURE 24—Soft-sediment deformation structures and body fossils. **(A–C)** Soft-sediment deformation structures: **(A)** cf. *Dendrophycus*—PE 44632. **(B)** cf. *Neantia*—PE 50982. **(C)** Amorphous structures—PE 51045. **(D)** *Anthracomedusa turnbulli* for comparison with Fig. 24E (reprinted with permission, Paul Selden, 2004). **(E)** cf. *Anthracomedusa* tentacles—PE 21581. **(F)** The worm-like animal *Mazoglossus ramsdelli*—PE 51534.

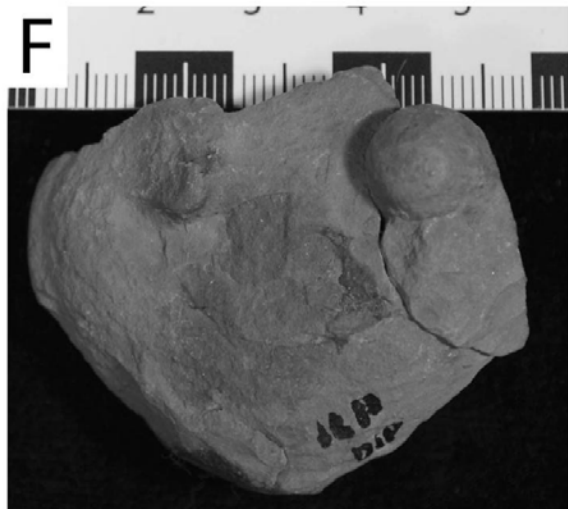
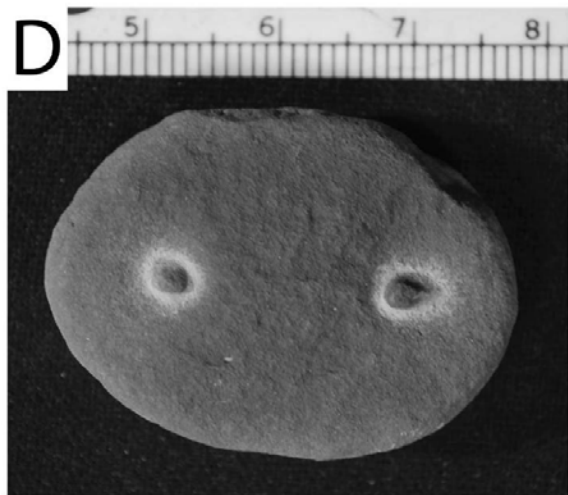
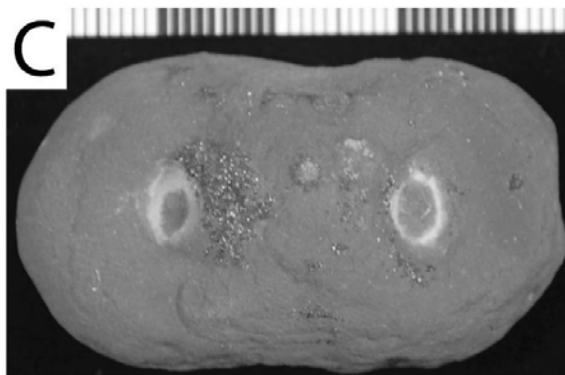
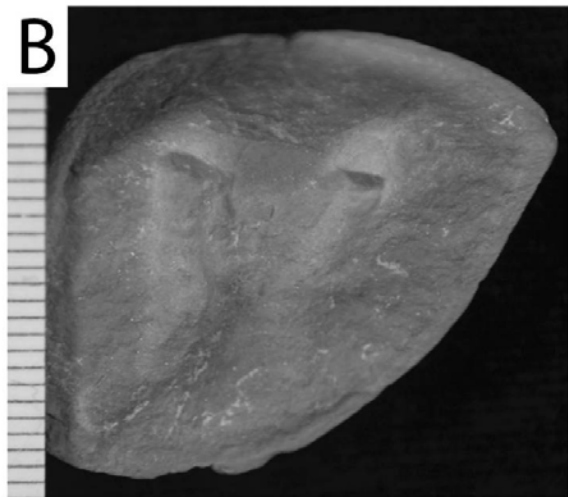
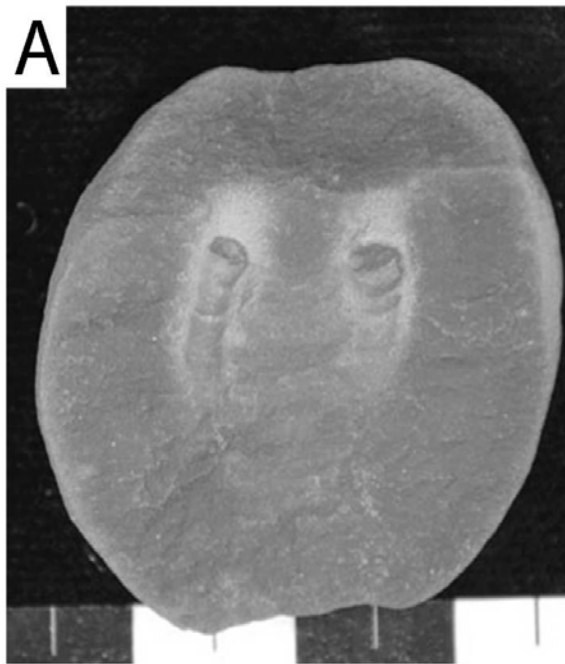
FIGURE 25—*Calamites*, cololite, and wrinkled texture on *Macroneuropteris*. **(A)** *Calamites* stem—PE 43654. **(B)** Wrinkled texture on *Macroneuropteris* pinnule—PP 26064. **(C)** Cololite—PE 12450. **(D)** Inset of 25C—close up of pelletal structures within cololite.

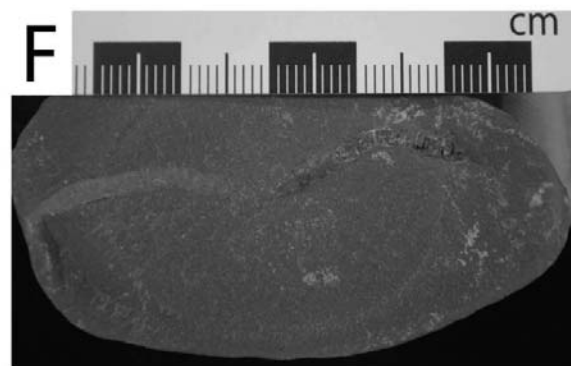
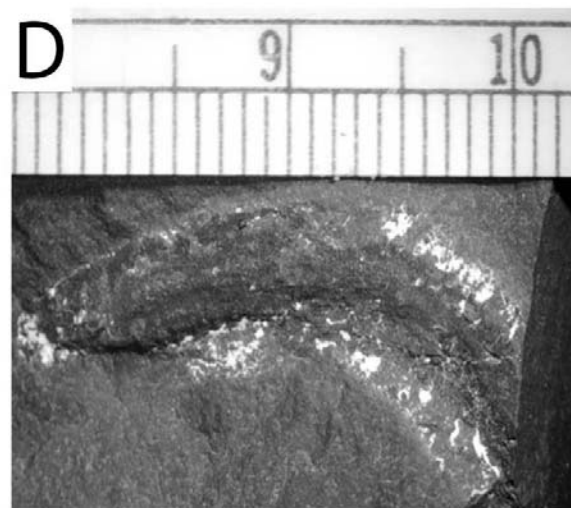
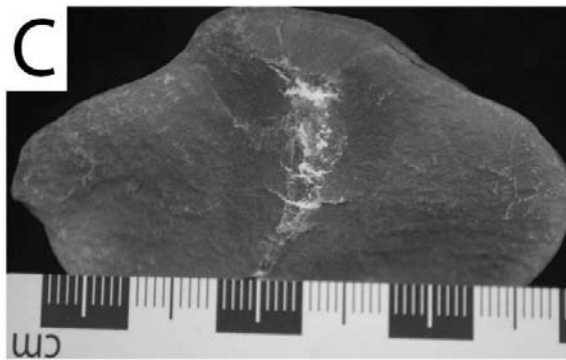
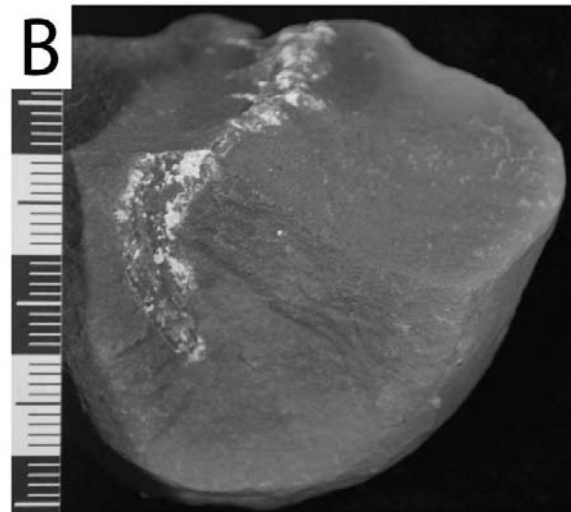
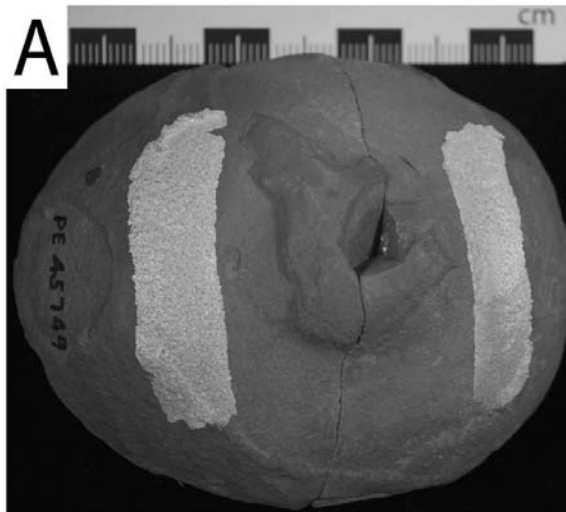


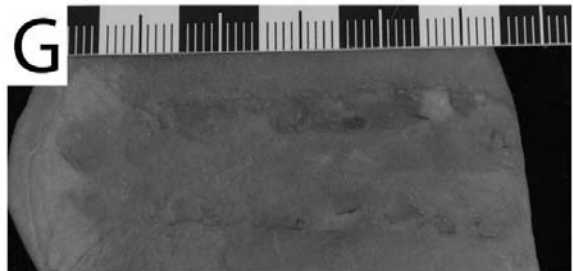
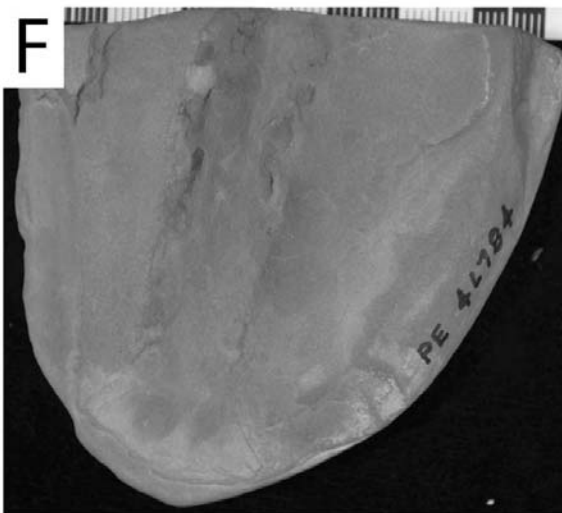
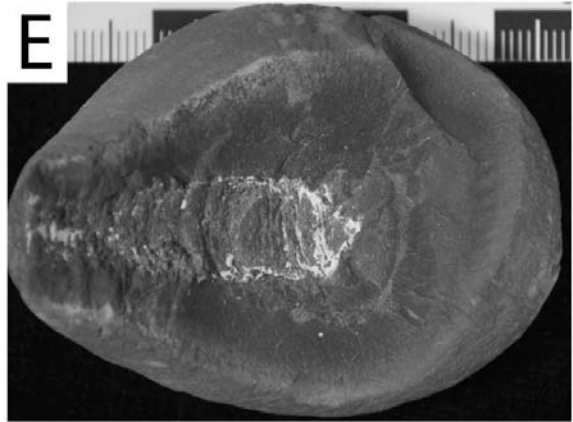
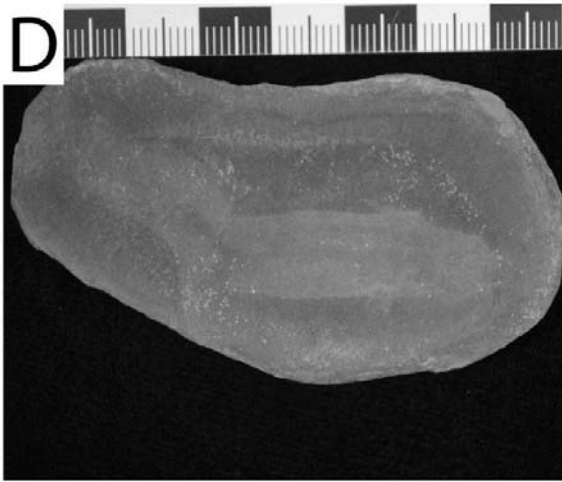
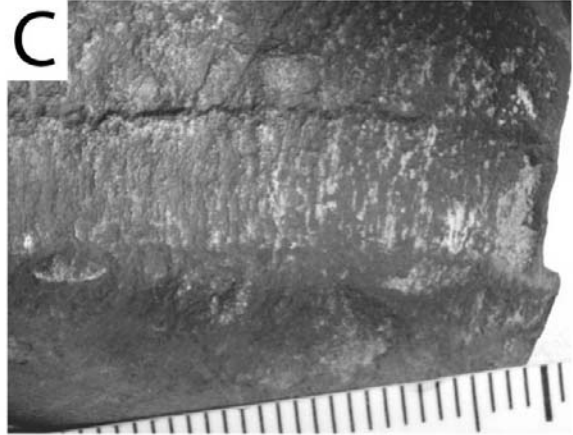
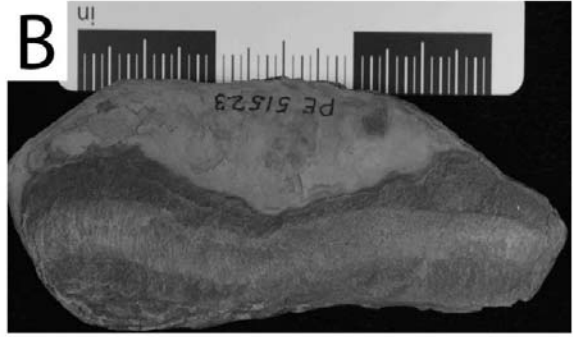
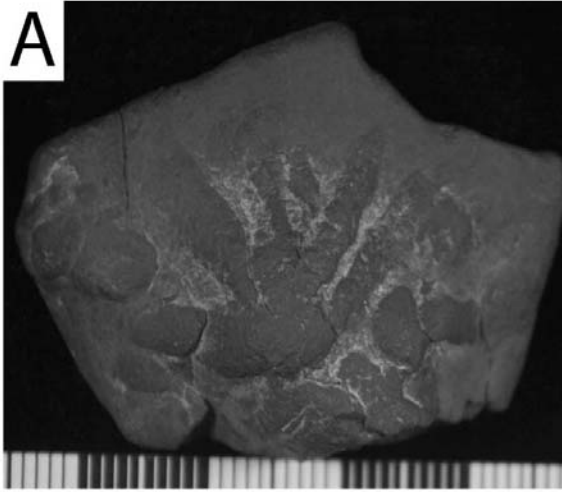


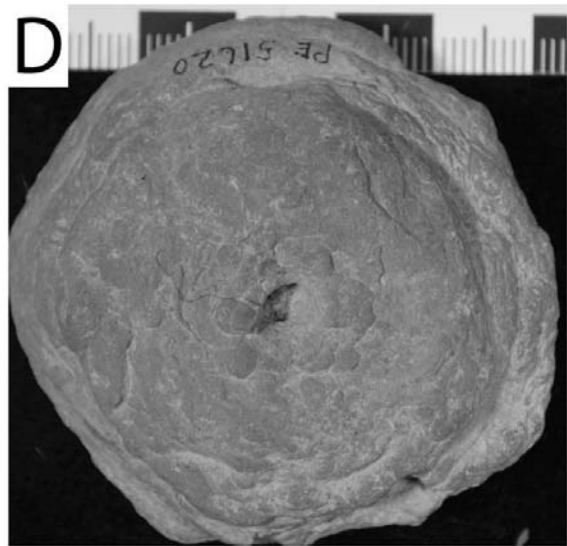
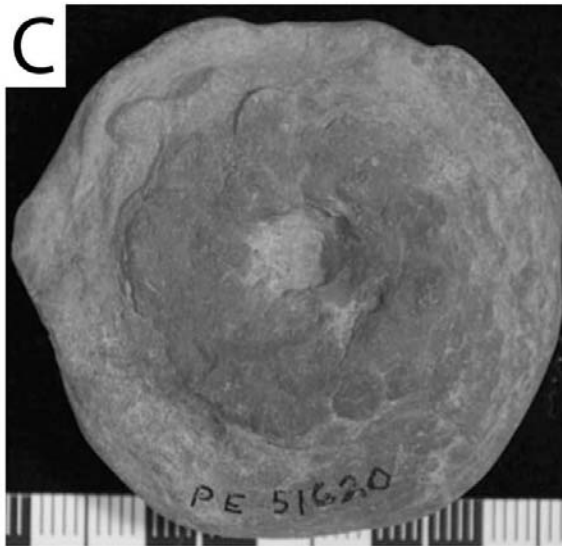
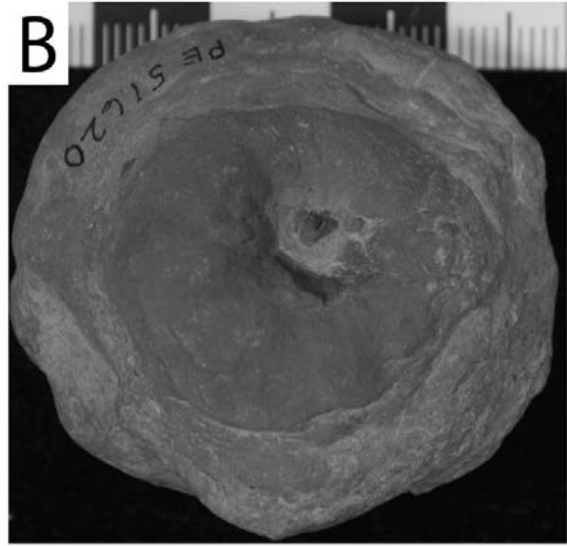
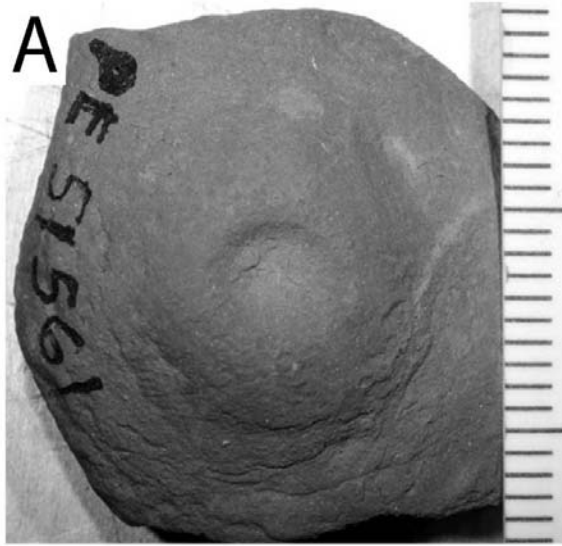


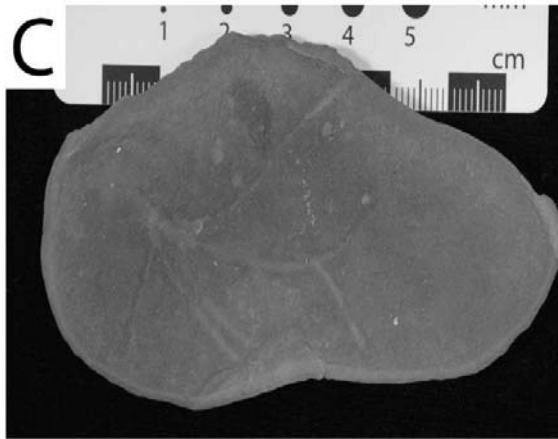
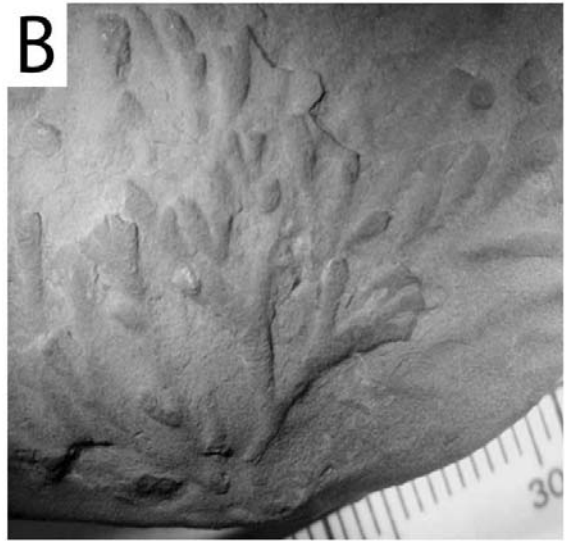
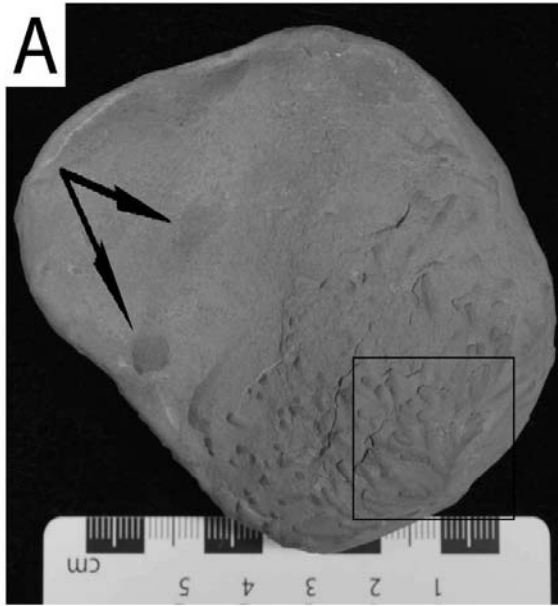


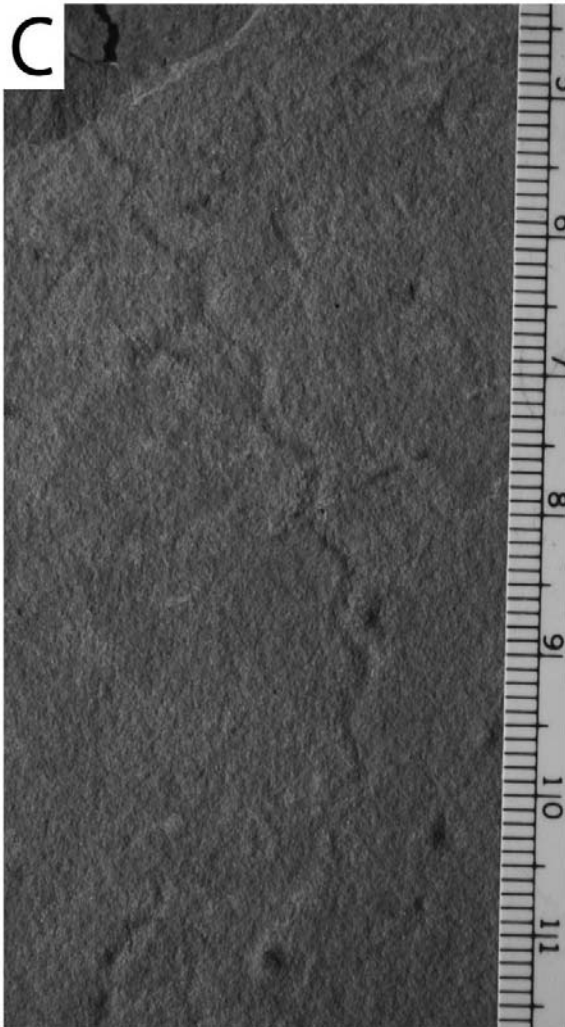
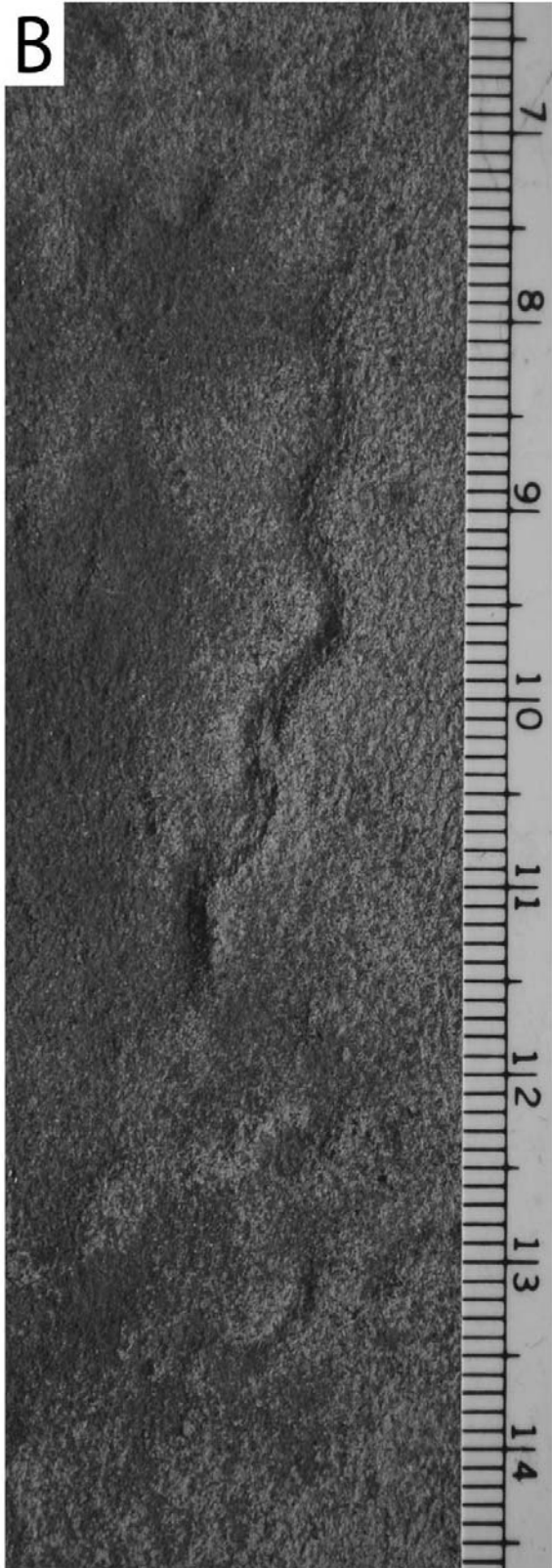
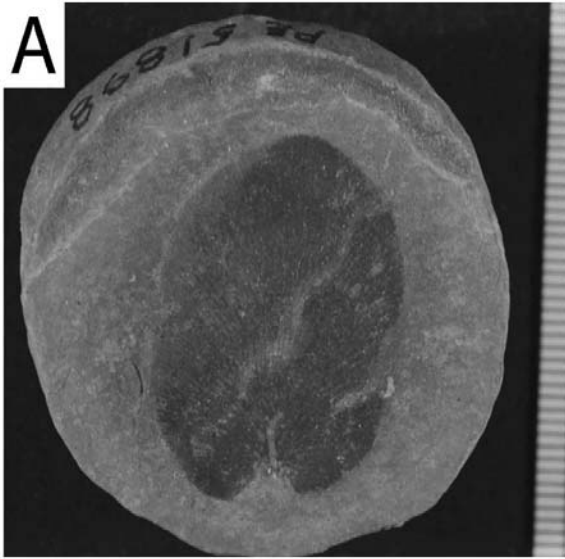


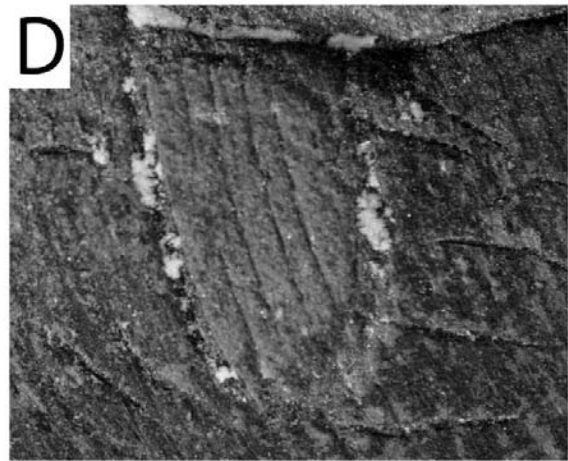
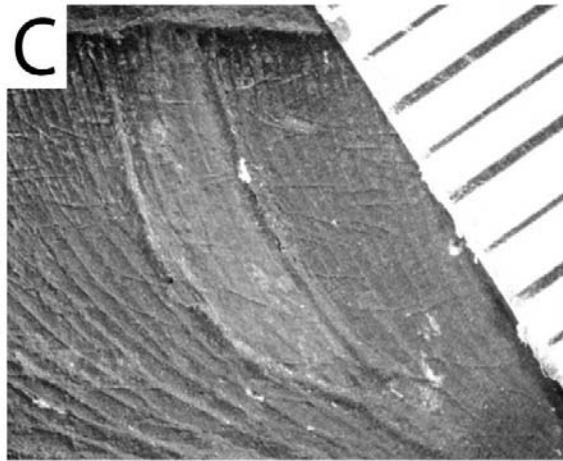
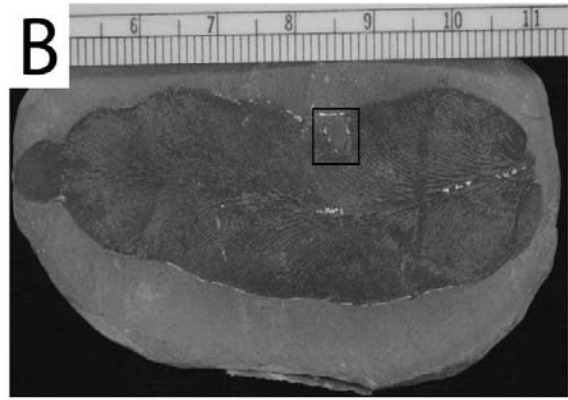
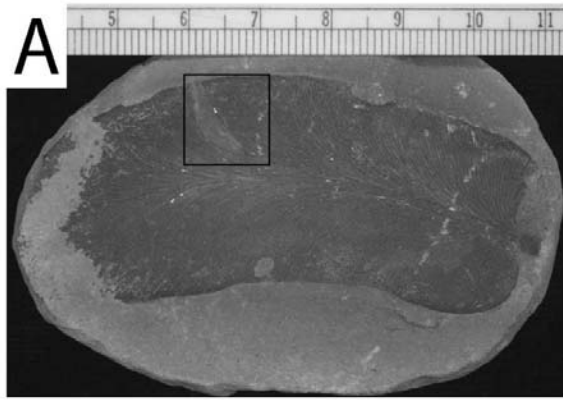


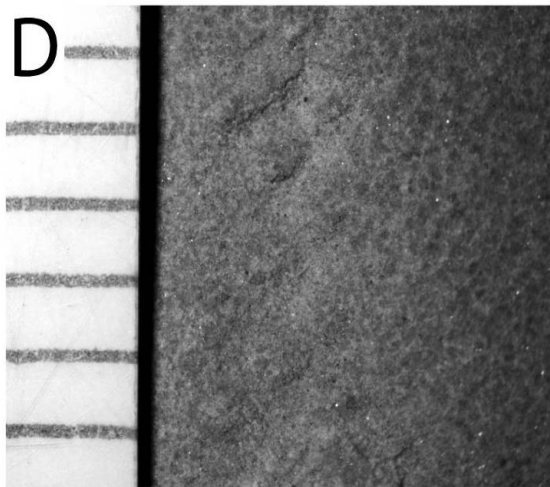
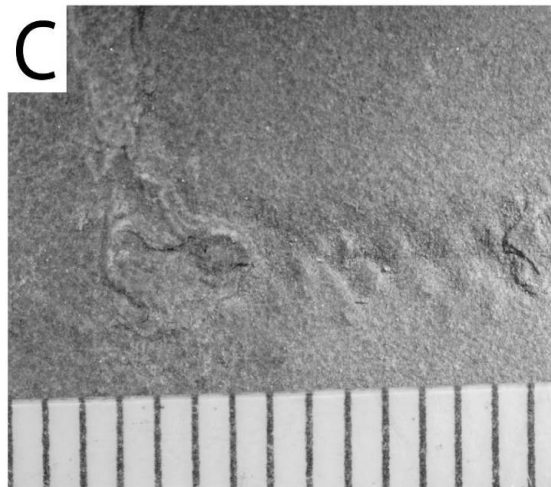
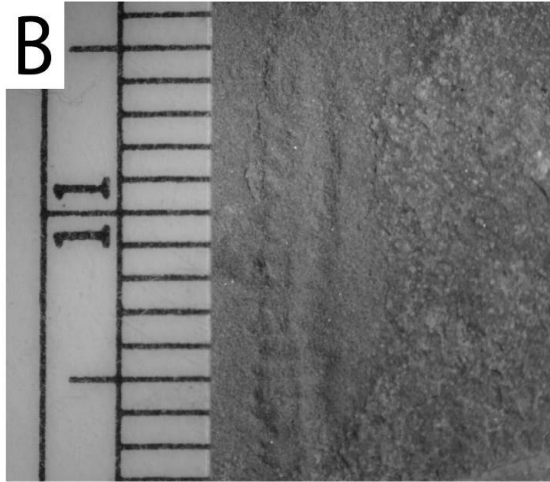
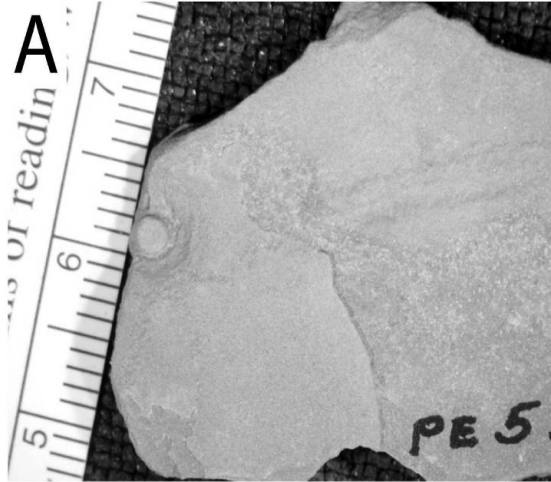


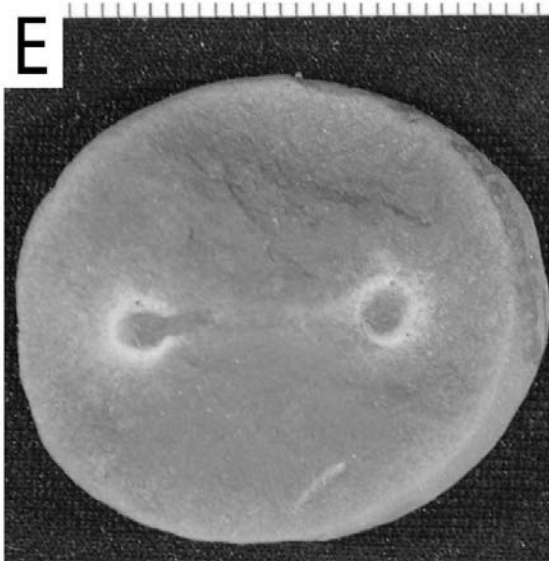
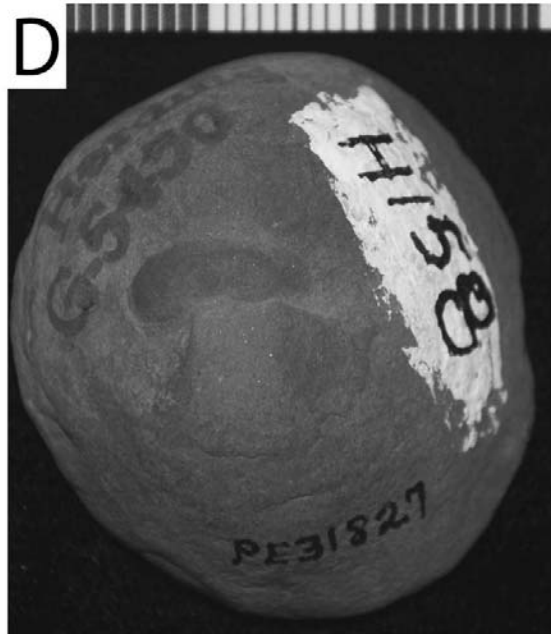
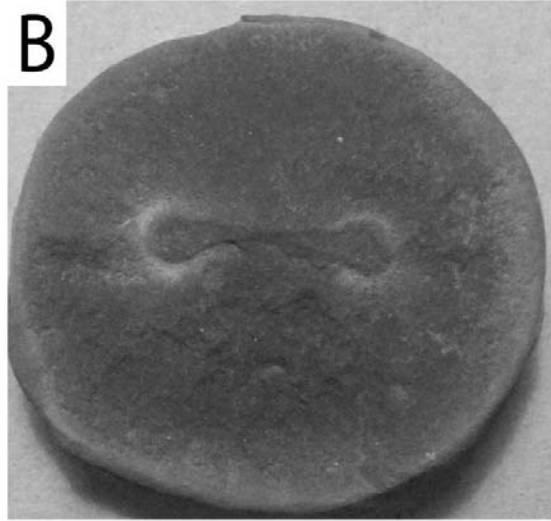
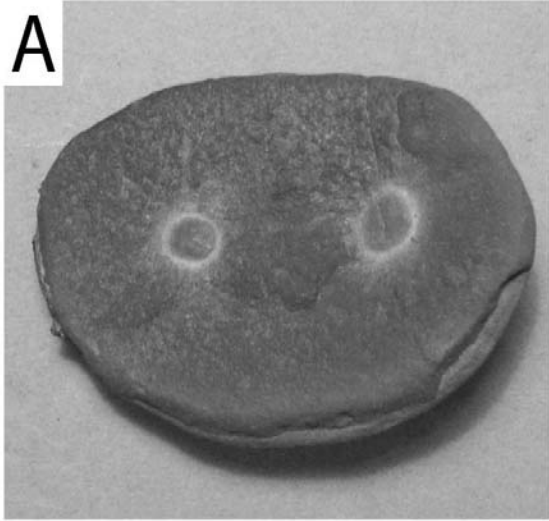


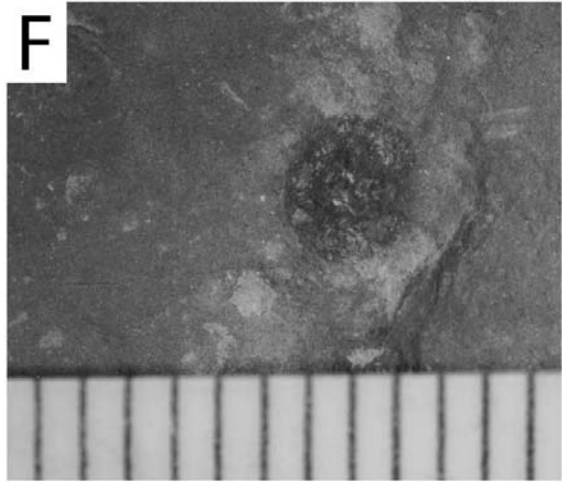
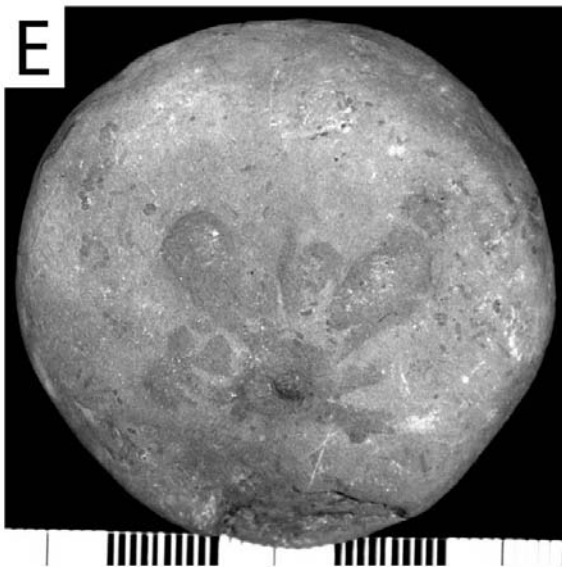
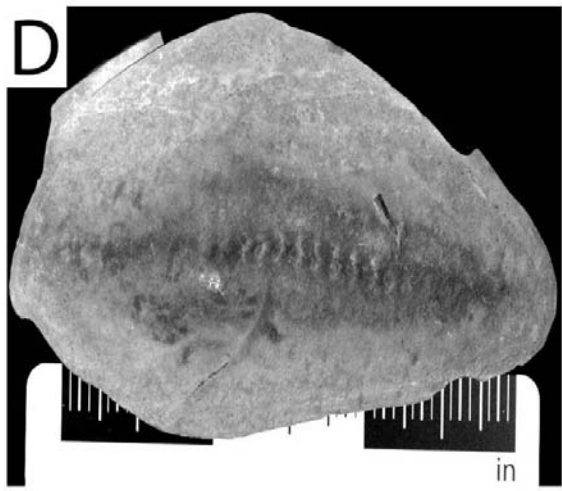
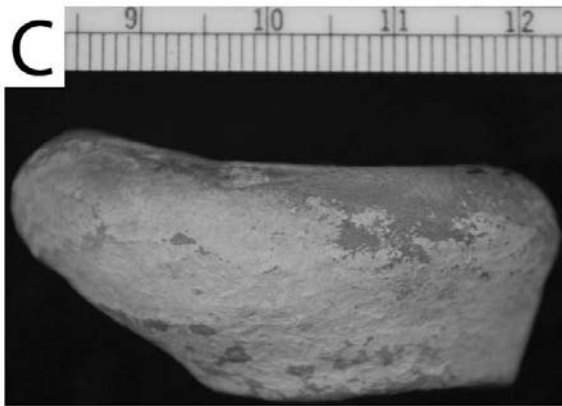
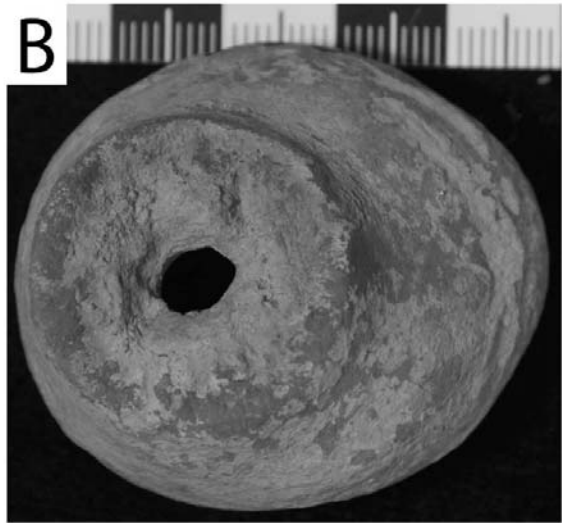


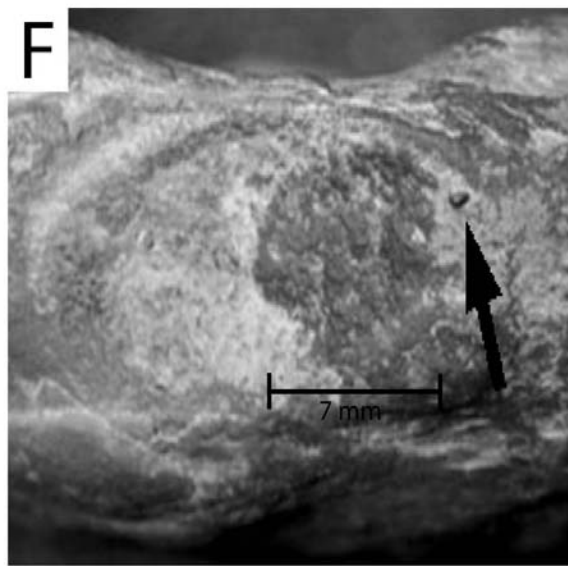
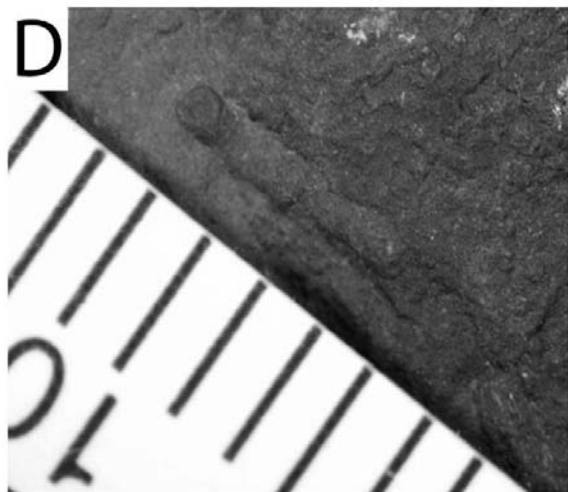
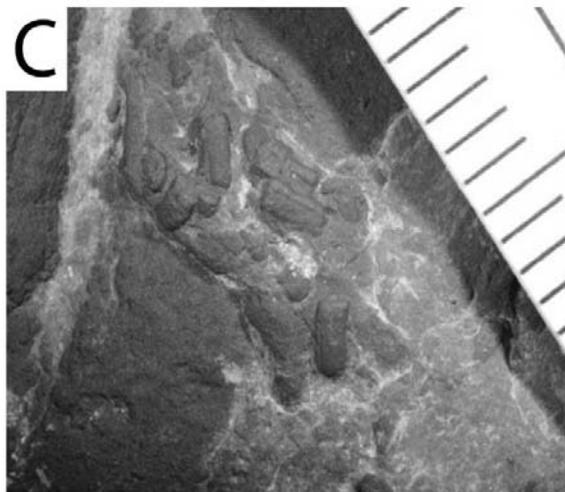
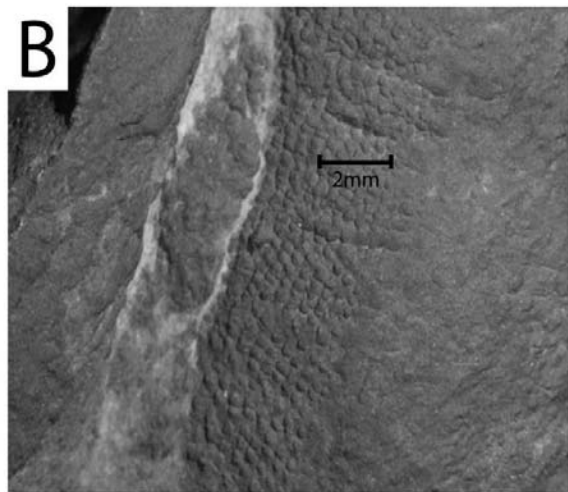
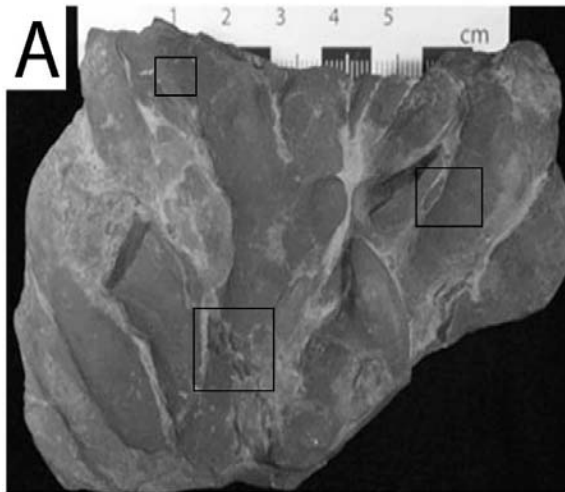


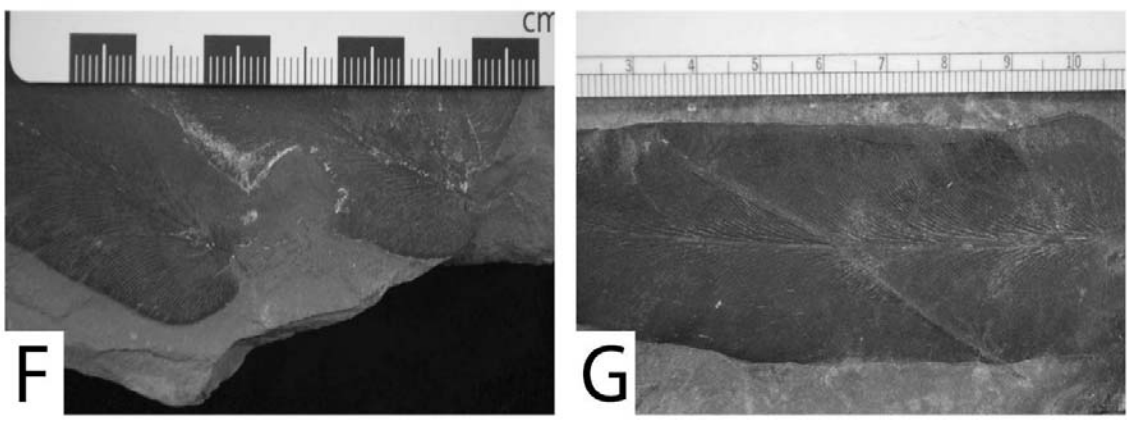
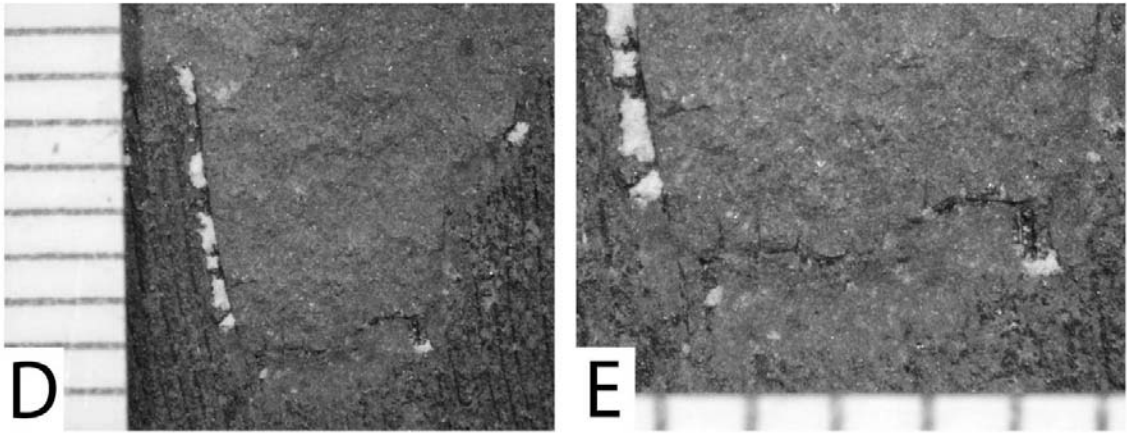
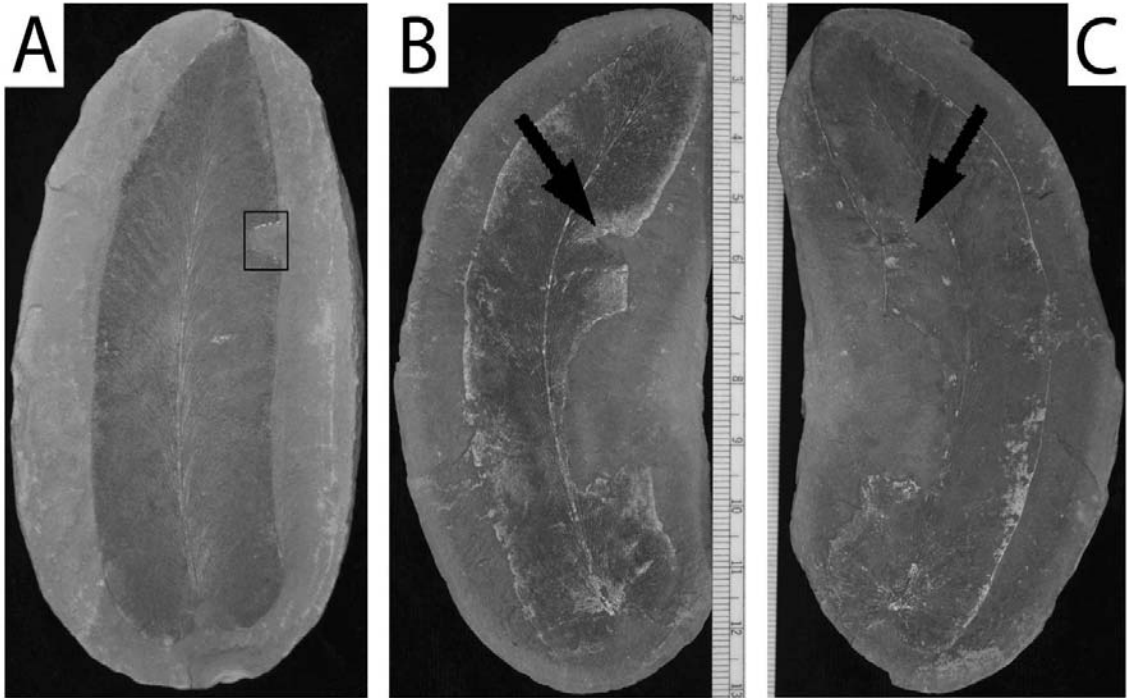


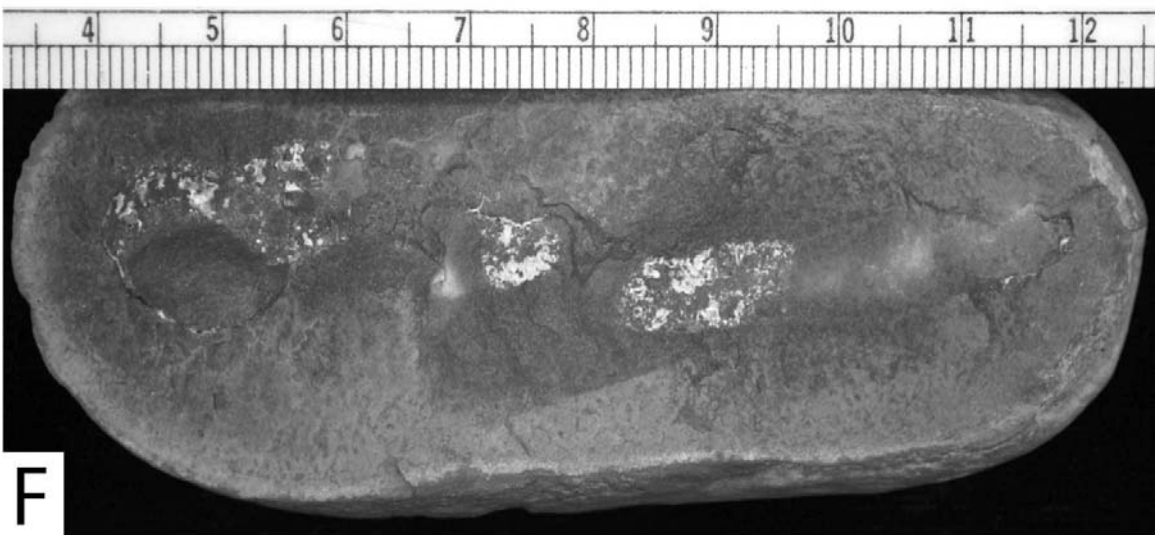
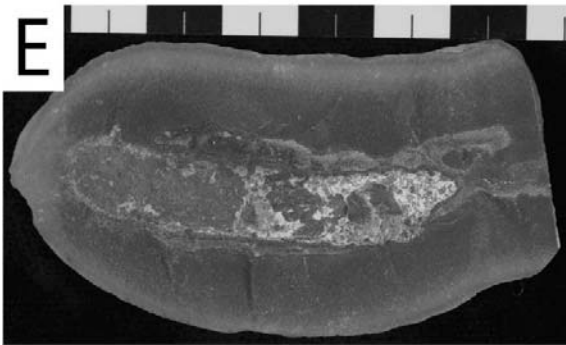
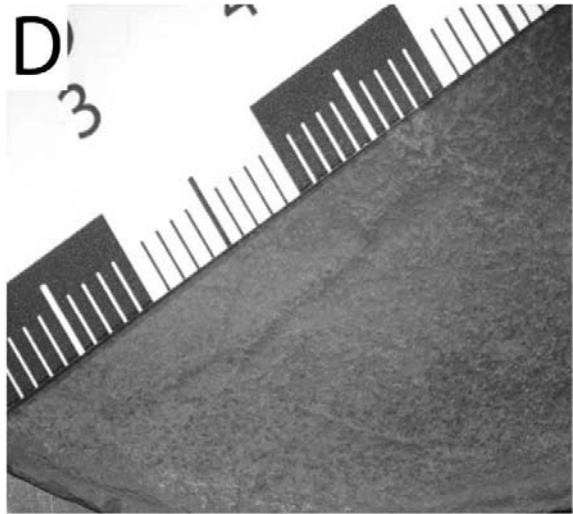
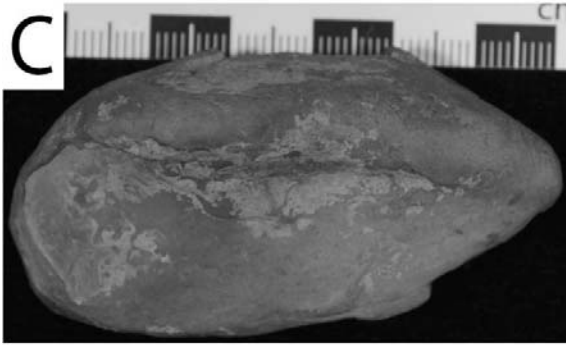
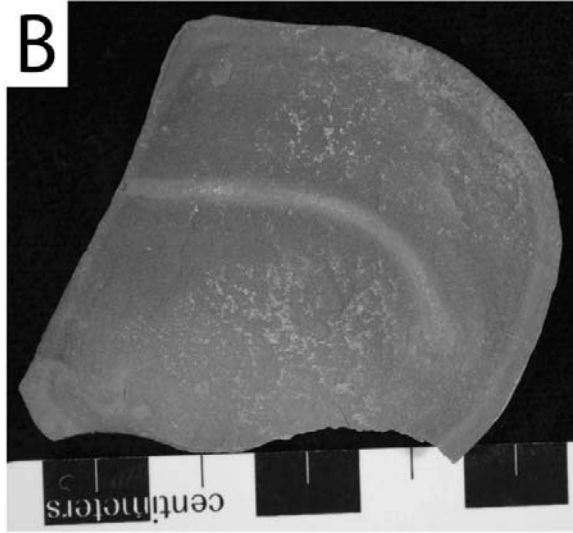
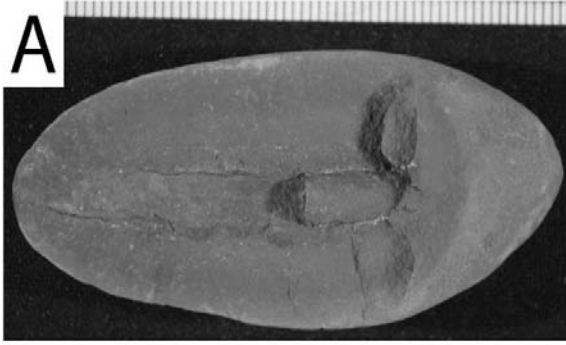


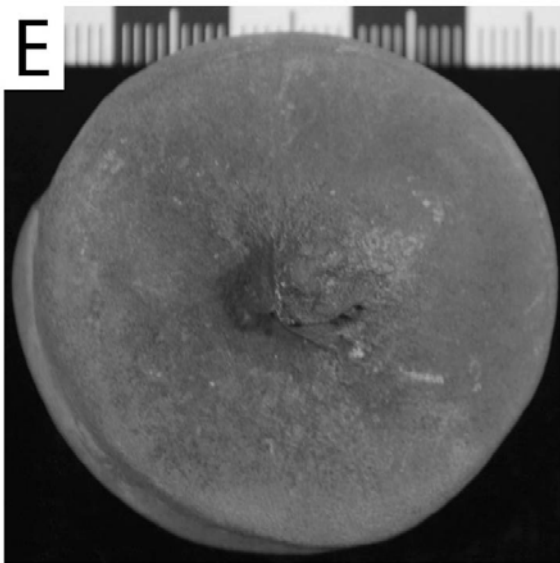
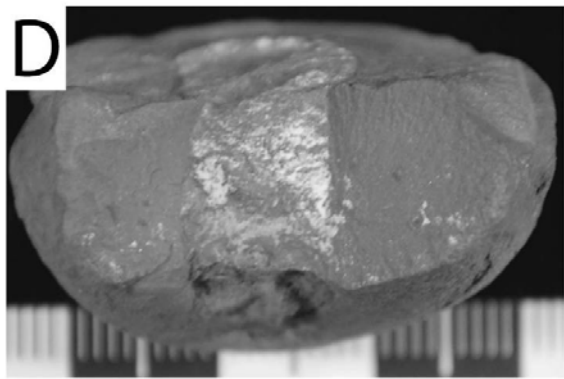
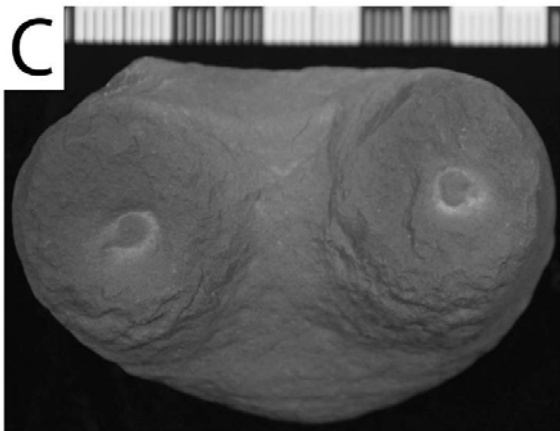
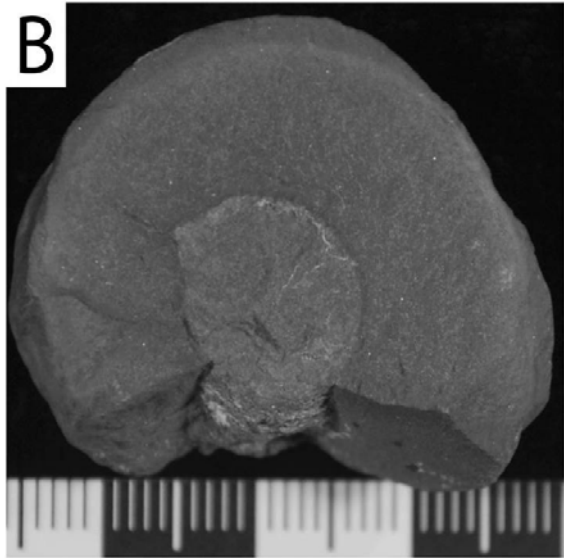
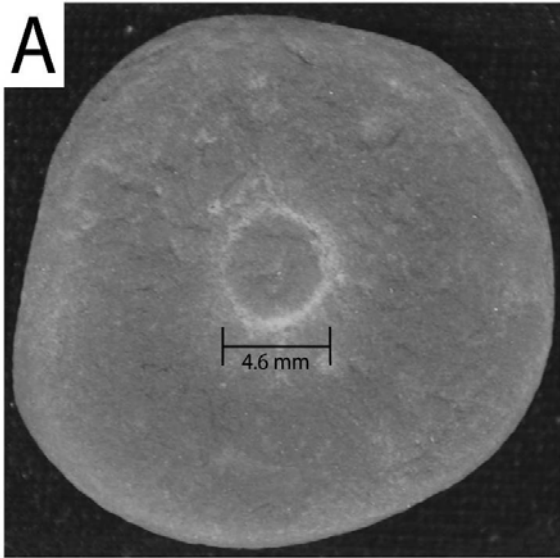


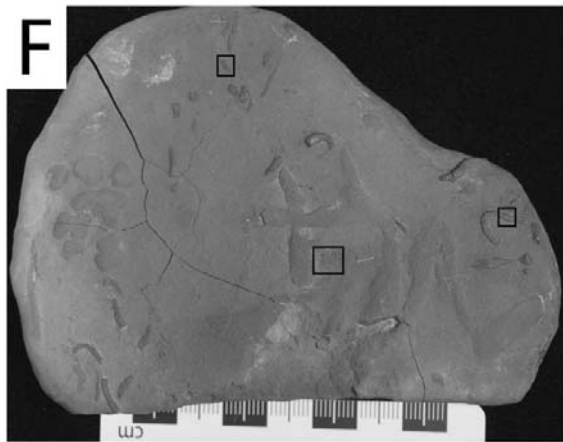
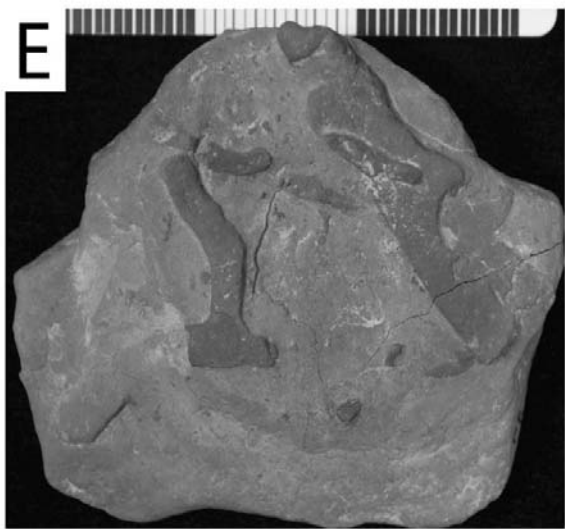
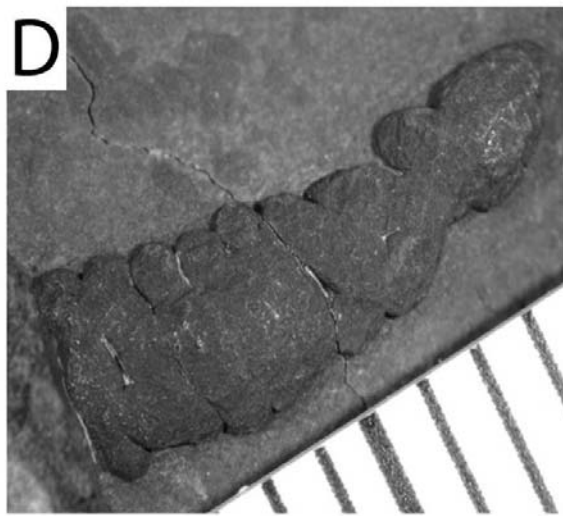
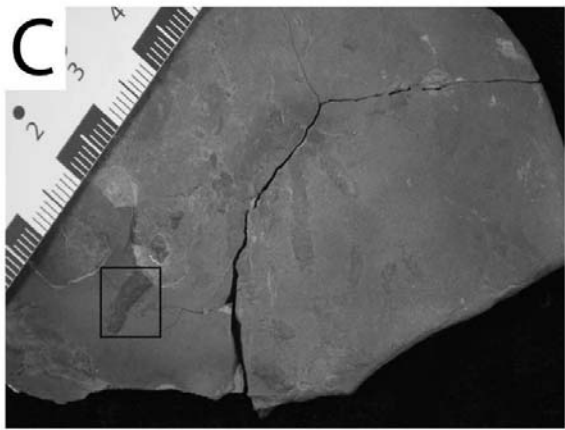


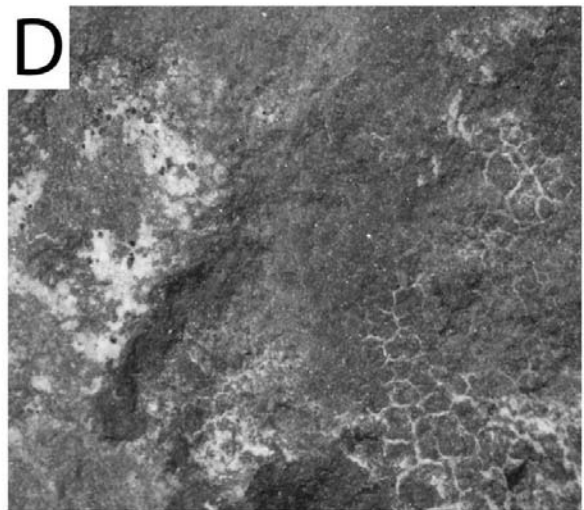
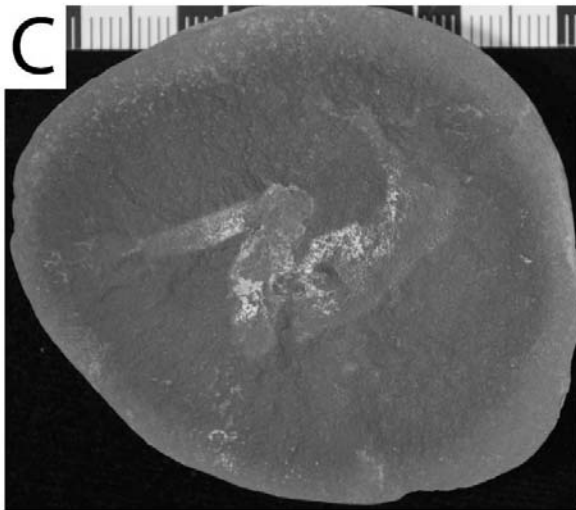
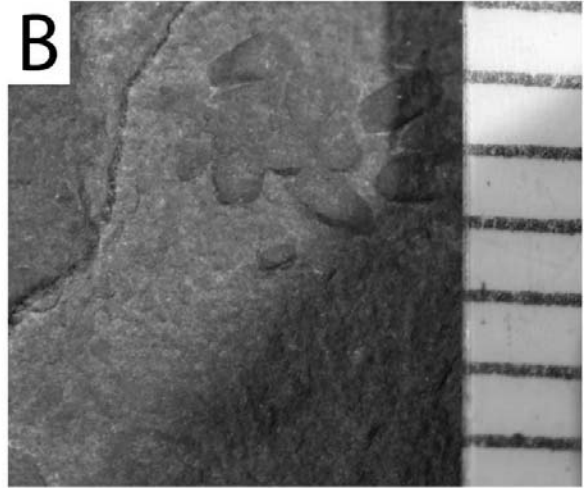
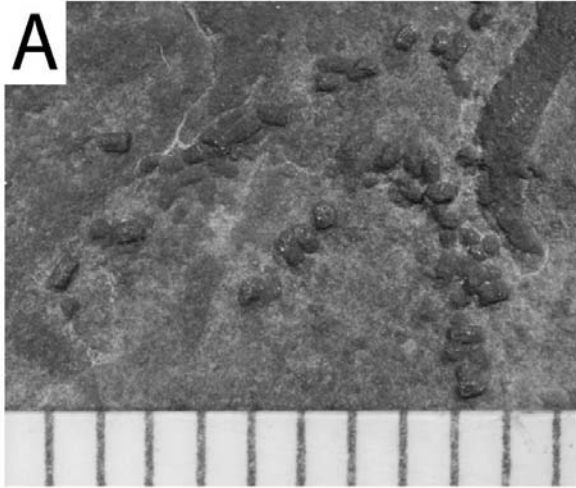


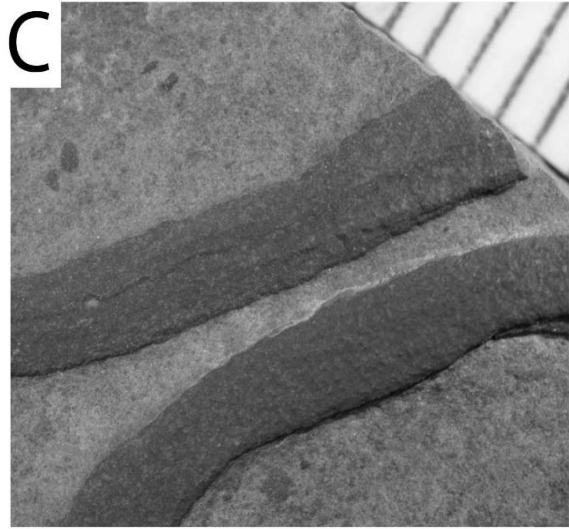
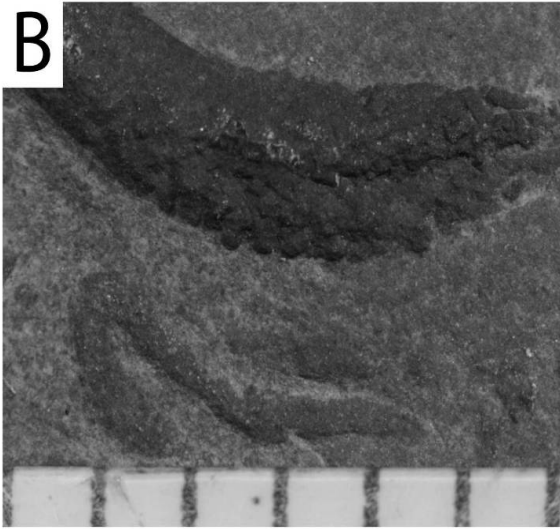
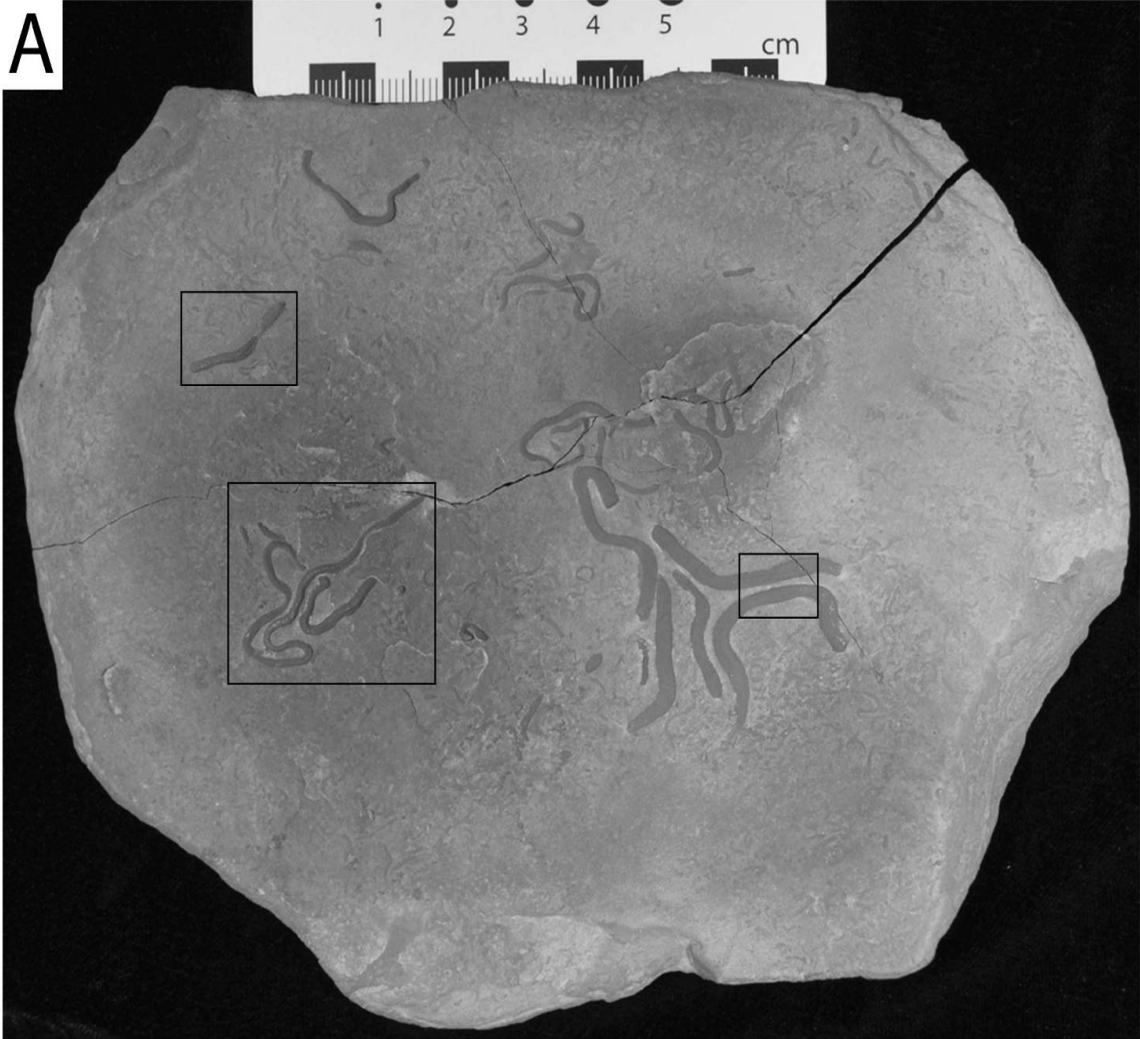


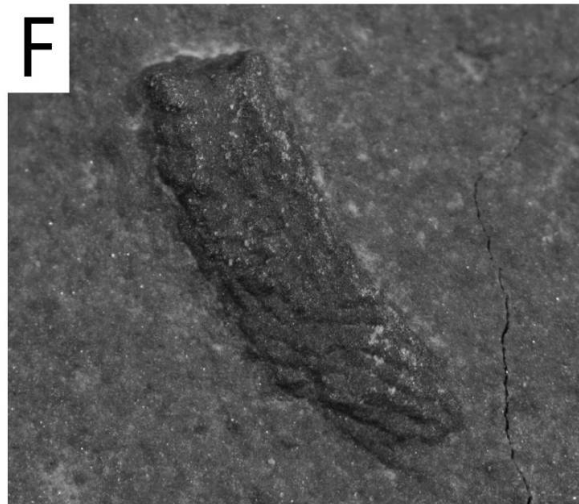
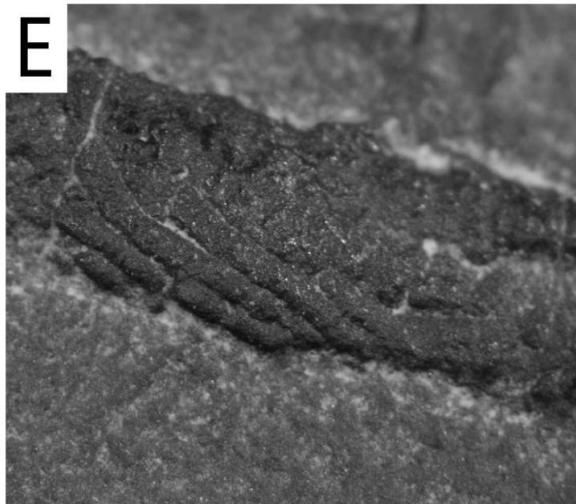
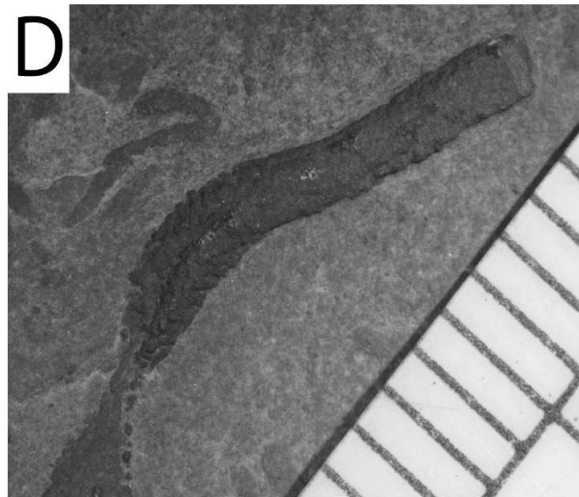
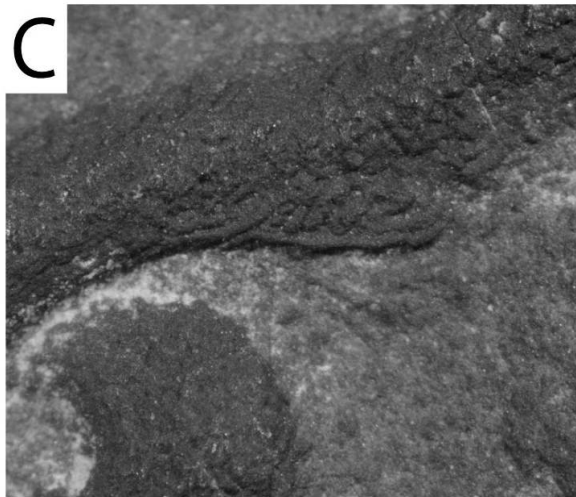
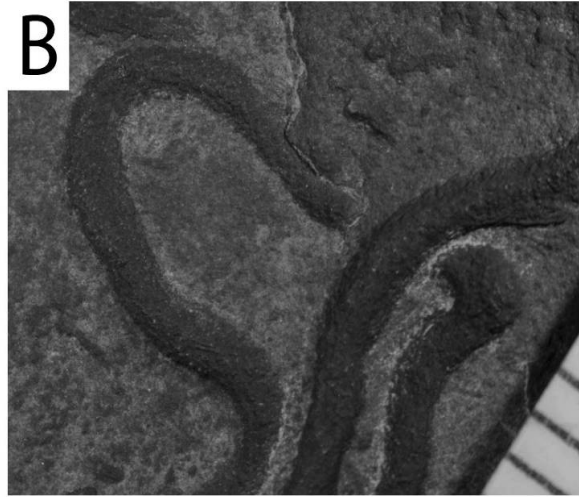


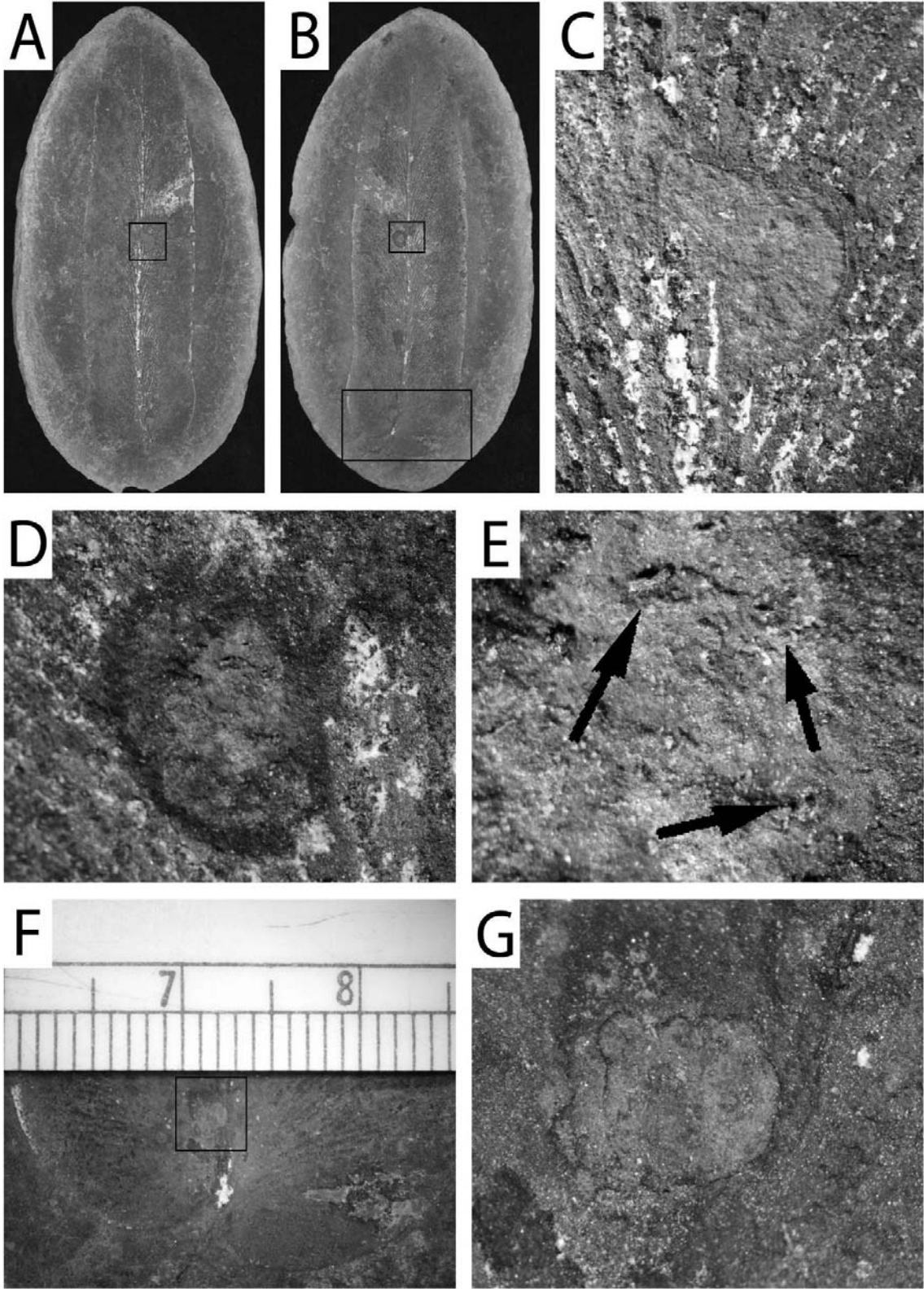


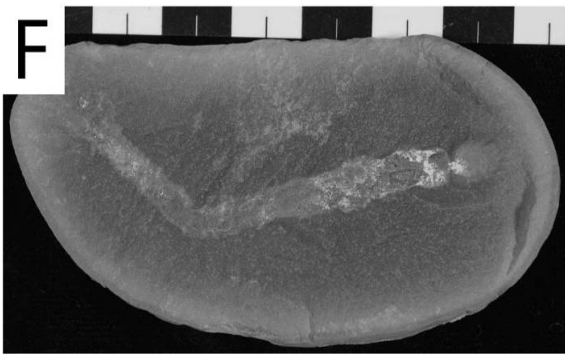
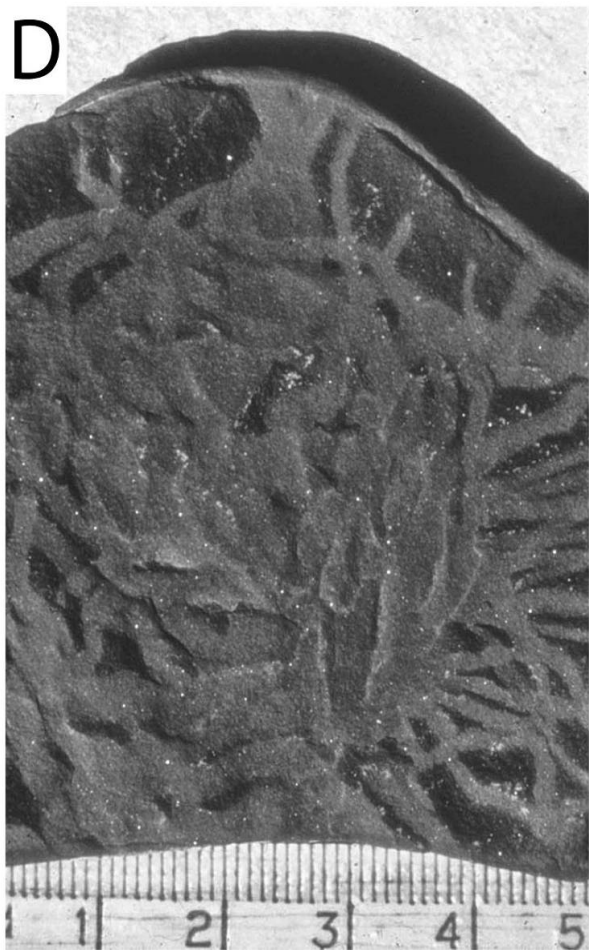
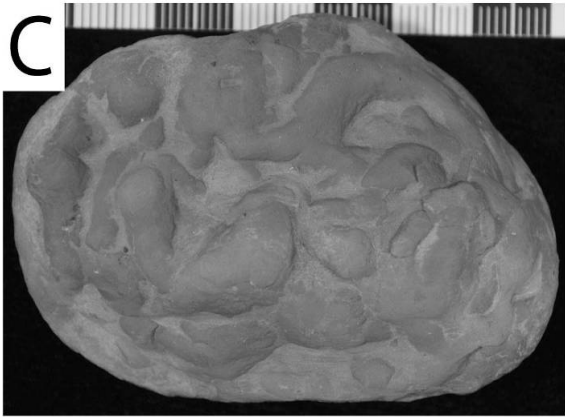
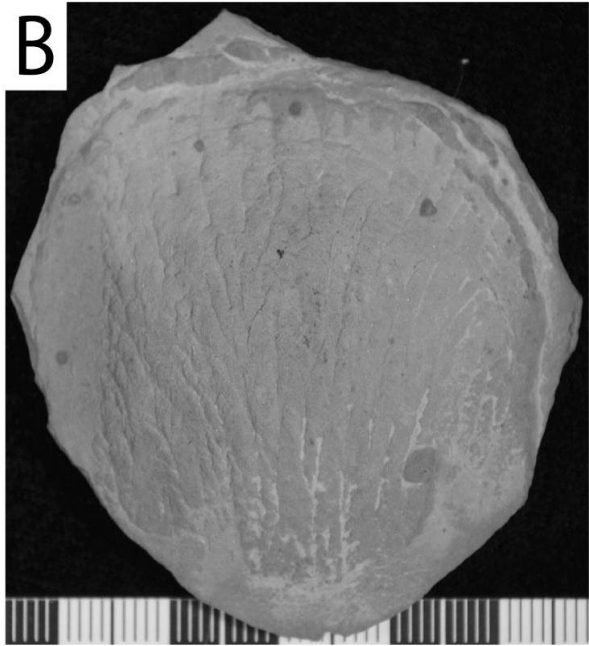
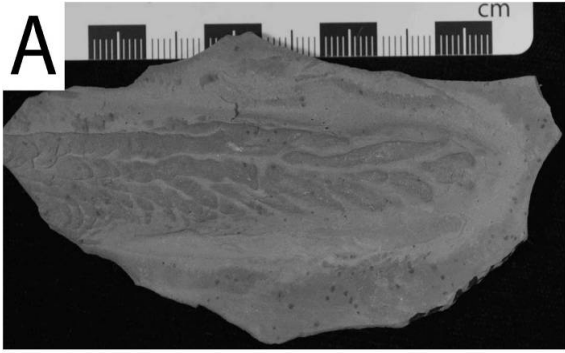


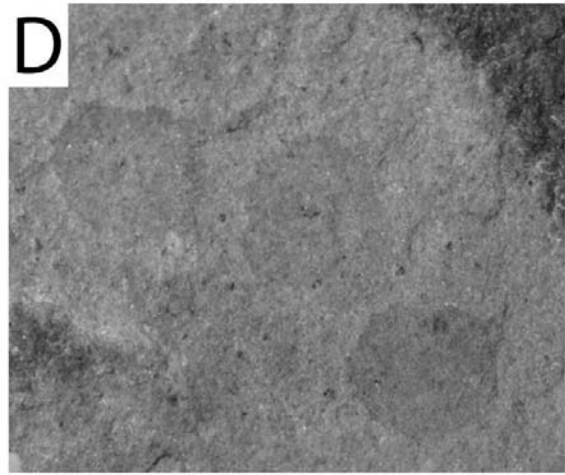
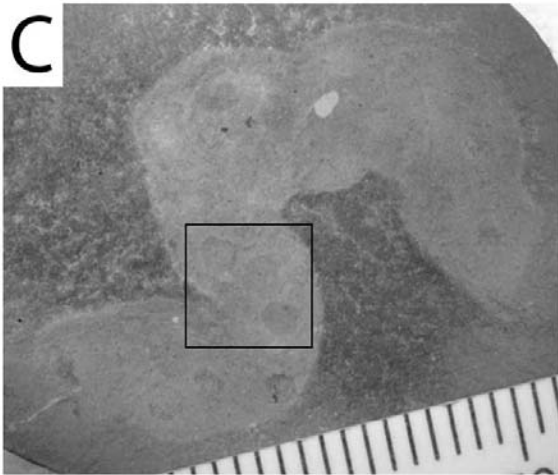
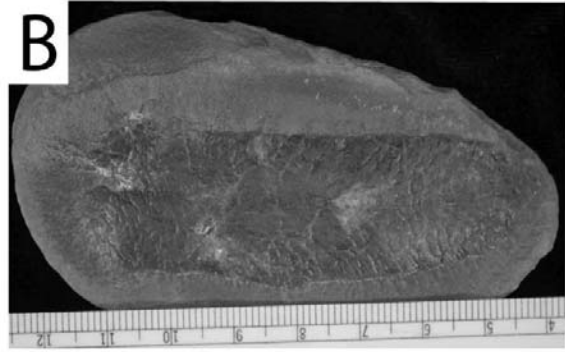
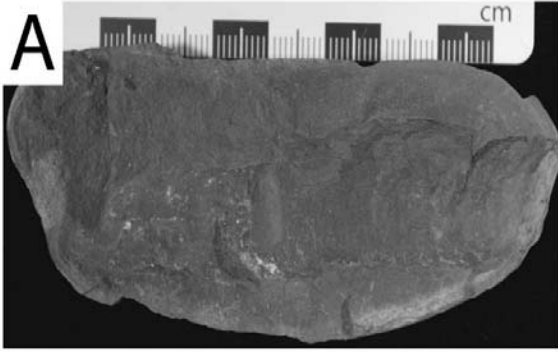












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