



The Ichnogenus *Kouphichnium* and Related Xiphosuran Traces from the Steven C. Minkin Paleozoic Footprint Site (Union Chapel Mine), Alabama, USA: Ichnotaxonomic and Paleoenvironmental Implications

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ABSTRACT

The ichnogenus *Kouphichnium* and associated ichnofossils attributed to xiphosuran activity are here re-examined from samples collected from the Pennsylvanian-age Steven C. Minkin Fossil Site at the Union Chapel Mine, in Walker County, Alabama, USA. The large sample size offers an unique opportunity to evaluate some *Kouphichnium* ichnospecies. Thus, the morphological variability resulting from the taphonomic, ethological, taxonomic variability and underprint fallout are evaluated using this large sample set. Three morphotypes have been segregated from the material previously assigned to *K. aspodon* discovered at this and adjacent sites. Ichnospecies of *Kouphichnium* identified at the Union Chapel Mine site include: *K. lithographicum*, *K. aspodon* and two new ichnospecies (*K. atkinsoni* and *K. minkinensis*). Additionally, *Kouphichnium*-like traces that are associated with “jumper” traces have been previously misinterpreted as *Kouphichnium* and *Selenichnites*, respectively, and are excluded from this study, leaving them in open nomenclature as they will be the subject of a subsequent publication. We here redescribe the holotype of *K. aspodon* and designate lectoparatypes to better define the ichnospecies. New trace makers for some *Kouphichnium* ichnospecies are hypothesized, in contrast to the traditional xiphosuran attribution.

KEYWORDS

Alabama; Carboniferous; ichnology; invertebrate; *Kouphichnium*

Introduction

The Steven C. Minkin Paleozoic Footprint Site (Union Chapel Mine (UCM) site; Hunt et al. 2005) is located in Walker County, Alabama (33° 48' 33.10 N; 87° 09' 58.90 W; Fig. 1A), in a partially reclaimed open pit coal mine (Allen 2005; Figs. 1B and C). Since the site's discovery, the UCM collection has become one of the world's largest caches of Upper Carboniferous terrestrial ichnofossils, including thousands of vertebrate and invertebrate trackways as well as infaunal and surface burrows. The abundance of tetrapod tracks has been the focus of extensive recent studies at UCM, with as many as six tetrapod ichnogenera being recognized (Hunt et al. 2010; Haubold et al. 2005; Hunt and Lucas 2005; Hunt et al. 2005; Martin and Pyenson 2005); however, the invertebrate trackways and burrows have not received as much attention (Buta et al. 2005; Lucas and Lerner 2005). Thus, the invertebrate traces from the UCM have

only been given a cursory study by Lucas and Lerner (2005) and are in dire need of further investigation. According to Lucas and Lerner (2005) and Buta et al. (2005), *Kouphichnium* traces are very common at UCM but are represented by a range of morphological variants, all currently assigned to *K. aspodon* or *K. isp.* (Buta et al. 2005; Lucas and Lerner 2005).

In addition to ichnofossils, the fossil record at UCM encompasses over 2000 other fossil specimens, including: allochthonous, but articulated and disarticulated plant fossils, and invertebrate body fossils (including both productid brachiopods, and rare arthropods; Wood 1963; Atkinson 2005; Dilcher et al. 2005; Buta and Kopaska-Merkel 2016). Plant fossils preserved within the UCM are thought to be detritus, transported from Pennsylvanian peat-accumulating swamps that were established inland, beyond the limits of the UCM site (Minkin 2005).

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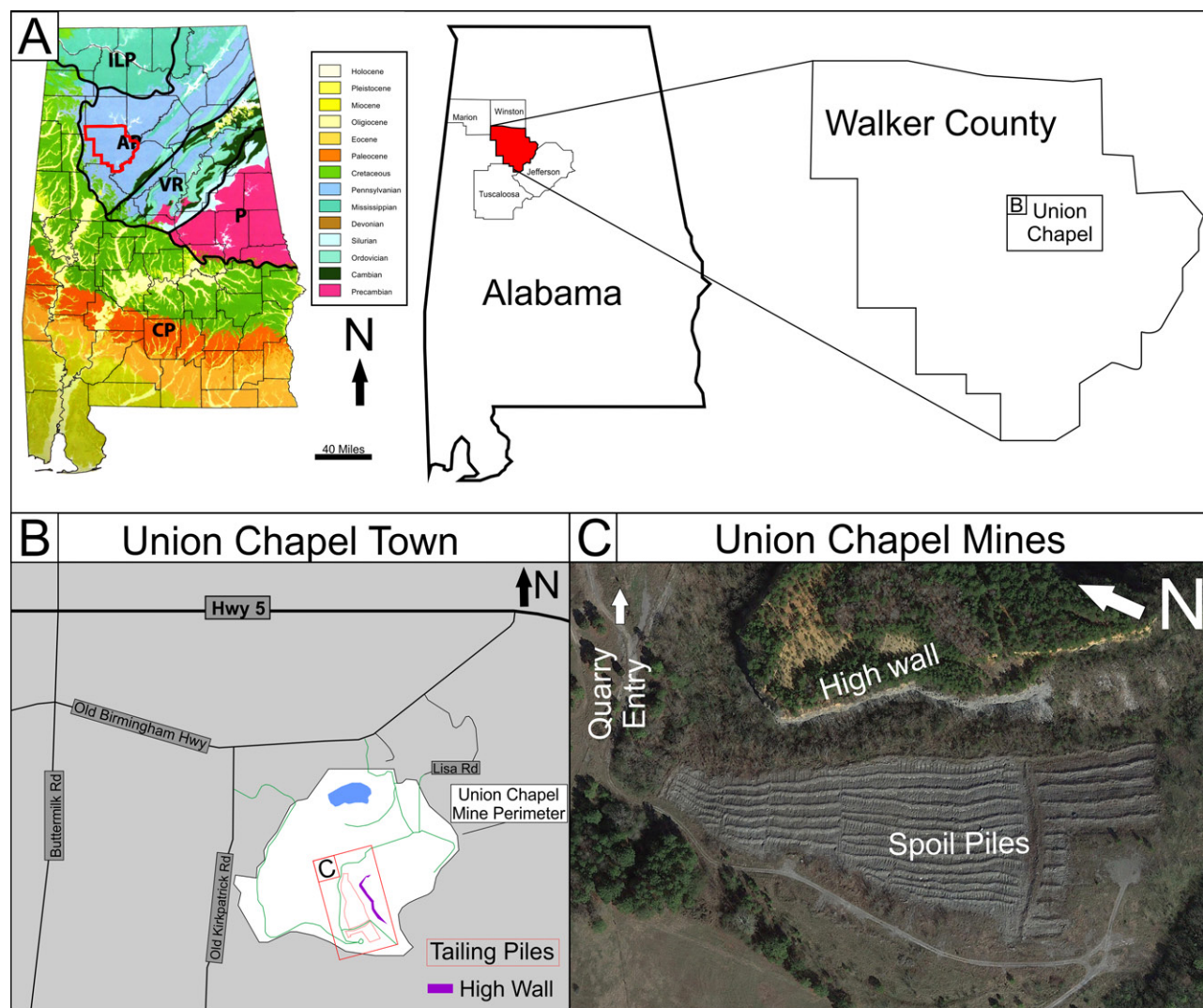


Figure 1. Location map; A) Geological map of Alabama and the site map for the Union Chapel Mine Fossil Site (modified from Buta and Kopaska-Merkel 2016) B) Local map for the town of Union Chapel and quarry map of the open pit site. C) Annotated Google image for the Union Chapel Mine locality (Modified from Google Earth images).

At the UCM, fossils have been collected from the spoil piles (Hooks 2005; Fig. 1C) that consist of the overburden strata of the Mary Lee Coal Bed of the Pottsville Formation (Hunt et al. 2005; Fig. 2), making studying these traces in their precise stratigraphic context difficult (Rindsberg 2005). Pashin (2005) has attempted to place the fossils from the spoil piles back into the strata in the high wall and has provided a preliminary interpretation of the biostratigraphy at UCM (Fig. 2).

In Alabama, Pottsville Formation trace fossils were first noted by Aldrich and Jones (1930) from the Jagger Coal Seam strata in the Number 11 mine of the Galloway Coal Company near Carbon Hill, Walker County, Alabama. Aldrich and Jones (1930) described a number of new ichnogenera and ichnospecies of vertebrate and invertebrate traces, including the type

specimen of *Bipedes aspodon* that was originally, and erroneously, described as an amphibian trackway (Aldrich and Jones 1930). The type specimen of *Bipedes aspodon* was described from three individual bifid impressions on the outer edge of a broken rock slab (Fig. 3). The holotype of the ichnospecies (*B. aspodon*) conforms with the ichnogenus *Kouphichnium* (Minter and Braddy 2009) but has never been formally reassigned to that ichnogenus. Many subsequent and more complete specimens discovered from UCM are assignable to this ichnogenus but have only been informally assigned to "*Kouphichnium aspodon*" without a detailed ichnotaxonomic restudy and ascribed to xiphosurid trace makers (Buta et al. 2005). Body fossils of xiphosurids have not been found in the Pottsville Formation of Alabama, although some of its ichnotaxa have been interpreted to have been produced by

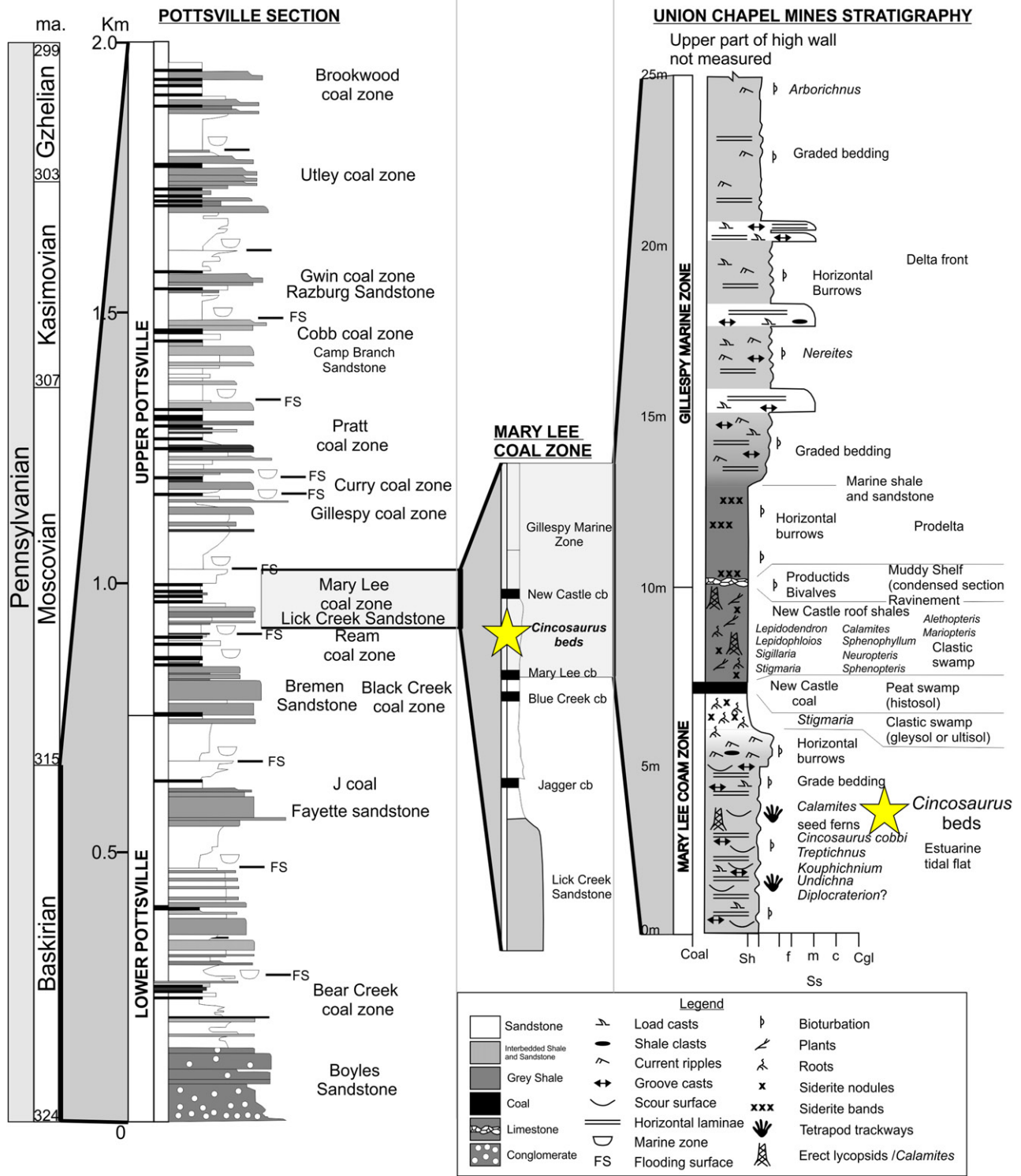


Figure 2. Stratigraphic log for the Pottsville Formation and the exposed strata at the Union Chapel Mine site (modified from Pashin 2005). The Star indicates the stratigraphic location of the trace fossil beds.

xiphosurans, including: *Kouphichnium*, *Selenichnites*, *Arborichnus* and the “unassigned xiphosuran traces” (Buta et al. 2005; Lucas and Lerner 2005).
The first recognition of the ichnogenus *Kouphichnium* isp. at UCM was made by Mángano

and Buatois (2004) and in Rindsberg and Kopaska-Merkel (2003). Subsequent work by Lucas and Lerner (2005), in a preliminary study of the ichnotaxonomy of invertebrate traces from the UCM, also used the name *Kouphichnium* isp. for traces that strongly



Figure 3. A) *Kouphichnium aspodon*, type specimen, AMNH 985.1.6 B) Interpretive sketch of complete trackway of type specimen, AMNH 985.1.6 C) Close-up of bifid impressions of the type specimen, AMNH 985.1.6, indicated by white arrows.

resemble morphologies described later in the same volume by Buta et al. (2005) as unassigned xiphosuran traces. Buta et al. (2005) were the first to informally reassign the ichnospecies *Bipedes aspodon* to the ichnogenus *Kouphichnium*, but this was done without proper systematic ichnological work. Buta et al. (2005) used the ichnospecies name liberally to encompass a wide array of morphologies for any walking traces they assumed to be made by xiphosurans. An exception in Buta et al. (2005) are trackways that were left, and remain, in open nomenclature and that were only identified as “unassigned xiphosuran traces”. These

unassigned xiphosuran traces are associated with cubichnia traces that have been erroneously assigned to the ichnogenus *Selenichnites*, although actual *Selenichnites* do exist in the UCM ichnofaunal assemblage (Lucas and Lerner 2005). We leave both the cubichnia and tracks assigned to unassigned xiphosuran traces in open nomenclature, as they do not conform to the *Kouphichnium* ichnogenus concept and are not interpreted as having been made by xiphosurans. Thus, they will only be mentioned briefly in this manuscript, as they will be the subject of a subsequent paper.

With the large sample size of invertebrate trackways now available for study from the UCM site, the ichnogenus *Kouphichnium* and its ichnospecies can now be re-examined to better characterize the morphology and distinguish the various *Kouphichnium* ichnospecies at this site with greater confidence. In particular, the purpose of this study is to re-examine the type of *B. aspodon*, and the multitude of specimens that have been assigned to *K. aspodon* from the UCM. We here segregate specimens assigned to this ichnospecies into four *Kouphichnium* ichnospecies, including a previously unidentified ichnospecies at UCM (*K. lithographicum*); we better define the ichnospecies *K. aspodon*, and name two new ichnospecies – *K. minkinensis* isp. nov., and *K. atkinsoni* isp. nov. Many specimens from the UCM that previous authors erroneously identified as *Kouphichnium* are provisionally excluded from this ichnogenus and are left in open nomenclature pending further study. Additional limulid activity at UCM has been attributed to a number of ichnogenera, including, *Selenichnites*, *Arborichnus* and unassigned xiphosuran traces (Lucas and Lerner 2005), that will be examined here.

Geological background and stratigraphy

Regional setting

The Union Chapel Mine exposes strata of the Pottsville Formation (Fig. 2) that have been dated to the Early Pennsylvanian (Morrowan Epoch; Langsettian Stage, Westphalian A; Fig. 2) by both palynology and marine invertebrate correlations (Butts 1926; Eble and Gillespie 1989; Eble et al. 1991). The Pottsville Formation was deposited in the Warrior Coal Basin, which is part of the broader Black Warrior Basin, a foreland basin, that formed at the junction of the Appalachian and Ouachita orogenic belts (Pashin 2005; Fig. 4). The siliclastic sediments of the Pottsville Formation were sourced from adjacent orogenic belts and accumulated within the Warrior Coal Basin from the Late Mississippian through the Pennsylvanian (Pashin 2005; Fig. 4C).

The sedimentology and paleontology of the Pottsville formation

The Pottsville Formation is a two-kilometer-thick heterogeneous sedimentary succession composed mainly of shale, sandstone, bituminous coal and nodular limestone (Aldrich and Jones 1930; Fig. 2). The formation is divided into upper and lower strata that are organized into “coal zones.” The 750-meter-thick, lower, sandstone-rich Pottsville Formation lacks

economic coal beds, whereas the 1.25 km-thick, upper, shale-rich Pottsville Formation contains abundant economic bituminous coal that includes the Mary Lee Coal Zone exposed at the UCM. The Mary Lee Coal Zone is stratigraphically located 1 km above the base of the formation (250 meters above the base of the upper part of the formation) and is composed of four coal seams, two of which were mined at UCM; the Mary Lee and New Castle coal beds (Pashin 2005; Fig. 2).

The upper Mary Lee Coal Zone strata, as exposed at the UCM, are 25 meters thick and are overlain by the Gillespie Marine Zone. The Mary Lee Coal Bed is directly overlain by the lower “*Cincosaurus* beds,” which contain all of the ichnofossils preserved at this site and other adjacent sites. The “*Cincosaurus* beds” preserve intervals dominated by tidal rhythmites of pinstripe-bedded mudstones, siltstone-shales and sandstone-shales that fine upwards. Individual beds range between 0.2 cm and 4 cm thick, with the trackways preserved on the tops of individual beds. These beds preserve an array of ichnofossils that include: tetrapod tracks (Haubold et al. 2005; Hunt et al. 2010), invertebrate traces (Buta et al. 2005; Lucas and Lerner 2005; Rindsberg and Kopaska-Merkel 2005a, 2005b; Lucas and Stimson 2013) and fish trails (Haubold et al. 2005; Martin and Pyenson 2005; Fig. 2).

Tetrapod and invertebrate tracks are often associated with articulated allochthonous plant detritus as described by Dilcher and Lott (2005) and Dilcher et al. (2005). Pashin (2005) noted the only autochthonous plants to the *Cincosaurus* beds were *Calamites* stems and a single fern stem. The paleoflora was studied by Dilcher et al. (2005) and found to be similar to a previously studied, temporally equivalent paleoflora in Indiana (Wood 1963). The paleoflora is dominated by *Calamites*, lycopods and understory plants, including seed ferns and pteridosperms. Riparian plants are represented by isolated foliage, seeds and pith casts of cordaitaleans that likely occupied the hinterlands (Falcon-Lang 2006; Falcon-Lang and Bashforth 2004; Dilcher et al. 2005). The UCM flora has a fine preservation and a high degree of articulation that suggest the detritus was not transported far before burial (Dilcher et al. 2005).

The upper strata of the *Cincosaurus* Beds include a light gray, fine-grained sandstone that preserves wavy ripple bedforms with discoidal shale and siderite pebbles, often with the invertebrate resting trace *Arborichnus repetitus*. The uppermost meter of strata is a reddish-hued sandy underclay that preserves stigmariian roots below the New Castle coal beds (Pashin

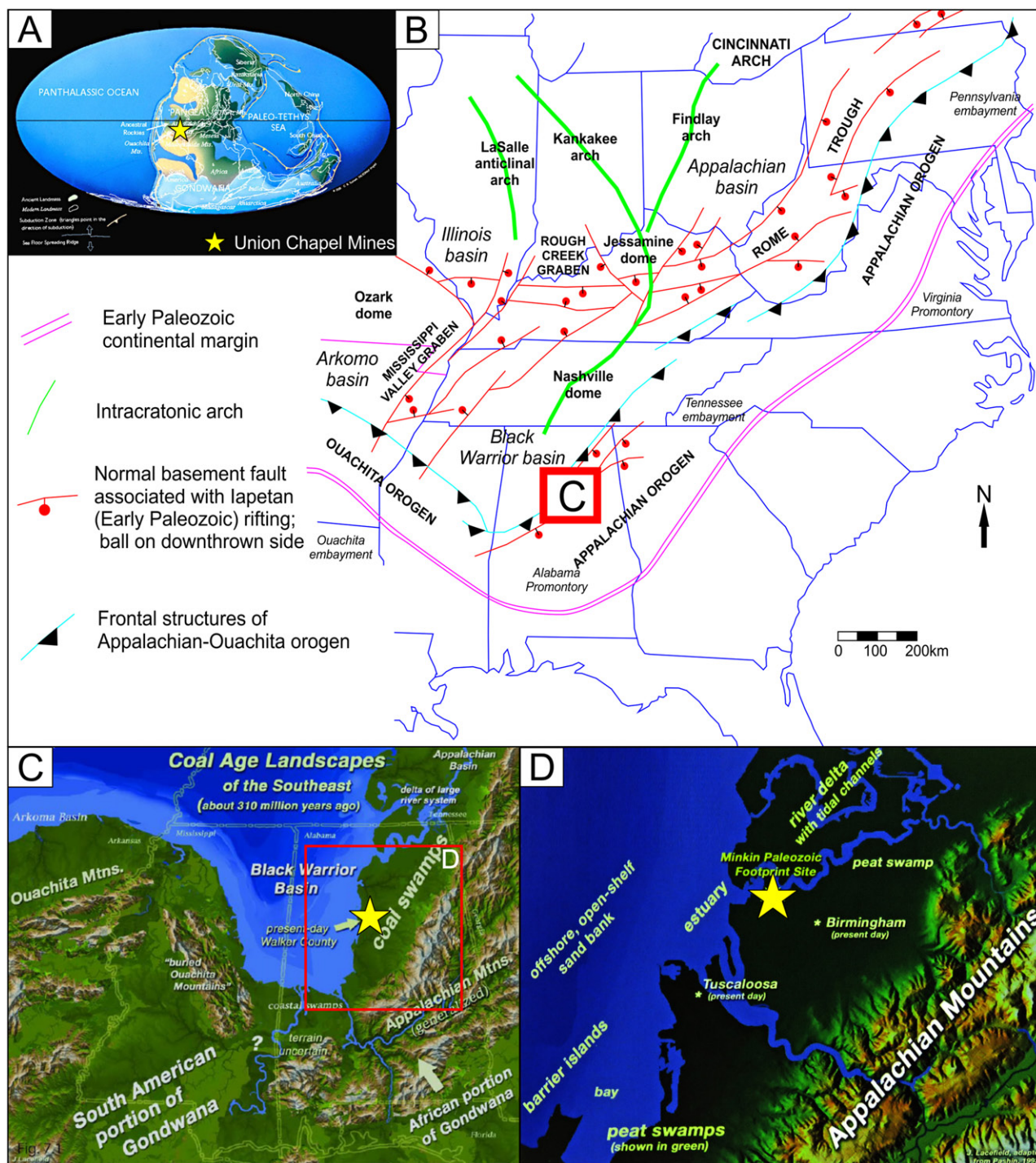


Figure 4. Paleogeographic location: A) Carboniferous global map (after Scotese 1997) B) Eastern USA Appalachian Orogen and Black Warrior Basin paleogeographical map (modified from Pashin 2005) C) Coal age landscape reconstruction for the Black Warrior Basin in Alabama and southeastern USA (after Buta and Kopaska-Merkel 2016) D) Coal age landscape reconstruction for the Black Warrior Basin in Walker County, Alabama (after Buta and Kopaska-Merkel 2016). Source: With permissions to reproduce by the original artist Jim Lacefield.

2005) and is overlain by the Gillespy Marine Zone (Fig. 2).

Paleoenvironmental interpretations

During the Pennsylvanian, peat swamps accumulated in equatorial, low lying humid, tropical environments that

extended from the American Midwest to Western Europe and Asia within the equatorial paleofloral belt (Gastaldo 1990; DiMichele and Phillips 1995; Dilcher et al. 2005; Fig. 4A). Paleogeographic reconstructions suggest that, during the Early Pennsylvanian, Alabama was located ~10 degrees latitude south of the equator

(Minkin 2005; Pashin 2005; Fig. 4A). River drainage from the Appalachian Orogen flowed northwest through peat-forming inter-distributary swamps, and through local, freshwater-dominated estuaries, preserved as mudflats, depositing heterogeneous shales and sandstones of the Pottsville Formation (Ferm et al. 1967; Pashin 2005). This estuary eventually drained into the coastal shallow marine environments and offshore open waters of the Black Warrior Basin, interpreted to be normal marine as evidenced by the Gillepsy Marine Zone (Buta and Kopaska-Merkel 2016; Figs. 4C and D). Pashin (1994a, 1994b) has demonstrated that marine and non-marine cycles within the Pottsville Formation are consistent with glacial eustasy and were primarily driven by polar ice sheet advance and retreat during the Pennsylvanian (Caputo and Crowell 1985; Frakes et al. 1992; Falcon-Lang 2003).

The Mary Lee Coal Bed represents a widespread rheotrophic peat swamp and forested wetlands dominated by arborescent lycopsids represented by the economic coal deposits of the upper Pottsville Formation. These wetlands are interpreted to have shed the articulated plants that have been transported to and preserved on the *Cincosaurus* beds mudflats that Pashin (2005) interpreted as a freshwater, intertidal mudflat deposit, and that agrees with previous studies (Hobday 1974; Demko and Gastaldo 1996; Pashin 2005). The *Cincosaurus* beds are thought to have formed during the inundation of the Mary Lee Coal Bed during episodic tidal cycles in a mesotidal environment (Hobday 1974; Horne 1979). Evidenced by the low sulfur content, it is thought that the Mary Lee Coal Bed and the inundating waters were freshwater. However, the intercalated limestones preserve marine fauna, indicating an estuarine environment that was a lateral sedimentary facies expressed at the UCM during periods of transgression, sea level high stand.

The tidally influenced deposits at UCM encompass a range of taphonomic conditions. The high degree of variability among the preservation of the trace fossils at UCM provides important insight into the paleoecology of coal-age Alabama (Lacefield and Relihan 2005) and the depositional environments that these animals were traversing (Pashin 2005). The exceedingly large collection also is an ideal opportunity to differentiate underprints from surface traces as well as to evaluate the extent of taphonomic variability such as extramorphological variants caused by sediment consistency, grain size and gait (Haubold et al. 2005; Davis et al. 2007), which all vary with paleoenvironmental conditions. This concept has to date only been applied at UCM to

the vertebrate ichnofossils in a precursory way at the UCM.

Methods and materials

Initially examined in the field at the Union Chapel Mine site, this large collection of fossil material was collected by the Alabama Paleontology Society. These specimens were given UCM numbers before being distributed to the McWane Science Centre (MSC), Anniston Museum of Natural History (ANNMNH), the Alabama Museum of Natural History (AMNH), The Smithsonian Institution (USAM) and the New Mexico Museum of Natural History and Science (NMMNH). Museum specimens have been photographed under low angle light, using halogen work lamps. Through the use of photo-editing software and drafting software, photographs have been gray-scaled and the white balance changed to accentuate the impressions. Using freeware software (Image J), measurements of the specimens were taken from the photos. The photos from which the measurements were taken are assumed to have a 1:1 aspect ratio. Interpretive sketches were drafted using drafting software.

Supporting Information Appendices are included in this manuscript, but they are not intended to be a comprehensive list of all UCM specimens, as the dataset is too vast, and many specimens in museum collections are not yet catalogued, and many other specimens remain in private collections that are not discussed here. Those specimens listed include only those observed from photo records provided by the Alabama Paleontology Society and McWane Science Center, and those observed by the authors in museum collections. Additionally, we have included a list of those specimens that have appeared in previous publications, reassigning ichnotaxonomic affinities as needed (see Supporting Information Appendices 1–7).

Systematic ichnology

Kouphichnium Nopsca 1923

- 1862 *Ichnites lithographicus*; Oppel, (*Type ichnospecies*)
- 1923 *Kouphichnium lithographus*; Nopsca,
- 1930 *Bipedes aspodon*; Aldrich,
- 1935 *Paramphibius didactylus*; Willard,
- 1939 *Kouphichnium didactylus*; Caster,
- 1926 *Micrichnus scotti*; Abel,
- 1943 *Limuludichnulus nagoldensis*; Linck,
- 1944 *Kouphichnium arizonae*; Caster,
- 1949 *Kouphichnium variabilis*; Linck,
- 1949 *Kouphichnium gracilis*; Linck,
- 1964 *Kouphichnium walchi*; Malz,

1978 *Kouphichnium minisculum*; Actinolaza,
1985 *Kouphichnium fernandez*; Romano and Melendez,
2005 *Kouphichnium pentapodus*; Erickson,

Emended Diagnosis: Oppositely symmetrical, heteropodous and highly variable tracks that consist of up to five impressions in a track row series. Impressions consist of bifurcating, trifold or quadrifid, oval or punctate impressions together with variable secondary morphologies; with or without a medial drag impression (modified from Häntzschel 1975; Minter and Braddy 2009).

Remarks: The ichnogenus *Kouphichnium* is typically attributed to limulid walking activity characterized by the distinctive “pusher” impressions in addition to secondary impressions produced by the anterior walking appendages (pedipalps: Caster 1938, 1944; Linck 1949). Originally named by Nopsca (1923) for trackways described by Oppel (1862) as *ichnites lithographicus*, there are now 13 named ichnospecies of *Kouphichnium*, ranging from Ordovician (Fischer 1978) to Paleocene strata (Erickson 2005).

Ichnospecies of *Kouphichnium* that are currently recognized in the fossil record, include: *K. arizonae* (Caster 1944), *K. didactylus* (Willard 1935; Caster 1938), *K. gracilis* (Linck 1949), *K. fernandez* (Romano and Melendez 1985), *K. aspodon* (Aldrich and Jones 1930), *K. walchi* (Malz 1964), *K. variabilis* (Linck 1949), *K. scotti* (Caster 1938), *K. pentapodus* (Erickson 2005) and *K. minisculum* (Actinolaza 1978). Two ichnospecies represent cubichnia rather than walking traces: *K. cordiformis* (Fischer 1978), and *K. rossendalensis* (Hardy 1970). Although many of these ichnospecies are suspected to be junior synonyms of others, a comprehensive revision of the ichnogenus is beyond the scope of this article.

Kouphichnium lithographicum Nopsca

Figured Specimens: UCM 1094 (ANNMNH 2003.2.23), UCM 1368 (AMNH 6021), UCM 1377 (AMNH 13020), UCM 1378 (MSC 27958), UCM 4049 (MSC 25149), UCM 5015 (NMMNH P-79691) NMMNH P-69055, NMMNH P-78227 and NMMNH P-78266 (Fig. 5; Fig. 6).

Referred Specimens: See Supporting Information Appendix 1.

Emended Diagnosis: Oppositely symmetrical, heteropodous and highly variable tracks that typically consist of a series of imprints, often arranged in an echelon fashion of up to five imprints on each side. The imprints consist of a chevron-like series, each of four imprints that may vary in morphology, including punctate, oval or bifid “V” or “Y” shaped impressions that sometimes exhibit bifurcations (also trifold or

quadrifid; occasionally on both sides of the impression), scratches or irregular impressions of similar size to one another. Impressions are often parallel to the mid-line, with the bifurcation opening posteriorly. One pair of larger and more deeply impressed bifid or trifold impressions is similar to the smaller, medial proximal impressions and is spaced at regular intervals. With or without medial (continuous or discontinuous) drag marks (Häntzschel 1975; Minter and Braddy 2009).

Description: Trackways are preserved in convex hyporelief (or concave epirelief). The trackway trajectory varies between straight to gently curved or sinuous. Outer widths vary between 9.3 mm and 23.8 mm, whereas inner widths vary from 2.4 mm to 3.4 mm. General foot morphology for the smaller imprints (pedipalps) is heteropodus, varying from punctate, to curvilinear, comma internal (external) or bifids. The pedipalp impressions are smaller and vary in size due to extramorphological distortion. The relatively larger pusher foot impressions are bifid and “Y” shaped, ranging from 1 mm to 1.9 mm in width, and 1.6 mm to 3.5 mm in length. The trackway is bilaterally symmetrical, with impressions arranged obliquely, and angled away from the midline. Pusher impressions can vary in position and distribution within a track series, depending on gait. Pusher impression width (new term: the distance between the middle of the large pusher impressions) consistently ranges from 7.6 mm to 18.5 mm. The repeat distance of the pusher footprint ranges from 3.6 mm to 12 mm. Trackways are often preserved with a telson drag that is continuous or discontinuous, however, it is not a defining feature (Caster 1938). Telson drags can be absent due to poor preservation, or if the specimen is likely an underprint (Fig. 6). Caster (1938) discusses modern examples where the tail can be raised by the limulid, leaving no telson drag when the limulid traversed firm, muddy surfaces.

Remarks: Originally named by Oppel (1862) as *Ichnites lithographicus*, Nopsca (1923) erected the ichnogenus *Kouphichnium*, reassigning the ichnospecies to *K. lithographicum*. Numerous interpretations of the ichnogenus were proposed, including footprints of pterodactyls, fish-like amphibian trackways, bipedal dinosaur tracks and the tracks of jumping mammals (e.g. Oppel 1862; Abel 1935; Willard 1935; Häntzschel 1975). Caster (1938) convincingly made the connection that these complex tracks were produced by horseshoe crabs (xiphosurans). Anatomically, living horseshoe crabs have eight smaller pedipalp walking

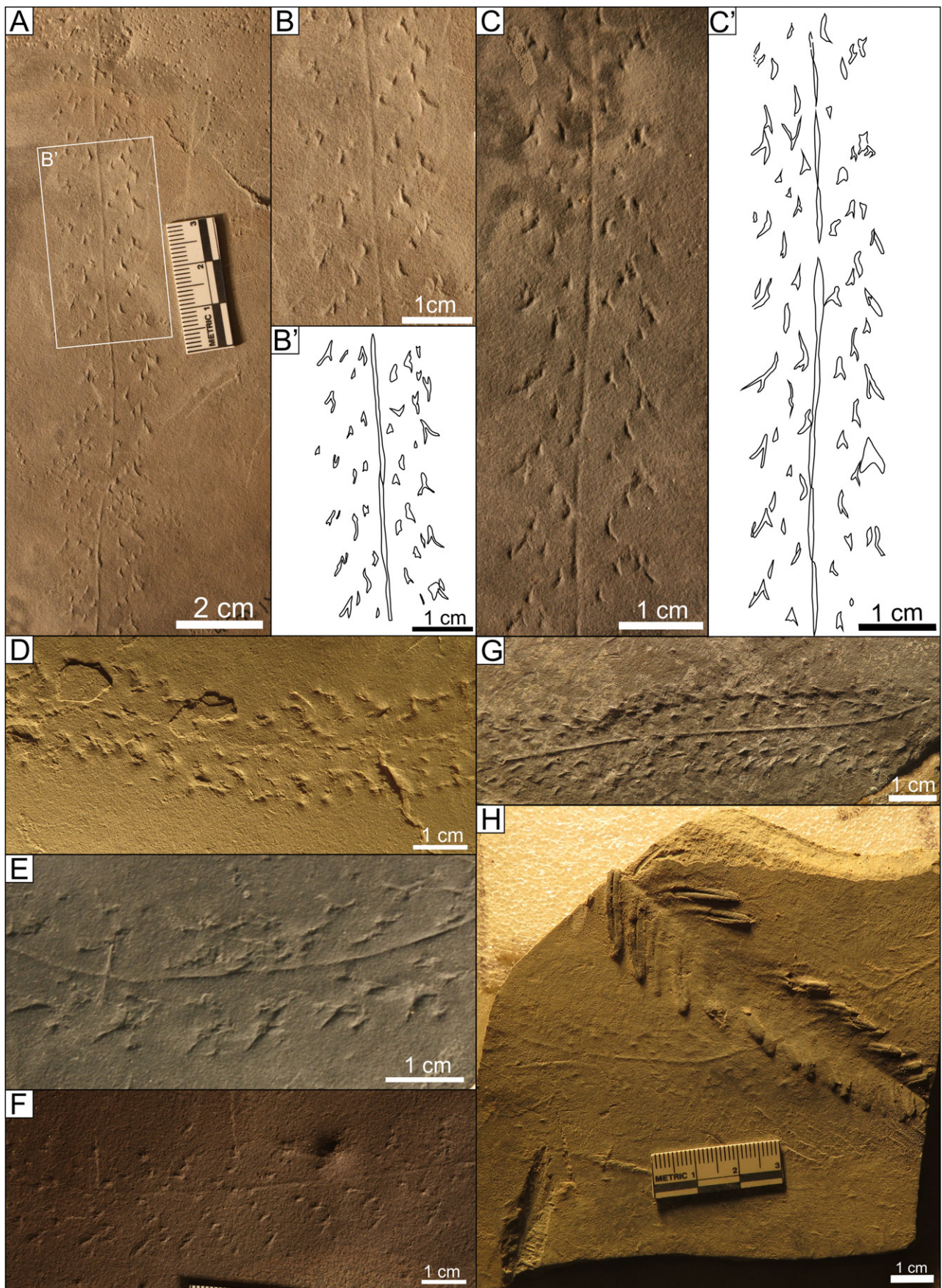


Figure 5. A) *Kouphichnium lithographicum* UCM 1377 (AMNH 13020) B) Close up of UCM 1377 (AMNH 13020) C) UCM 1378 (MSC 27958) D) UCM 5015 (NMMNH P-79691) E) UCM 1094 (ANNMNH 2003.2.23) F) UCM 1368 (MSC 27958) G) NMMNH P-78227 H) NMMNH P-78266.

legs and a set of larger “pusher” feet, for a total of 10 appendages, with five on each side of their bilaterally symmetrical carapace (Shuster et al. 2003).

The *Kouphichnium lithographicum* specimens preserved at the UCM site are conspecific with the type (Oppel 1862; Minter and Braddy 2009). It is suspected that many of the named *Kouphichnium* ichnospecies are junior synonyms of the type ichnospecies; however, the revision of the ichnogenus is beyond the scope of this article. Minter and Braddy (2009) commented on the ichnotaxonomic issues related to *Kouphichnium*. The UCM *Kouphichnium* specimens are assigned to *K. lithographicum* as they are most similar to the type ichno species in having larger bifid impressions (pusher foot) accompanied by smaller heteropodus impressions (pedipalps).

Kouphichnium aspodon Aldrich 1930

(Fig. 3; Fig. 7; Fig. 8; Fig. 9; Fig. 10; Fig. 11)

Type: AMNH 985.1.6 (Fig. 3)

Lectoparatypes: UCM 437 (ANNMNH 2003.2.76/74), UCM 544 (MSC 27749), UCM 662 (MSC uncatalogued), UCM 1072 (AMNH 13199), UCM 1505 (AMNH 13017), UCM 2517 (MSC uncatalogued), UCM 2716 (MSC 28058), UCM 2902 (MSC uncatalogued), UCM 5009 (NMMNH P-79689), UCM 5157(MSC 38454), UCM 5540 (MSC 38456), NMMNH P-68994.

Referred specimens: See Supporting Information Appendix 2.

Emended diagnosis: Individual impressions are small relative to the outer width of the trackway compared to other ichnospecies of *Kouphichnium*. All bifid impressions are of similar size, and bifurcate on one, or both ends, with no distinct, larger “pusher” impressions present. Medial telson impressions are rarely preserved, except in surface traces, or very shallow underprints. *K. aspodon* is distinguished from *K. minkinensis* based on morphology indicative of different behavior. Thus, *K. aspodon* represents continuous walking trackways, whereas *K. minkinensis* are characterized by clusters of impressions representing a jumping or hopping locomotion (see below).

Description: The type specimen was described from a partial specimen consisting of only three distinct, equal sized, well separated, distinct bifid tracks and with a depression for a pad (Aldrich 1930, in Aldrich and Jones 1930, 25 plate 5; Fig. 3). Subsequent specimens collected from the UCM site are preserved in concave epirelief and convex hyporelief, and the trackways are linear to gently curved or sinuous. Track row series consist of up to five impressions on either

side of the midline of individual heteropodus impressions, ranging from bifurcating to punctate. Specimens exhibit bifid and double bifid impressions (bifurcating on both sides, separated by a linear impression). All impressions are small relative to the outer width and are of similar size and morphology to each other, with no distinct, larger “pusher” impressions. Impressions may be oriented parallel to the midline or obliquely, often with at least one track oriented perpendicular to the midline. This impression is frequently the most distal impression (i.e. Fig. 7B).

The type specimen is the largest known representative of the ichnospecies, with impressions that measure 11 mm by 5 mm and have a repeat distance of 53.2 mm and 56.7 mm in successive impressions. In more complete but smaller examples, outer widths vary between 39.5 mm and 84.4 mm, whereas inner widths vary from 11.8 mm to 21 mm. Bifid impressions measure between 4.9 mm and 5.9 mm in length and 1.6 mm and 2.8 mm in width. Bifids have a repeat distance between 12.5 mm and 19.5 mm. The preservation of these tracks is predominantly as underprints that lack a telson drag (Figs. 7–9). Rare examples with telson drags are suspected to be surface traces assignable to *K. aspodon* (Fig. 10A). In these examples, and in shallow underprints, a telson drag is observed, alongside digit drags and appendage impressions that exhibit a high degree of extramorphological variability that implies that the surface in which these traces are preserved was water saturated (Figs. 10B and C). In *K. aspodon*, the dominant morphological feature of *K. lithographicum* and many other ichnospecies, the impression of the pusher foot is not present or is not larger than the walking impressions of the pedipalps. This contrasts with the more typical larger size of the pusher foot in all other *Kouphichnium* ichnospecies. *K. aspodon* exhibits appendage impressions of equal size that are morphologically similar to one another, predominantly as bifids, although some morphological variants occur.

Remarks: *Kouphichnium (Bipedes) aspodon* was originally described by Aldrich, in Aldrich and Jones (1930), as an amphibian track. Cotton et al. (1995) also apparently considered it to be a tetrapod track, as it appeared in their taxonomic list for USA Paleozoic tetrapod localities at Carbon Hill Mine, Alabama. The ichnospecies was later used as an ichnospecies of *Kouphichnium* and an invertebrate trackway by Buta et al. (2005), but they did not conduct any systematic ichnological work. Minter and Braddy (2009) list the various ichnospecies of *Kouphichnium* and include *K. aspodon*, referencing Aldrich and Jones (1930), but

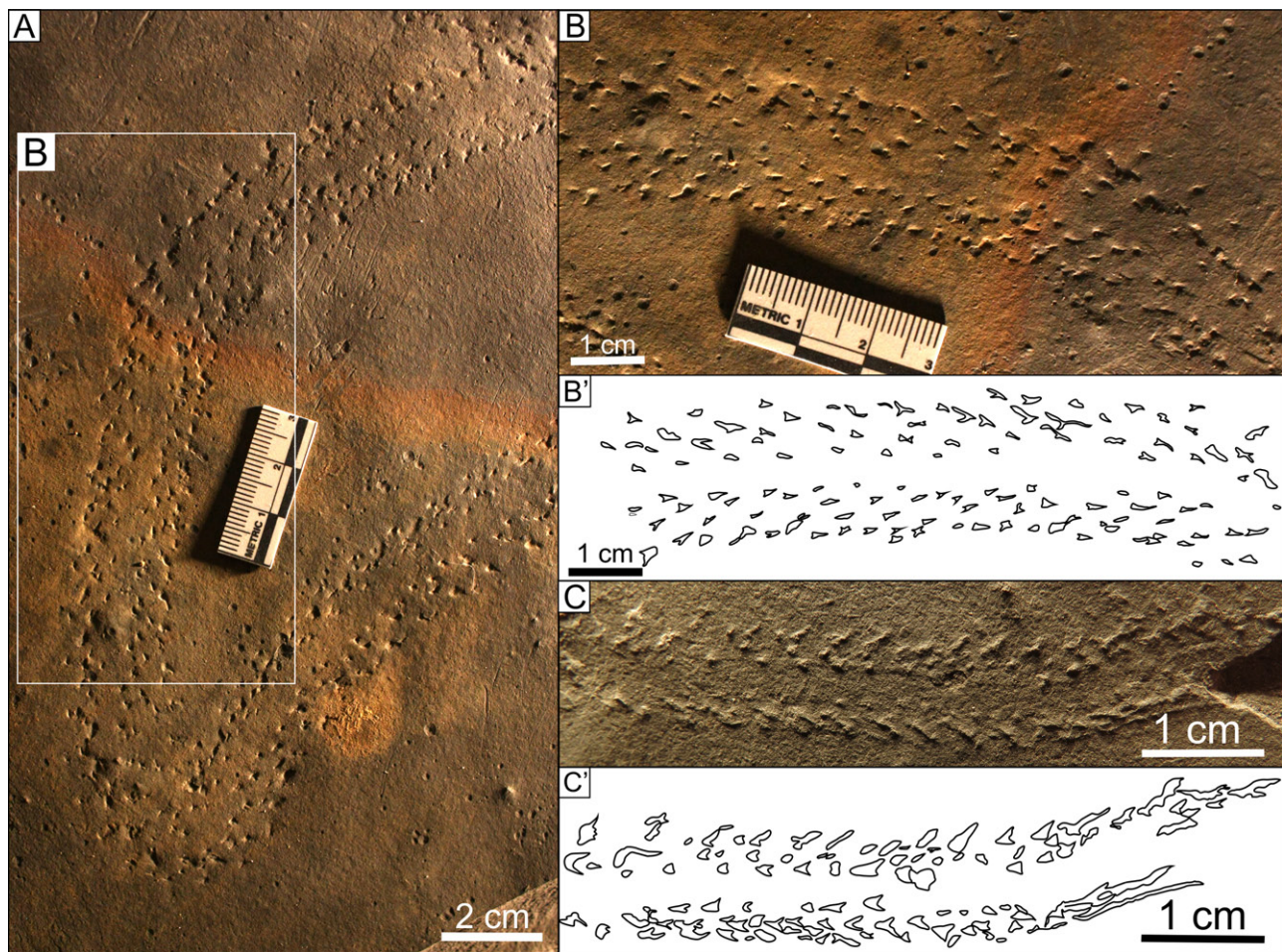


Figure 6. *Koupichnium lithographicum*: A) UCM 4049 (MSC 25149) B) Close up of UCM 4049 (MSC 25149) C) NMMNH P-69055.

without formal reassignment of the ichnospecies *Bipedes aspodon* to the ichnogenus *Koupichnium*.

Rarely found with a telson drag, *Koupichnium aspodon* conforms to the ichnogenus concept in that impressions are heteropodous and, in most cases, bifurcate. However, due to the lack of a larger, prominent “pusher” impression, this trackway could be produced by a different tracemaker than the limulids that are normally identified as the trackmakers of *Koupichnium*. Nevertheless, due to the bifurcations of the footprints, *K. aspodon* was likely made by an arthropod in the same family as xiphosurids (Merostomata). The trackway itself is orders of magnitude larger than those of *Koupichnium* described from elsewhere in the Carboniferous (e.g. Goldring and Seilacher 1971; Chrisholm 1983; Romano and Melendez 1985; Archer et al. 1995; Buatois et al. 1998, 2005; Prescott et al. 2014) and is larger than all of the known xiphosurid body fossils from the late Paleozoic (Meek and Worthen 1865; Copeland 1957; Anderson et al. 1997; Shabica and Hay 1997; Babcock et al. 2000; Lerner et al. 2016).

Indeed, the type specimen of *Koupichnium aspodon* is double the size of all other known limulid trackway specimens from the Pottsville Formation. Assuming allometric growth, if the smaller, more complete specimens are scaled up to match the holotype specimen, it would suggest that the type specimen would have an outer width of nearly 100 mm in width. This is, again, significantly large than any known Carboniferous xiphosuran.

On two specimens, UCM 5540 (MSC 38456; Figs. 9A and B) and UCM 5157 (MSC 38454; Figs. 9C and D), trackways begin abruptly as elongated foot impressions. Specimen UCM 5540 (MSC 38456; Figs. 9A and B) is a short trackway that terminates abruptly as well. Both examples are preserved on large slabs that contain other ichnofossils (i.e. *Diplichnites gouldi*; Figs. 9C and D). The abrupt beginning and end of these trackways, with no obvious continuation, suggest that the animal was suspended in the water column before landing on the sediment surface. The abrupt end of the trackway indicates that the animal re-entered the water column,

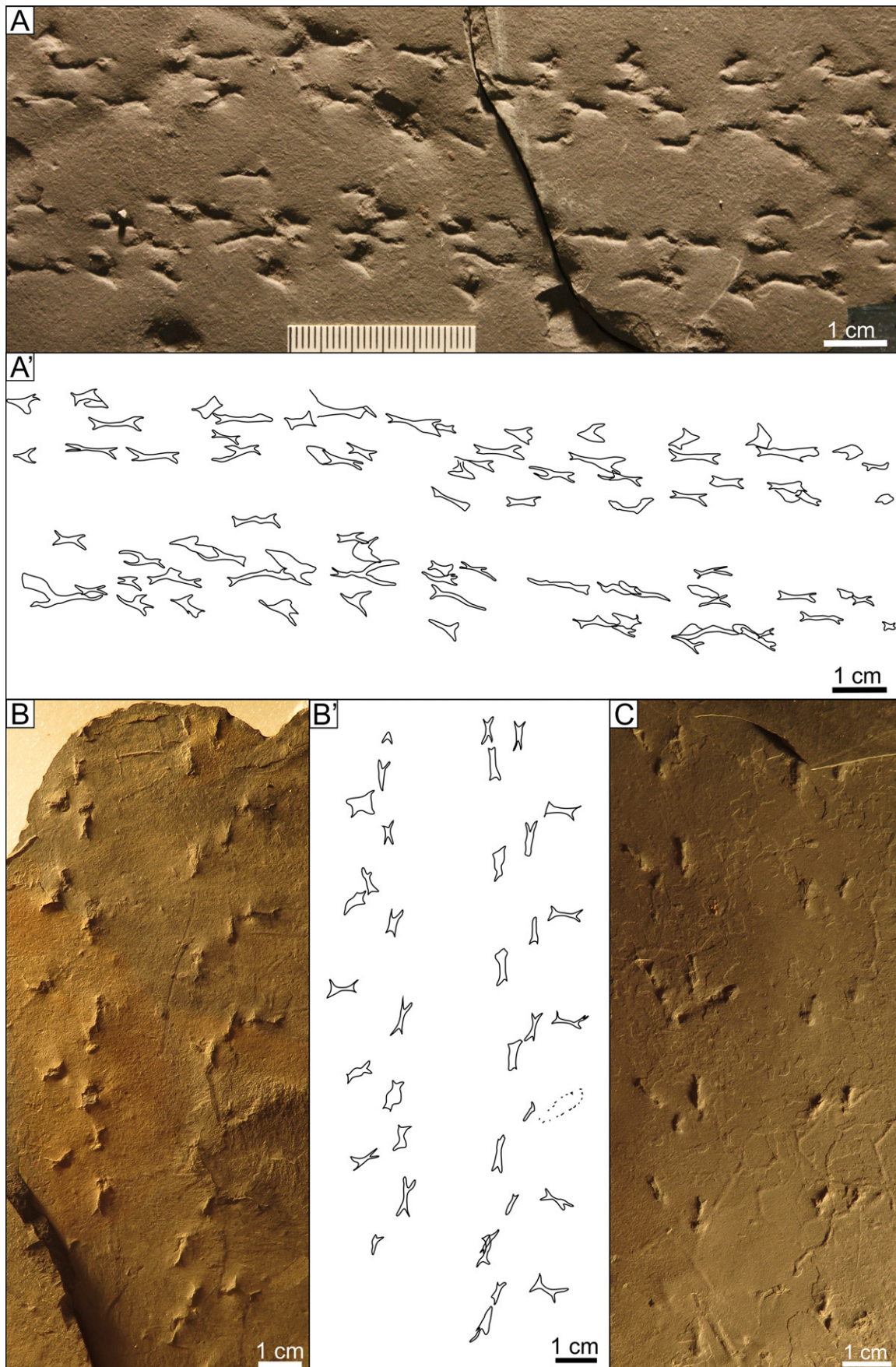


Figure 7. *Koupichnium aspodon*: A) UCM 437 (ANNMNH 2003.2.76/74) B) UCM 5009 (NMMNH P-79689) C) NMMNH P-68994.

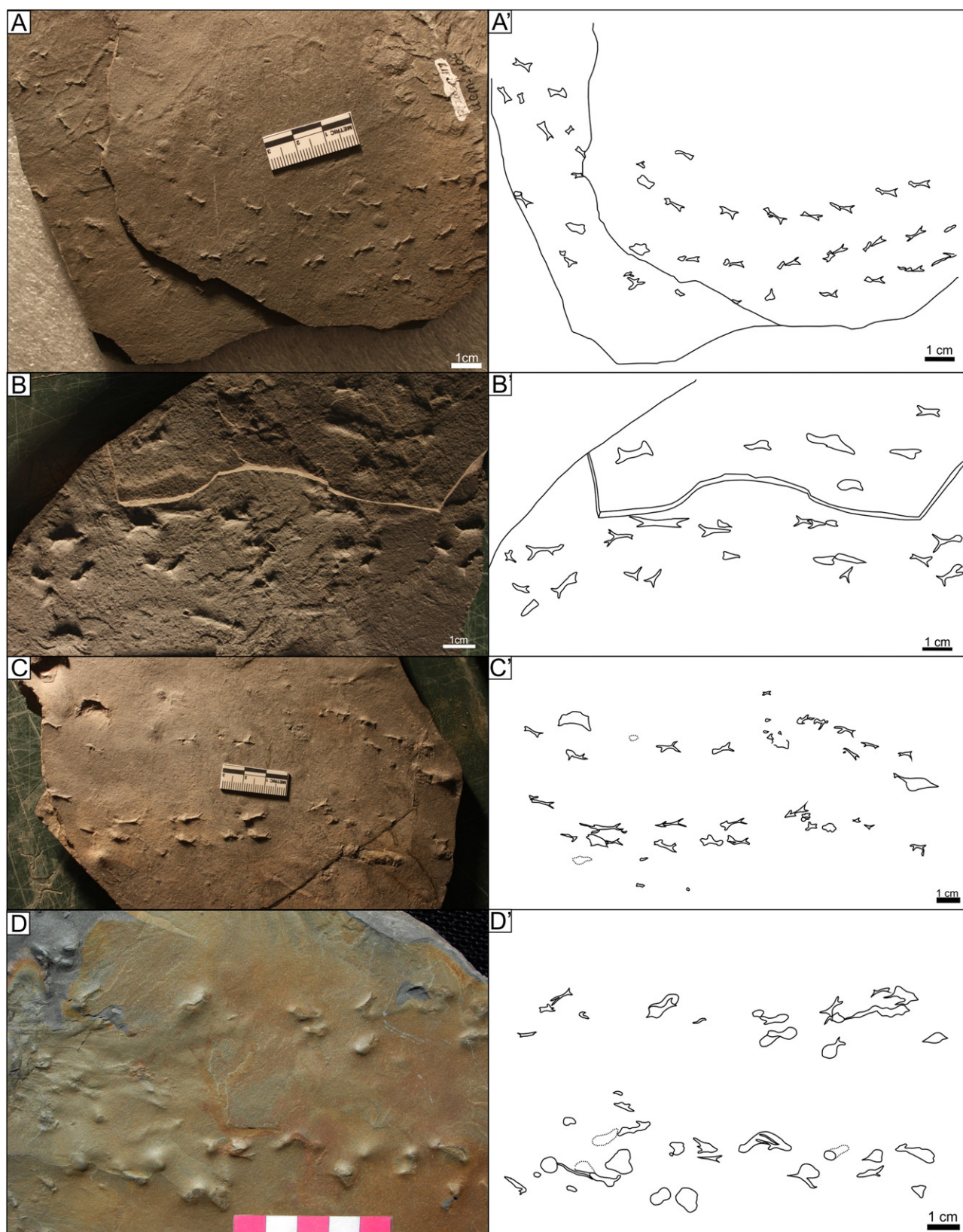


Figure 8. *Koupichnium aspodon* underprints: A) UCM 1505 (AMNH 13017) B) UCM 544 (MSC 27749) C) UCM 2716 (MSC 28058) D) UCM 2517 (MSC uncatalogued).

suggesting it was likely a swimmer in addition to walking along the sediment surface.

Kouphichnium minkinensis isp. nov.

(Fig. 12; Fig. 13)

Holotype: UCM 227 (ANNMNH 2003.5.24).

Paratypes: UCM 508 (ANNMNH 2003.20.10), UCM 2242 (MSC 9324), NMMNH P-69078.

Referred specimens: See Supporting Information Appendix 3.

Diagnosis: Similar to *Kouphichnium aspodon*, the distinctive, larger “pusher” impressions, characteristic of most *Kouphichnium* ichnospecies, are not present, and all bifid impressions are of equal size. Bifid impressions are closely clustered together and are made up of a maximum of five individual impressions that vary in orientation. Clusters of impressions are well spaced from each other and are the distinguishing characteristic of the ichnospecies when compared to *K. aspodon*.

Description: Preserved in concave epirelief (or convex hyperrelief), these trackways are linear to gently curved. Outer widths vary between 55.8 mm and 80.3 mm, whereas inner widths vary from 20.7 mm to 37.4 mm. The preservation of these tracks is predominantly as underprints. *Kouphichnium minkinensis* exhibits appendage impressions of equal size and is morphologically similar to *K. aspodon*, and thus similarly lacks the defining “pusher” impression that is characteristic of other ichnospecies of *Kouphichnium*. The “pusher” foot appendage (if present) is the same size as the smaller pedipalp walking appendage impressions. Impression dimensions measure 7.4–6.4 mm (length) by 2.9 mm (width).

Remarks: Morphologically similar to *Kouphichnium aspodon*, *K. minkinensis* consists of bifurcating and double bifurcating impressions of equal size and lacks the larger “pusher” impression. This trace is within the same size range as *K. aspodon*. These two ichnospecies have the potential of having a similar trace-maker and may be found in future samples in taphoserries but are distinguished based on inferred ethological differences. Thus, *K. aspodon* represents a walking trackway, whereas *K. minkinensis* represents a semi-buoyant, “bouncing” or saltation trackway, perhaps due to locomotion within a water current. *K. aspodon* and *K. minkinensis* likely represent end members of an ichnological taphoserries with a gradation between them, so that transitional trackways may be difficult to classify into one end member taxon or the other.

The difference in locomotion represents different behaviors, so the traces are separated at the

ichnospecific level, as ethology is considered a major source of morphological variation that provides a good ichnotaxobase for a new ichnospecies. Telson drags have not been observed in this ichnospecies of *Kouphichnium*. Telson drags have, however, been observed in *K. aspodon* surface and shallow underprints. The suspicion that *K. aspodon* and *K. minkinensis* are produced by the same trace maker suggests that the trace maker of *K. minkinensis* had a telson.

Etymology: This new ichnospecies is named for the late Steven Minkin, for his extensive contributions to the science of the UCM site.

Kouphichnium atkinsoni isp. nov. (Fig. 14)

Holotype: UCM 2737 (NMMNH P-69048).

Lectoparatypes: MSC 28063

Referred specimens: See Supporting Information Appendix 4.

Diagnosis: Trackways with well-spaced, bifurcating appendage impressions that are long, with multiple bifurcations and trifurcations forming a dendritic morphology that distinguishes *K. atkinsoni* from other ichnospecies of *Kouphichnium*.

Description: Preserved in either concave epirelief (or convex hyporelief), trackways are linear to gently curved and may be asymmetrical. Outer widths vary between 71.3 mm and 90.2 mm, whereas inner widths are 18.6 mm to 18.7 mm. The appendage impressions are heteropodus and arranged as well-spaced, complex impressions within each trackrow series with a repeat distance of 34.4 to 51.5 mm. Impressions are longer than wide and are oriented perpendicular to the midline. Proximally, impressions begin as circular to elliptical, punctate impressions and extend out distally as a thin, linear trace that bifurcates dendritically. Impressions are 24.1 mm to 24.5 mm long and 11.1 mm to 12.1 mm wide. Often, one bifurcating impression is short, spur-like, and tapers sharply at its distal end, whereas the second bifurcation continues and bifurcates a second or third time to the distal edges of the trackway. In asymmetric examples, one track row series has the appendage impressions curved proximally towards the midline and may be entirely overturned, likely representing extramorphological distortion. Known examples of *K. atkinsoni* lack a medial tail drag.

Remarks: *Kouphichnium atkinsoni* is consistent with the ichnogeneric concept of *Kouphichnium* in that it consists of heteropodous trackways that include bifurcating impressions, but these are unique in that they have dendritic, bifurcating impressions. The known examples of *K. atkinsoni* consist of shallow underprints, as compared to other full relief

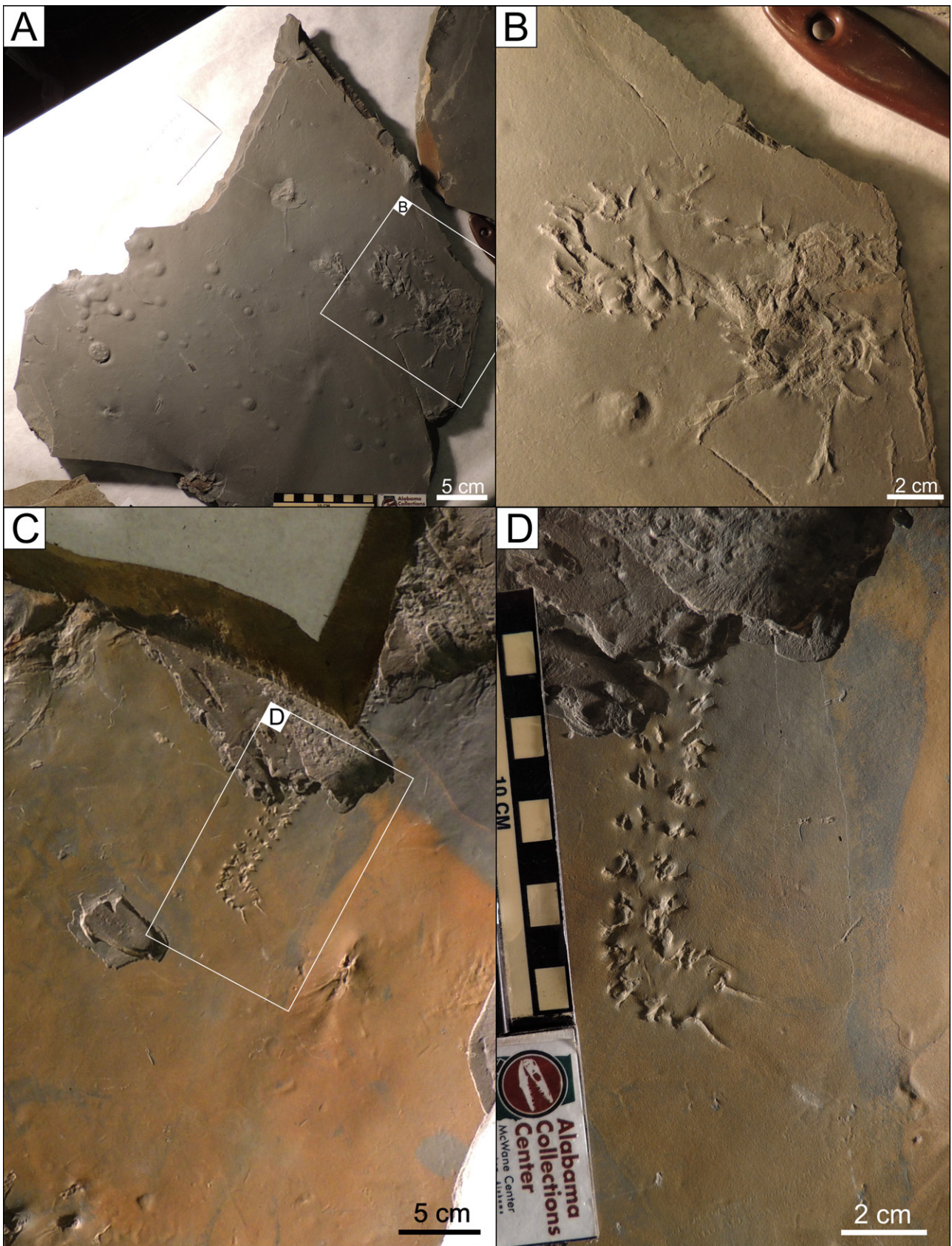


Figure 9. *Kouphichnium aspodon*: A) UCM 5540 (MSC 38456) B) Close up of UCM 5540 (MSC 38456) C) UCM 5157 (MSC 38454) D) Close up of UCM 5157 (MSC 38454).

Kouphichnium specimens prints at UCM that are preserved in what was a soupy substrate and that often exhibits a wide range of extramorphological variation (Fig. 10A). The bifurcation and trifurcation of the appendage impressions is a unique morphology, and it could be argued that that this represents a new ichnogenus. However, we take a conservative approach to the ichnotaxonomy pending further discoveries.

Etymology: This new ichnospecies is named for Dr. Prescott Atkinson for his continued contributions to scientific understanding of the UCM site. The unusual morphology of the type specimen was also first recognized by Dr. Atkinson.

Selenichnites Romano and Whyte 1987

Selenichnites rossendalensis Hardy 1970 (Fig. 15)

Figured Specimens: UCM 107 (AMNH 5920), UCM 1612 (MSC uncatalogued), UCM 3790 (MSC uncatalogued), NMMNH P-78237, MSC 27086.

Referred specimens: See Supporting Information Appendix 5.

Emended diagnosis: Shallow, sub-oval traces occurring as isolated or in a series. Traces are semi-lunate in morphology and are generally slightly wider than long, with a rounded anterior margin and are strongly convex (in hyporelief) or concave (in epirelief) lunate or are paired crescent-shaped lobes directly anterolaterally with or without scratch marks and an anterior ridge (Romano and Whyte 2015; Buhler and Grey 2017)

Description: Five specimens have been identified from the UCM. Three specimens of *Selenichnites* are compound traces of *Selenichnites* x *Cruziana* isp., and *Selenichnites* x *Dendroidichnites* isp. A small specimen (UCM 107 (AMNH 5920)) described provisionally by Lucas and Lerner (2005) exhibits a number of semilunate impressions preserved in convex hyporelief (Figs. 15A and B). Impressions are wider than long and taper on either side posteriorly, resembling the genal angles of a trilobite cephalon. The resting trace preserves a *Cruziana* trackway in taphoseries with the *Selenichnites* trace. The *Selenichnites* trace is 13.5 mm wide and 7.4 mm long, with a prosomal ridge 2 mm thick. The associated *Cruziana* is 6 mm wide and preserves two parallel trackrows of scratch marks, each 2.3 mm wide, with a medial furrow 1.24 mm wide. The trace is 19.7 mm long. Scratch marks are oriented oblique to the midline at 67°.

On the same surface a subsequent specimen (UCM 1612 [MSC uncatalogued]; Fig. 15C) preserves only the semilunate headshield impression with no posterior ridge or taphoseries trackway associated. Another

specimen (NMMNH P-78237; Fig. 15D) is larger (17.2 mm long by 24.5 mm wide) and is more typical of the morphology of other known *Selenichnites* specimens. The semilunate impression has an 18.3 mm long posterior ridge (telson impression). The semilunate convex impression is directly associated with *Dendroidichnites*-like trace with elongate, curvilinear impressions that taper laterally from a medial drag and are similar to chevron tool marks. A similar trace (UCM 3790 [MSC uncatalogued]; Fig. 15E) was noted to be in taphoseries with a sinuous, ribbon-like trail terminating as an elliptical, semi-lunate convex impression.

Specimen MSC 27086 (Fig. 15F) strongly resembles specimens described by Chrisholm (1985) as *Selenichnites bradfordensis*, as it consists of a series of semilunate impressions that overlap one another consecutively. The *Selenichnites* on specimen MSC 27086 is in taphoseries with a *Dendroidichnites*-like trackway that is similar to specimen NMMNH P-78237.

Remarks: In examples of *Selenichnites* from other localities, traces are often associated with *Kouphichnium* or other arthropod traces (cf. Romano and Whyte 1987). *Selenichnites* has classically been ascribed to xiphosuran activity whereby the prosomal head shield is projected into the sediment in a burrowing fashion (Hardy 1970; Romano and Whyte 1987; Lerner and Lucas 2015; Buhler and Grey 2017). A recent revision of the ichnogenus *Selenichnites* was conducted by Romano and Whyte (2015) that divided it into several ichnogenera. We do not accept the subdivision here, as most of the ichnospecies they recognize are suspected to be extramorphological variants and are thus in need of an ichnotaxonomic revision beyond our scope. We thus follow the ichnotaxonomy of Lerner and Lucas (2015).

This is the first published example of a *Selenichnites* specimen that is preserved in taphoseries with *Cruziana*, and the first *Selenichnites* associated with *Dendroidichnites*. It has been suggested that other *Cruziana* specimens at the UCM were produced by trilobites (Crimes 1975; Fillion and Pickerill 1990; Buta et al. 2005). If a marine incursion were present at UCM, which could be indicated by the presence of productid brachiopods (NMMNH P-69097) in the Gillespy limestone that stratigraphically overlies maximum flooding surfaces (Fig. 2) in the exposed strata at the UCM site, then a trilobite origin is possible, especially as trilobites are known from the marine bands. This would suggest that the cephalon impression of trilobites may be responsible for some *Selenichnites* specimens. This is not unlike interpretations of Gibb et al. (2011), where the oldest known examples of *Selenichnites* are of

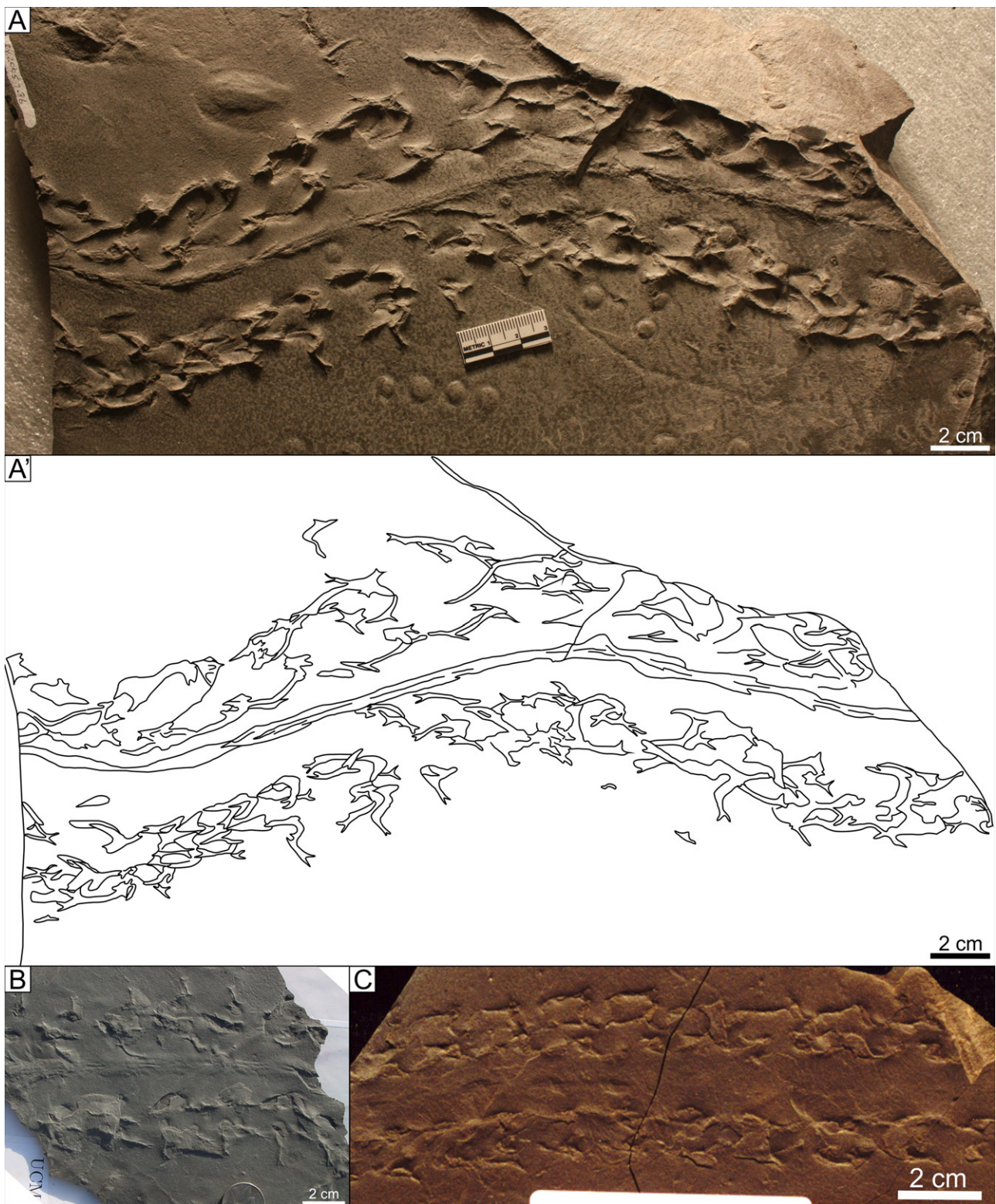


Figure 10. *Kouphichnium aspodon* with tail drag: A) UCM 1072 (NLMNH 13199); [Counterpart UCM 1070 (AMNH 6); not figured] B) Shallow underprint of *Kouphichnium aspodon* with tail drag, UCM 2902 (MSC uncatalogued) C) Shallow underprint of *Kouphichnium aspodon* with tail drag transitioning to *Kouphichnium aspodon* without a tail drag, UCM 662 (MSC uncatalogued).

Cambrian-age from Morocco where they have been interpreted to have been made by trilobites.

Specimens NMMNH P-78237 and MSC 27086 described here are associated with a *Dendroidichnites*-

like trace that suggests the trace was made in a soupy substrate and likely represents a surface trace. Given the poor preservation of the associated trackway it is difficult to determine the trace maker. However, some

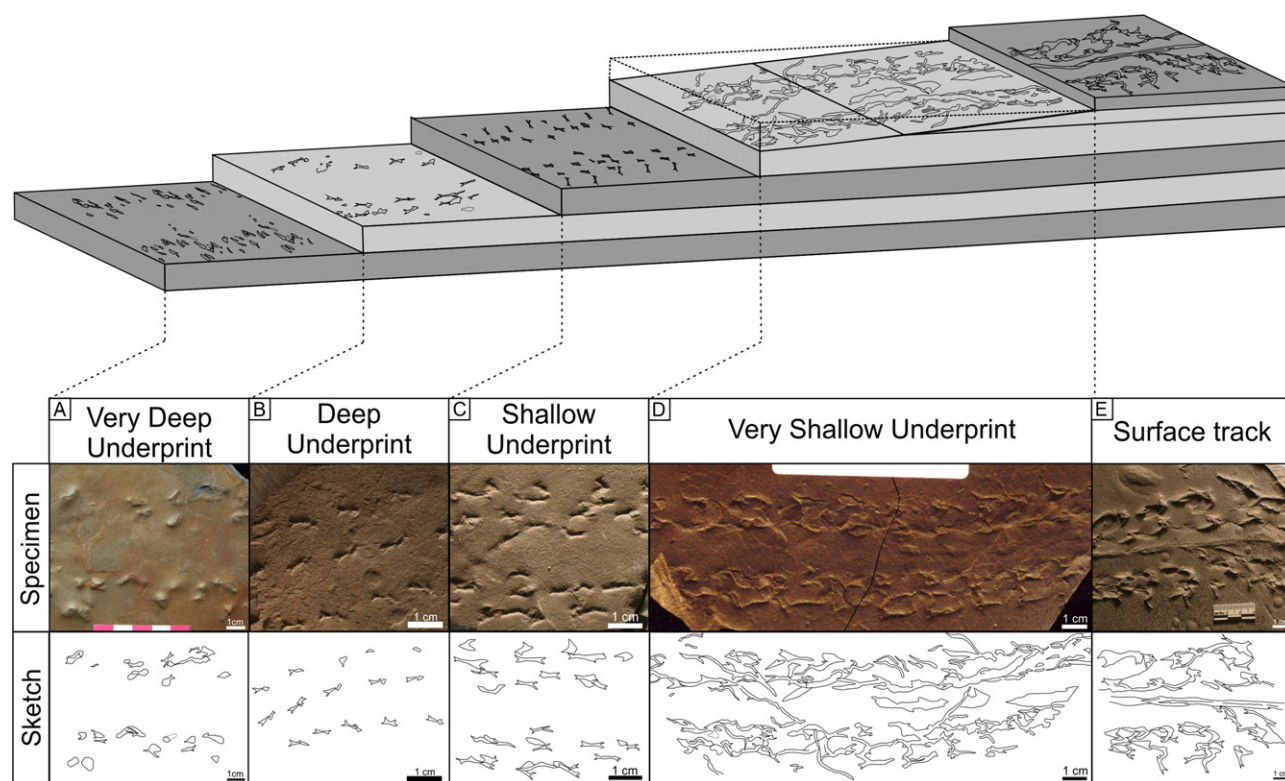


Figure 11. *Koupichnium aspodon* underprint fallout interpretation: A) UCM 2517 (MSC) B) UCM 544 (MSC 27749) C) UCM 437 (ANNMNH 2003.2.76/74) D) UCM 662 (MSC uncatalogued) E) UCM 1072 (AMNH 13199).

of the *Selenichnites* at UCM match well to the size and morphology of Carboniferous limulids and match well to the size of the *Koupichnium lithographicum* at the UCM.

Although xiphosurans are the classic interpretation for *Selenichnites* impressions, large examples at UCM may be attributed to any other chelicerate with a semilunate cephalon, including trilobites, eurypterids or synxiphosurans, given the association with *Cruziana* trackways.

At UCM, underprints of cubichnia (Fig. 16) associated with trackways previously referred to as “unassigned xiphosuran traces” (Fig. 17; Fig. 18) were misinterpreted as *Selenichnites* resting traces and, by affiliation, many of the associated trackways were erroneously labeled as *Koupichnium* (Buta et al 2005; Lucas and Lerner 2005; see Supporting Information Appendix 7). These resting or colloquially named “jumper” traces (Fig. 16) and their associated trackways do not conform to the ichnogenetic concept of *Koupichnium* or *Selenichnites* and are thus excluded from these ichnotaxa. The traces are here left in open nomenclature pending a subsequent publication.

Lerner and Lucas (2015) discuss *Selenichnites bradfordensis* from specimens recovered from New Mexico.

In their paper, *S. bradfordensis* is considered a poorly preserved *S. rossendalensis* due to similarities to specimens preserved on the type specimen described by Hardy (1970). We here agree with Lerner and Lucas (2015) and consider this ichnospecies a minor morphological variation on the type ichnospecies and consider specimen MSC 27086 to be an extramorphological variation of *Selenichnites rossendalensis*.

Ichnogenus *Arborichnus* Romano and Meléndez, 1985
Arborichnus repetitus Romano and Meléndez, 1985
 (Fig. 19)

1985 *Arborichnus repetita*: Romano and Meléndez,
 fig. 1, pls.1, pls.2, fig. 3,

2005 *Arborichnus repetita*: Lucas and Lerner,
 p. 150, fig. 2F.

2005 *Arborichnus repetitus*: Buta et al., pls. 103A-B,
 104A-B, 105A-B, 106A-B.

2013 *Arborichnus repetitus*: Buta et al., pls. 3A-B.

2016 *Arborichnus repetitus*: Buta and
 Kopaska-Merkel, fig. 16.11.

Figured Specimens: UCM 4646 (MSC 25968),
 UCM 3549 (MSC 27905).

Referred specimens: See Supporting Information
 Appendix 6.

Emended diagnosis: Sets of up to five pairs of symmetrical scratch marks. At the anterior end of the set, the scratch marks are short and directed inward and backward; the posterior scratches are aligned at about right angles to the mid-line of the set. Scratch marks are repeated as a track with the distance between the sets being approximately equal to the length of the set.

Description: Numerous UCM specimens are bilaterally symmetrical traces that consist of up to five sets of paired scratch marks (grooves in concave epirelief; or as paired ridges in convex hyporelief) that are oriented perpendicular to the midline. These traces flank a central, oval-shaped disturbed area. Impressions are straight to strongly curved and splay outwards from the oval-shaped center, with the posterior pairs of grooves being slightly longer in some specimens (Buta et al. 2013; Kopaska-Merkel and Buta 2013). Spacing between sets is approximately equal distance apart. These distinctive traces closely resemble the original diagnosis of *Arborichnus repetita* by Romano and Melendez (1985).

Remarks: *Arborichnus* was not formally described until Romano and Melendez (1985), although it had been known for a considerable time (see Caster 1938, fig. 1, plate 9, figs. 3 and 4). Other than Romano and Melendez's (1985) type descriptions from the Carboniferous of Spain, there are few recent reports of this ichnotaxon in the literature (Buta et al. 2005; Lucas et al. 2005; Lucas and Lerner 2005; Mansky and Lucas 2013; Buta et al. 2013; Buta and Kopaska-Merkel 2016). The large number of UCM *A. repetita* specimens, which number in the hundreds, provides an extensive sample with which to broaden our understanding of this trace and further clarify the taxonomy of this ichnogenus.

Specimens from the Crescent Valley Mine described by Buta et al. (2013) in the Pottsville Formation were interpreted to have been made by xiphosurans and represented both swimming and grazing behavior in more distal facies in deep waters (Buta et al. 2013). A re-description of specimens from the UCM (Buta and Kopaska-Merkel 2016) has led them to suggest these traces were not made by xiphosurans, as was previously thought (Romano and Melendez 1985; Buta et al. 2005; Lucas and Lerner 2005). Buta et al. (2013) and Buta and Kopaska-Merkel (2016) have taken a conservative approach and interpreted *Arborichnus* as the resting traces of decapod crustaceans but admitted that the trace maker was probably not a horseshoe crab.

Discussion

Kouphichnium tracks were originally attributed to an array of possible trace makers, including: amphibians,

bipedal dinosaurs, pterodactyls, reptiles and jumping mammals or other precursor tracemakers (Oppel 1862; Nopsca 1923; Aldrich and Jones 1930; Abel 1935; Häntzschel 1975). Caster (1938) was the first to theorize and compare modern limulid footprints to *Kouphichnium* trackways preserved in the fossil record. It was then confirmed as the trace maker when a xiphosurid *Mesolimulus* was discovered at the end of a *Kouphichnium* trace in the famous Jurassic limestones of Solnhofen, Germany (*K. walchii*: Malz 1964). Thus, limulids as the tracemaker for *Kouphichnium* trackways has been widely accepted in the literature. The pusher foot is interpreted as the largest and deepest impression that occurs in a *Kouphichnium* trackway, whereas the smaller pedipalps produce a range of different and smaller morphologies, ranging from punctate to bifid (Caster 1938, 1944; Linck 1949).

Trace fossil interpretations can have profound implications for the understanding of Carboniferous paleoenvironments (e.g. Calder 1998; Buatois et al. 2005; Falcon-Lang et al. 2006). Modern day limulids are marine organisms that periodically migrate into brackish and freshwater shorelines to mate and reproduce. Xiphosurids and their ancestors date back to the early Paleozoic (Rudkin et al. 2008). In the Pennsylvanian, only three genera of limulids are well documented: *Euproops*, *Paleolimulus* and *Belinurus*. All have been recorded from classic Carboniferous sections such as Mazon Creek, Illinois (Nitecki 2013), Joggins, Nova Scotia (Calder 1998; Falcon-Lang 2006; Stimson and MacRae 2010; Buhler and Grey 2017), West Bay, Nova Scotia (Copeland 1957) and Sydney, Cape Breton, Nova Scotia (Copeland 1957; Calder 1998). Historically, reconciling Carboniferous localities and marine xiphosurids has posed challenges where classic Carboniferous localities such as Joggins and Horton Bluff were interpreted as freshwater environments. As a result, many of the associated xiphosurids were interpreted to be fresh water organisms (Moore 1955). New data from historical localities (i.e. Joggins, Nova Scotia; Grey et al. 2011; Horton Bluff, Nova Scotia; Mansky and Lucas 2013) imply a distal marine connection, that may change our interpretation of Carboniferous xiphosurid ecologies.

Currently at the UCM, xiphosurid body fossils have not been found. However, the presence of *Kouphichnium lithographicum* implies xiphosurans were present at the UCM location. Unlike classic sections such as Joggins, the marine connection here is not ambiguous, as local limestones representing sea level high stands contain productid brachiopods (NMMNH P-69097) that are interpreted as being

derived from marine environments (Fig. 2). The depositional environments of the trace-fossil-bearing strata are thought to be estuarine, freshwater-dominated mudflats with a marine connection. Thus, the trace makers for *Kouphichnium* at the UCM were likely xiphosurids or other similar, euryhaline chelicerates.

Taxonomy and taphonomy

The majority of traces found at the UCM of both vertebrates and invertebrates are underprints (Goldring and Seilacher 1971; Haubold et al. 2005). Traces on the walking surface are present, but they are much less common and are preserved with a high degree of extramorphological distortion due to the water-saturated substrate (Fig. 10A; Fig. 11; and Fig. 20). In rare examples of surface tracks made by tetrapods, the shallow underprints are plantigrade, while the surface traces are highly distorted, with extramorphological digit extraction and elongated drag impressions, sometimes resembling *Dendroidichnites* (Fig. 21, P-43509). This variance is interpreted to be due to water saturation in the surface layer at the sediment-water interface that is influenced by inundating tidal waters, while the more cohesive subsurface sedimentary layers preserved a higher degree of detail in the trackways that penetrate the surface layers (commonly they preserve appendage impressions but no telson drag). The sediment was predominantly mud or very fine-grained sand or silt, periodically inundated by water, while the underlying layers were more compacted in the subsurface. Previous workers (Rindsberg 2005) have noted that there is no direct sign of prolonged subaerial exposure (i.e. mudcracks, rain pit impressions, ripple bedforms), suggesting that either the traces observed at the UCM are all underprints, and the walking surface is rarely encountered, or the sedimentary surface was at no point subaerially exposed or it was subaerially exposed for a very short time. However, there are no tetrapod swim tracks, so if the sediments were perpetually submerged, they were only submerged by a shallow film of water or not exposed long enough to desiccate.

Biofilms have been interpreted at the UCM based on the presence of microbial bubbles associated with trackways (Rindsberg 2005). Biofilms allow for the preservation of fine details in fossil trackways and can stabilize the sediments by early cementation (Seilacher 2008; Marty et al. 2009). Generally, a clear print will occur after the appendage has passed the initial layer of soft, water saturated sediment and

made contact with the first compacted layer in the subsurface, which, in turn, allows for a high preservation potential, while the unconsolidated sediments at the surface are mobile, with poor preservation potential (Fig. 11). At the UCM, the high-resolution traces preserved as shallow underprints decrease in detail with depth (Lucas and Lerner 2005; Buta and Kopaska-Merkel 2016; Stimson and MacRae 2010; Milàn and Bromley 2007; Fig. 21). Evidence of this underprint fallout has been noted (Kopaska-Merkel and Buta 2013; Buta and Kopaska-Merkle 2016) before at the UCM site and can be seen in the preservation of “*Cincosaurus*” tracks (P-43509, Fig. 21), as the walking surface and consecutive layers preserve such phenomena.

Trace makers

Kouphichnium tracks at the UCM are associated with both aquatic (*Undichna*) and terrestrial (tetrapod track) ichnofossils on different surfaces, and all ichnofossils occur in association with infaunal and surface burrows (Fig. 20). This suggests that the tracemaker of *Kouphichnium* was tolerant of both subaquatic and subaerial conditions.

It is likely that xiphosurids are the tracemaker of most *Kouphichnium* based on the behavior of modern day limulids. Modern day horseshoe crabs have a high salinity tolerance for both fresh and salt water environments (Chatterji and Abidi 1993). They live the majority of their lives in normal marine water, and return to the shoreline where they were born, to reproduce. Reproduction occurs under specific sedimentary conditions in freshwater or brackish, low energy environments, such as Delaware Bay (Shuster and Botton 1985) and is comparable to the freshwater-dominated environment at the UCM.

Given the high preservation of articulated plant fossils (organic matter) at the UCM, if xiphosurids inhabited the shorelines, bodies and molts should populate this environment as well. However, no evidence of limulid body fossils or molts have yet to be found at this site, suggesting that migration to this brackish environment could be interpreted as temporary, comparable to modern day limulid ecologies (Shuster and Botton 1985). Alternatively, taphonomic factors, such as sediment rates, could have precluded the burial and preservation of limulid body fossils.

Kouphichnium has traditionally been interpreted to be of limulid origin. However, four distinguishable ichnospecies have been identified at Union Chapel

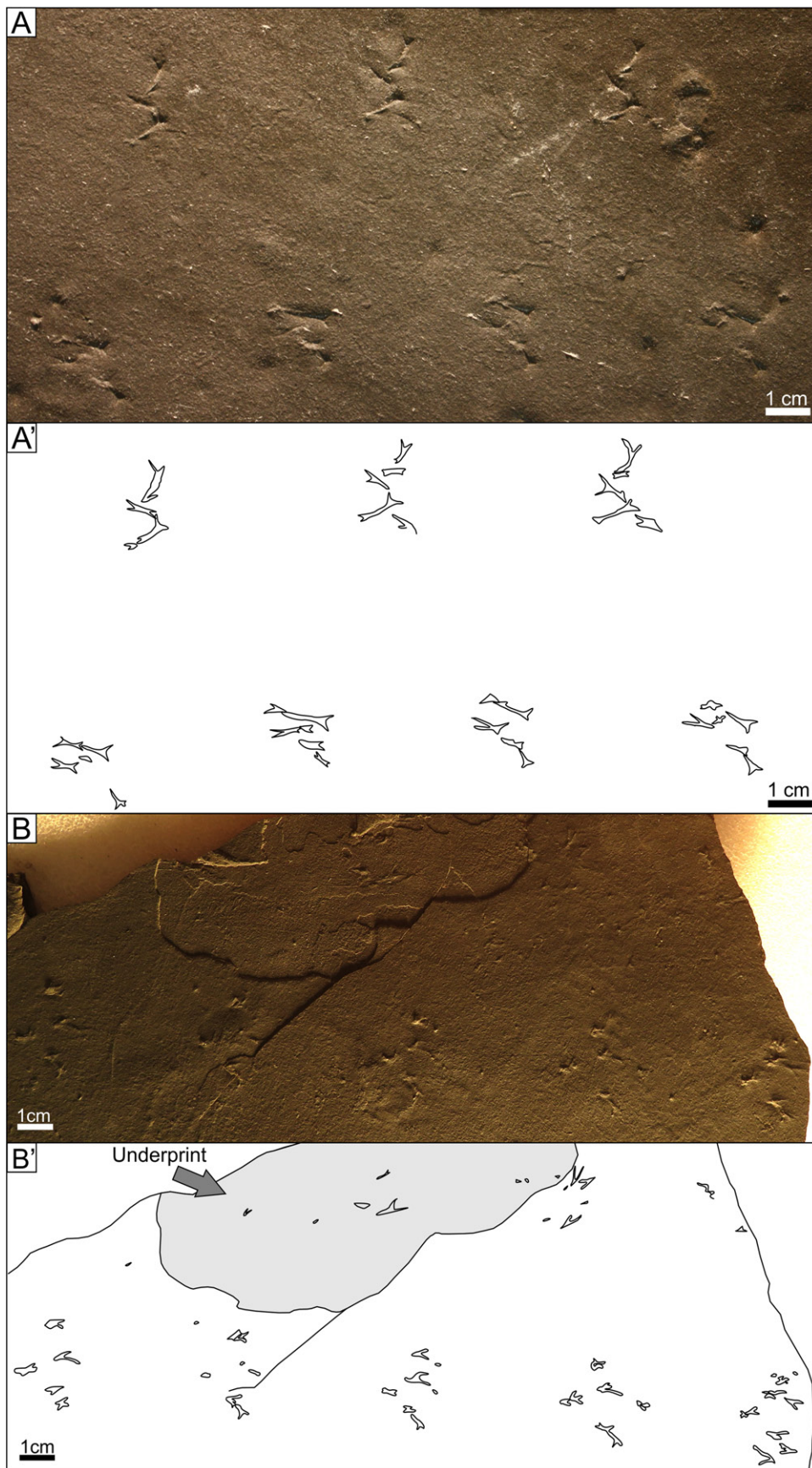


Figure 12. A) *Koupichnium minkinensis*, type specimen UCM 227 (ANNMNH 2003.5.24) B) UCM 2242 (MSC 9324).

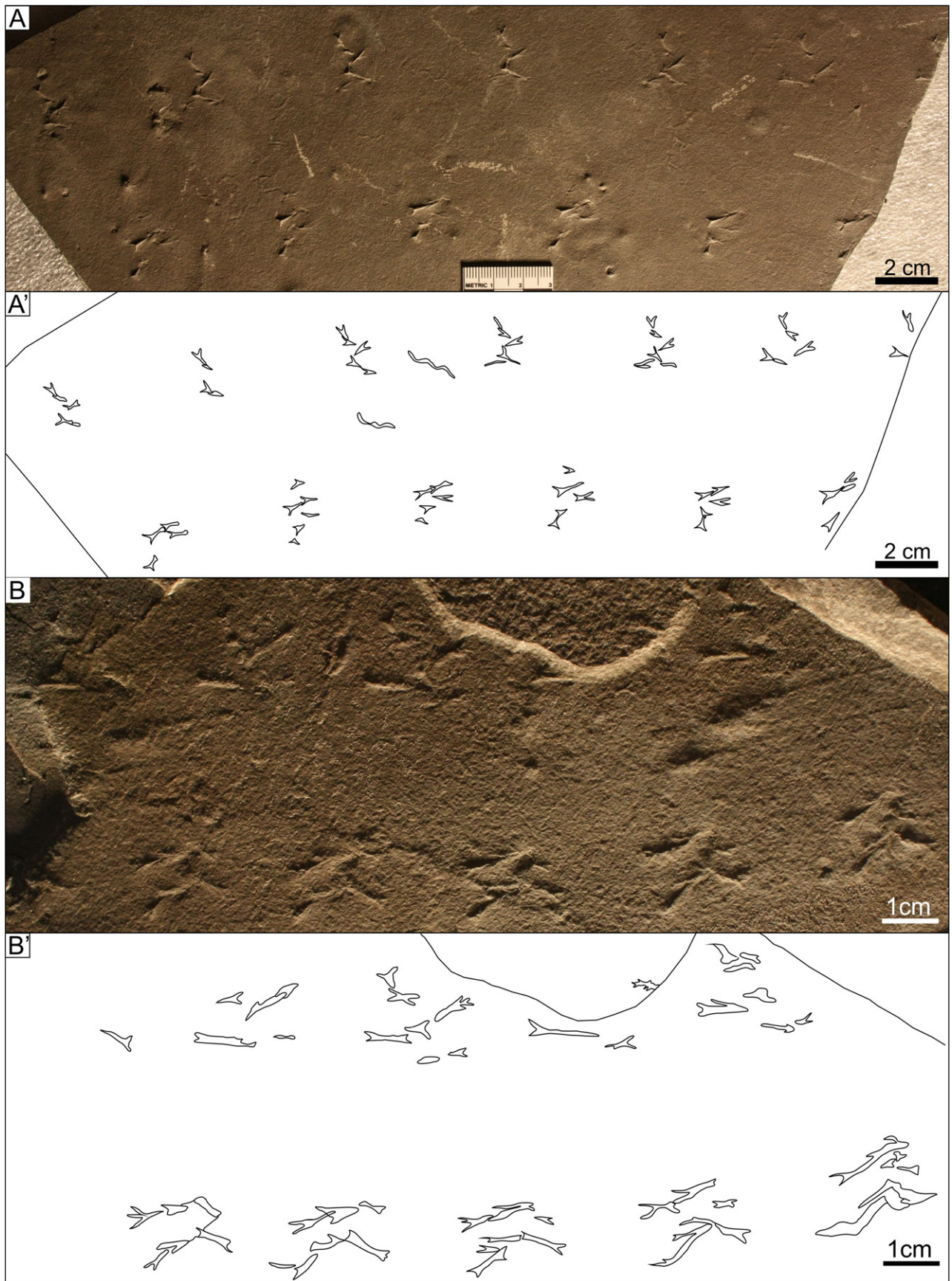


Figure 13. *Koupichnium minkinensis*: A) UCM 508 (ANMNH 2003.20.10) B) NMMNH P-69078.

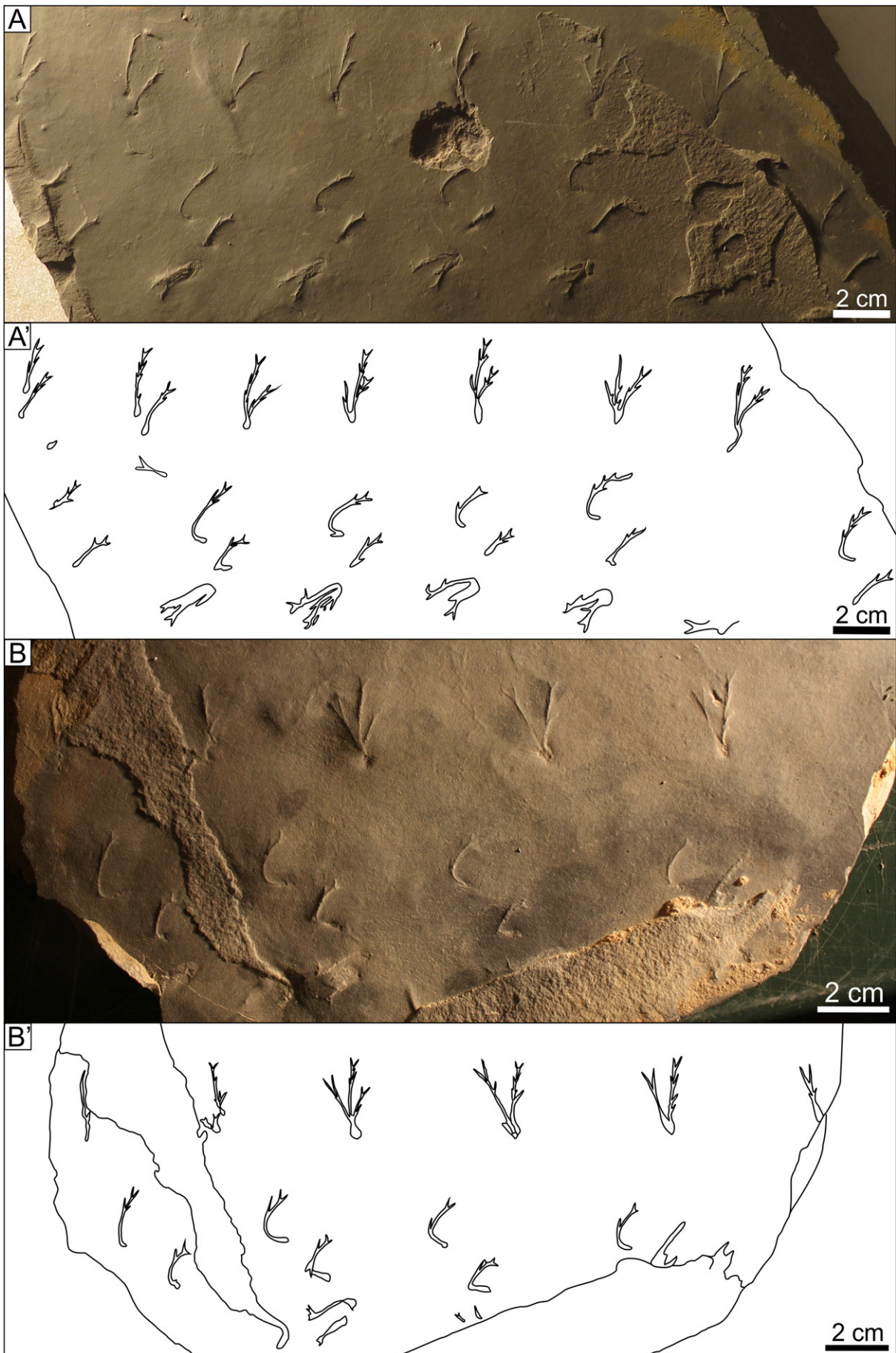


Figure 14. A) *Koupichnium atkinsoni*, type specimen NMMNH P-69048 B) MSC 28063.

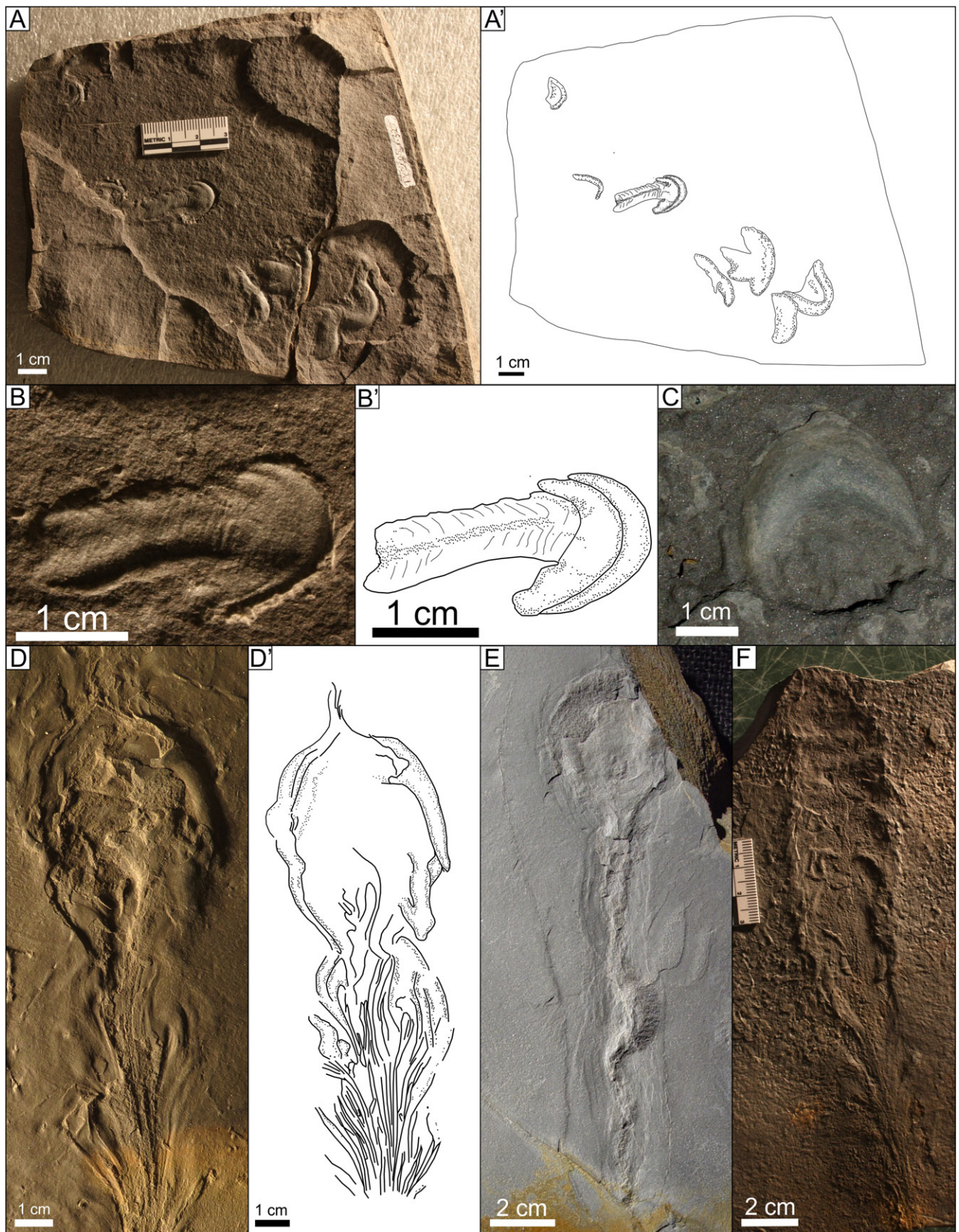


Figure 15. *Selenichnites rossendalensis*: A) UCM 107 (AMNH 5920) B) Close-up of UCM 107 (AMNH 5920) C) UCM 1612 (MSC uncatagued) D) NMMNH P-78237) E) UCM 3790 (MSC uncatagued) F) MSC 27086.

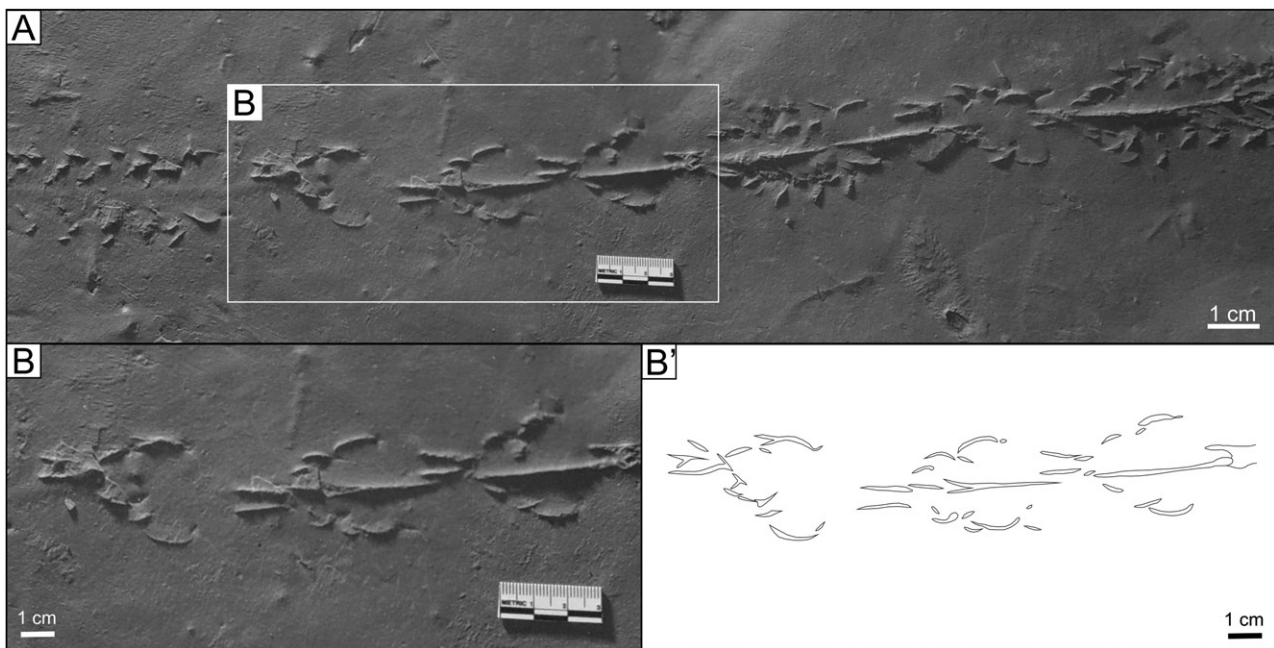


Figure 16. Unassigned “jumper” tracks: A) “jumper trace” associated with unassigned “xiphosurid tracks”, UCM 5000b (MSC 38462) B) close up of UCM 5000b (MSC 38462).

Mine, and likely represent at least three different trace makers discussed below.

Kouphichnium lithographicum

Classic *Kouphichnium lithographicum* morphologies are preserved at the UCM. However, this ichnospecies at the UCM is smaller than its Jurassic holotype specimen (Oppel 1862; Nopsca 1923; Abel 1935; Caster 1938, 1944; Malz 1964). Previous work has misidentified some small scale *Kouphichnium* traces at UCM as *Paleohelcura* and *Stiaria* (Buta et al. 2005; Buta and Kopaska-Merkel 2016; Supporting Information Appendix 7), which would have suggested arachnid trace makers such as spiders or scorpions. Larger examples of real *Paleohelcura* and *Stiaria* are known from the UCM (Buta and Kopaska-Merkel 2016) but are not discussed further here.

Specimens of *Kouphichnium lithographicum* from the Jurassic type locality at Solnhofen are found in association with the trace maker *Mesolimulus*. Limulids from the Mesozoic to present day are considerably larger than those from the Carboniferous and Permian (Copeland 1957; Haug et al. 2012; Lerner et al. 2016). The only known genera of horseshoe crabs in the Carboniferous are *Paleolimulus* and the poorly distinguished *Euproops* and *Belinurus* (Haug et al. 2012), known from various Carboniferous localities (Copeland 1957; Calder 1998; Falcon-Lang 2006; Mansky and Lucas 2013; Nitecki 2013; Lerner et al. 2016). They are considerably smaller than their

younger limulid descendants (i.e. *Mesolimulus*: Malz 1964), and this accounts for the size difference between Mesozoic and Paleozoic *Kouphichnium* examples, as seen here. Large xiphosurans (> 5 cm) are known from older strata (Rudkin et al. 2008) but are not yet known from the Carboniferous. The smaller examples of *K. lithographicum* found at the UCM have a width similar to that of the known limulids of the Upper Carboniferous and exhibit the diagnostic larger “Y” shaped pusher impressions that distinguish them from *Stiaria* and *Paleohelcura* (Minter and Braddy 2009).

The examples at UCM are often preserved as light surficial tracks (Fig. 5) that do not have deep underprints. If underprints occur they are relatively shallow (sub-mm) compared to the trackway surface, and generally lack a telson drag, with reduced resolution of the bifid-trifid pusher and pedipalp impressions (Fig. 6).

Kouphichnium aspodon

Kouphichnium aspodon has been identified from the UCM and other outcrops of the Pottsville Formation in Alabama, including its type locality at the Carbon Hill Mine, and the recently described Crescent Valley Mine (Buta et al. 2013). It is also known from the Mississippian (Visean) Mauch Chunk Formation of Pennsylvania (Fillmore et al. 2012). With re-examination and re-description of the ichnospecies at UCM, the Mauch Chunk examples will require re-examination, but this is beyond the scope of this manuscript.

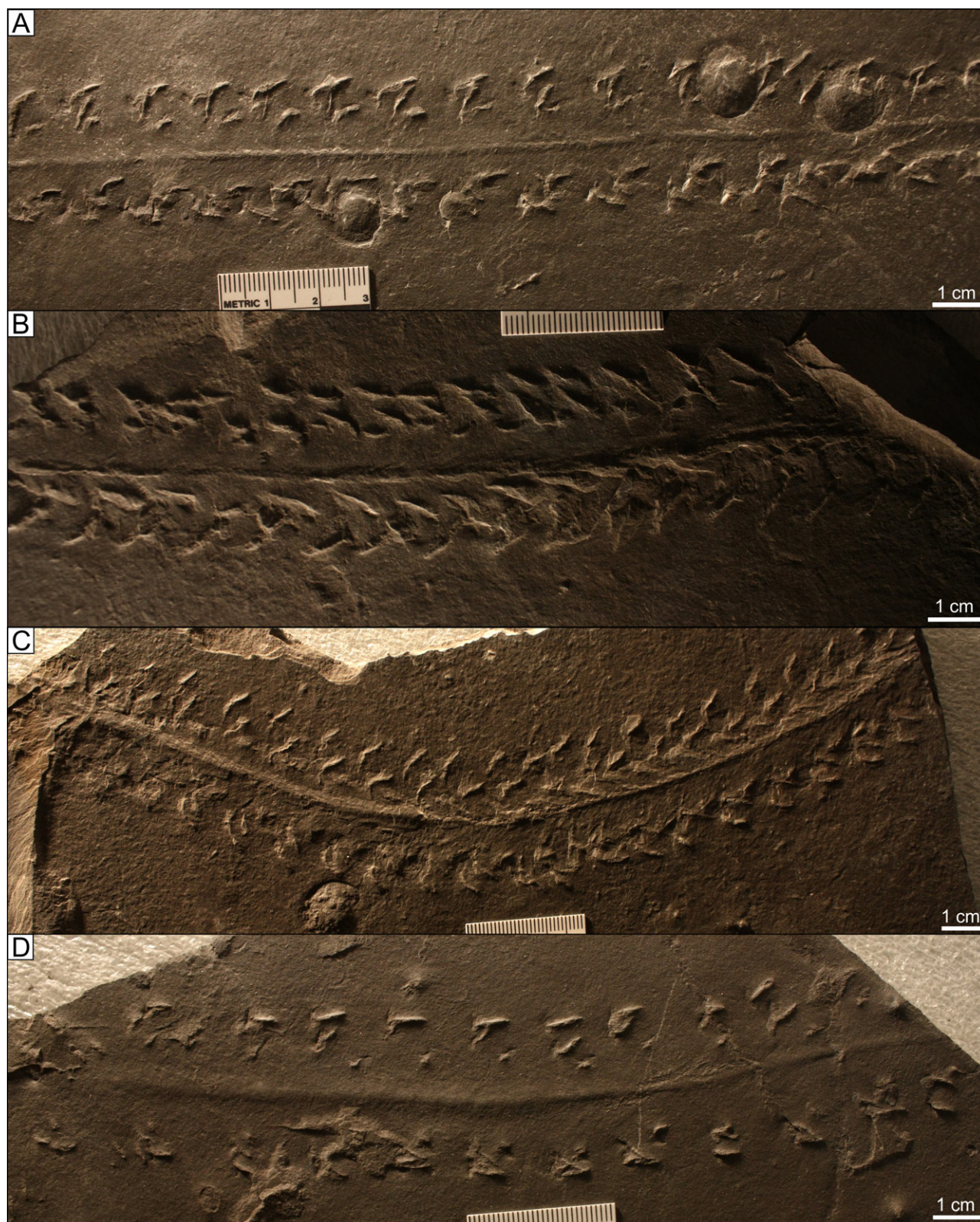


Figure 17. Unassigned “xiphosurid” tracks: A-B) UCM 1752 (AMNH 13108; counterpart to UCM 1740 (AMNH 6003) C) UCM 1119 (AMNH 5950) D) UCM 723 (AMNH 5959).

Kouphichnium aspodon trackways are larger by an order of magnitude, with deeper impressions, than all other Paleozoic *Kouphichnium* specimens described previously (Buta et al. 2005; Lucas and Lerner 2005; Buta and Kopaska-Merkel 2016). *K. aspodon* differs from the *K. lithographicum* ichnospecies concept as it lacks a larger “pusher” impression. Additionally, the bifid impressions are double bifid impressions with a bifurcation on either end and are all equal in size but vary in length and orientation. In previously described underprint fallout studies of *Kouphichnium*, the pusher impressions are the deepest impressions, with the resolution of the smaller pedipalp impressions lessening with depth and the loss of a medial telson drag (Goldring and Seilacher 1971; Stimson and MacRae 2010). In the case of *K. aspodon*, if the pusher foot was anatomically present on the trace maker, it should be observed as the deepest impression in all *K. aspodon* examples (Fig. 3; Figs. 7–11; Supporting Information Appendix 2). However, in the rare surface traces (Fig. 10) and underprints (that comprise the majority of encountered specimens; Figs. 7–11) the bifid impressions are the same size, and no pusher impression is observed, suggesting that they were produced by a tracemaker other than a limulid.

Also notable is that a shallow telson drag impression is only preserved on the rare surface specimens where the trackways exhibit a high degree of extramorphological distortion, likely due to highly water-saturated sediments, but they still do not exhibit pusher feet morphologies. Telson drags do not appear to be present in any known examples of underprint fallout (Fig. 10; Fig. 11). However, it was also noted by Caster (1938; plate 13, fig. 7) that when modern *Limulus polyphemus* walked on stiff mud surfaces, the telson was raised off the sediment surface, leaving no impressions. The animal walked on the blade-edged pedipalps and pusher appendages, producing comma-like impressions. The pusher impression was still recognizable, so the trackway differs from *Kouphichnium aspodon* in that way.

The Carboniferous Period was inhabited by a number of arthropods that are known to have traversed both freshwater and marine environments and frequented brackish-euryhaline paleoenvironmental niches (Kjellesvig-Waering 1964; Buatois et al. 2005; Tetlie 2007). The oldest chelicerates known to have lived in euryhaline environments, at least habitually for mating and molting, are the eurypterids (Braddy 2001; Vrazo and Braddy 2011), though xiphosurans are now known from the Ordovician (Rudkin et al. 2008). A number of Carboniferous eurypterid groups

are known in the Pennsylvanian, belonging to the Hibberopteridae and Adelophthalmidae (Tetlie 2007). These eurypterid families include both walking and swimming forms that encompass an array of morphologies that likely reflect different paleohabitats. Within these two groups, there is a wide diversity of eurypterids that are found in shallow marine, estuarine, fluvial or lacustrine environments, as well as representatives that were able to make short terrestrial excursions (Braddy 2001; Tetlie 2007; King et al. 2017). This would allow for a greater diversity of size and appendage morphology, so that *Kouphichnium aspodon* may have been made by eurypterids or synxiphosurids, though eurypterid walking traces are typically assigned to the ichnogenus *Palmichnium* (Briggs and Rolfe 1983; Minter and Braddy 2009).

At present, no eurypterid body fossils, molts or cuticle have been discovered at the UCM, and there is no direct evidence of paddle appendages associated with *Kouphichnium aspodon* specimens (Vrazo and Ciuca 2017). However, it was Buta et al. (2013) who first suggested that *Kouphichnium* traces at both UCM and the Crescent Valley Mine may have been produced by a more diverse group of arthropods than simply xiphosurans. The broader group Merostomata was suggested and includes chelicerates such as eurypterids.

Close relatives to the xiphosurans are the synxiphosurans (Moore et al. 2007). They are morphologically similar to xiphosurans, but, whereas they lack the pusher foot, these animals could easily produce traces similar to *Kouphichnium aspodon*. Synxiphosurans are well known in rocks of Silurian through Devonian age, but they are rare in rocks of the Carboniferous (Moore et al. 2007). Only a single example of a Carboniferous synxiphosuran has been reported in the fossil record and is of Namurian (Serpukhovian) age (Moore et al. 2007). This rare example extended the fossil record of synxiphosurans into the Carboniferous, thus synxiphosurans are a plausible trace maker of *K. aspodon*.

Kouphichnium minkinensis

Morphologically, the individual impressions of *Kouphichnium minkinensis* (Fig. 12; Fig. 13) resemble those assigned to *K. aspodon*, however, they differ in ethology. Thus, the trace exhibits well-spaced clusters of impressions that suggest a major change in gait and activity. It is possible that the animal was using the water currents to move, being suspended buoyantly in the water, touching down on the surface due to gravity and providing thrust and directionality for the next leap at regular intervals. Given that the specimens preserve

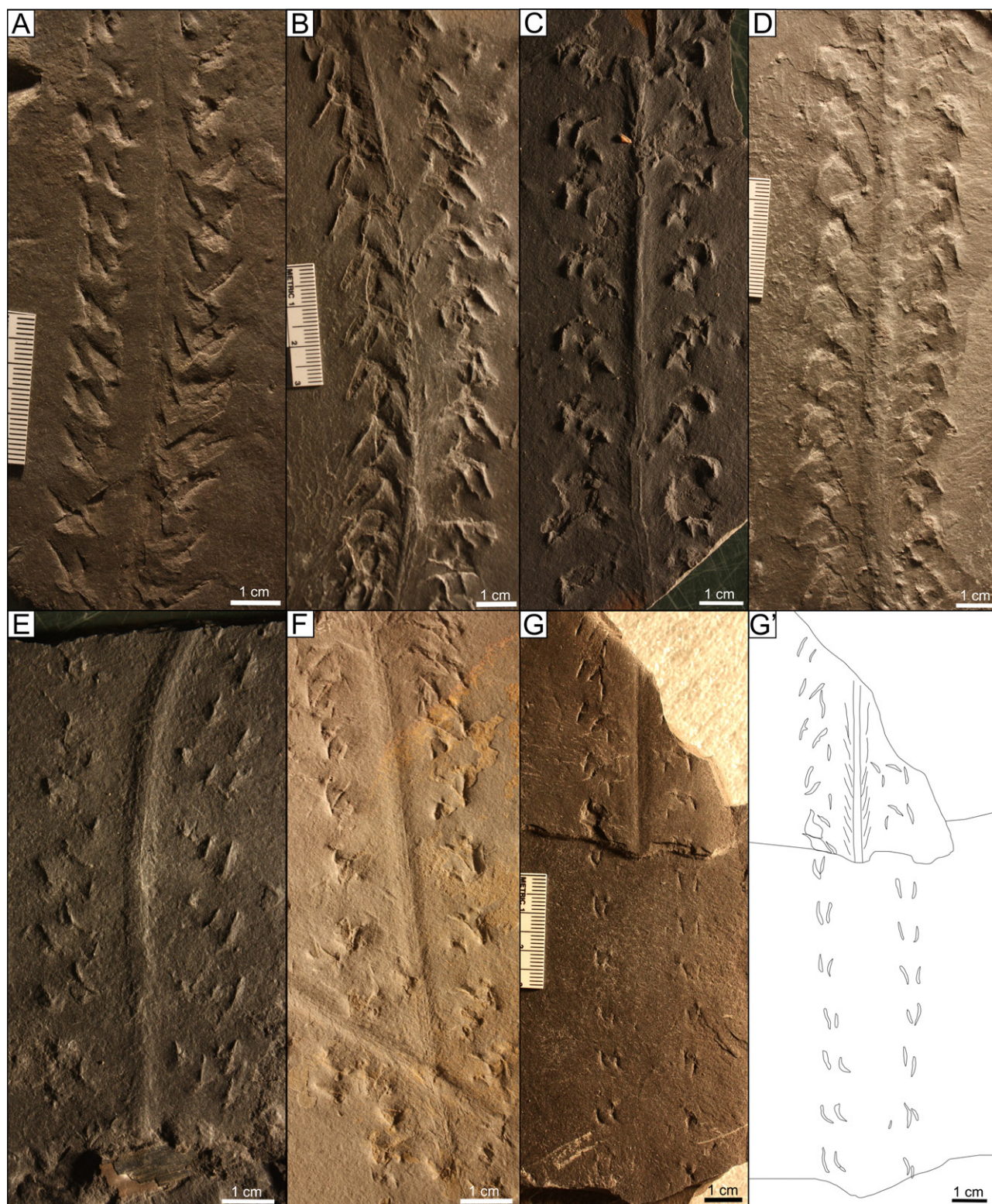


Figure 18. Unassigned “xiphosurid” tracks: A) UCM 1740 (AMNH 6003) B) UCM 1738 (MSC uncatalogued) C) UCM 722 (MSC 27764) D) UCM 1748 (AMNH 6014) E) UCM 1356 (MSC 27781) F) UCM 1414 (MSC uncatalogued) G) UCM 1781 (AMNH 6012).

underprints, sedimentary structures that would be at the sediment-water interface are not observed to confirm the movement of water. However, the “*Cincosaurus* beds” do exhibit tidal rhythmites, which suggests there were bidirectional currents. It is thus possible that the

trace maker was moving with either an incoming or an outgoing tidal current aiding its locomotion.

Invertebrate ichnotaxonomy is based on the ethology (the behavior) of a trace fossil as opposed to the taxonomy of the trace makers and extramorphological

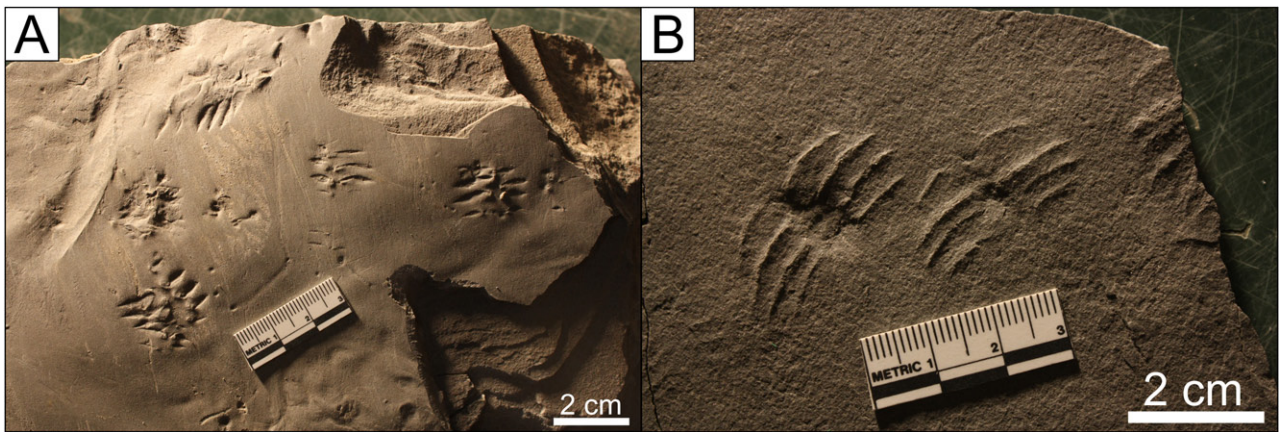


Figure 19. *Arborichnus repetitus*: A) UCM 4646 (MSC 25968) B) UCM 3549 (MSC 27905).

variation within a single ichnotaxon. Minter and Braddy (2009) discussed the difference between major and minor morphological variation. Major morphological variation includes ethological differences that are considered to be useful as an ichnotaxobase, whereas minor morphological variants such as gait variants are not. The morphological differences between *Kouphichnium minkinensis* and *K. aspodon* are likely changes in the locomotion style rather than gait, but no taphoseries has yet been noted. Despite morphological similarities in the individual appendage impressions, the mode of locomotion is different in *K. minkinensis* compared to *K. aspodon*, suggesting an ethological variant. *K. aspodon* represents a walking mode of locomotion as opposed to *K. minkinensis*, which represents a saltation mode of locomotion whereby the tracemaker undertook semi-buoyant locomotion while being carried in a current, periodically touching the bottom with all of its appendages. This behavioral difference dictates the morphological difference and what distinguishes the two ichnospecies. Thus, eurypterids, synxiphosurans or other chelicerates, as noted above for *K. aspodon*, are trace maker candidates.

Kouphichnium atkinsoni

Kouphichnium atkinsoni follows the ichnogenus concept in that the impressions are heteropodous and bifurcating. However, its dendritic morphology with multiple bifurcations per imprint is not similar to any other known ichnospecies of *Kouphichnium*, thus justifying a new ichnospecies. Two specimens of this ichnospecies have been found at the UCM and are among the largest invertebrate trackways currently known at this site (Fig. 14; Supporting Information Appendix 4). *K. atkinsoni* has an outer width that is approximately 9 cm, which is larger than other

Carboniferous *Kouphichnium* specimens and approximately 30% larger than most *K. aspodon* and *K. minkinensis*, with no growth series between them. The size is comparable to the type specimen of *K. aspodon* and likely represents a similar walking behavior.

Kouphichnium atkinsoni is a shallow underprint that preserves a series of dendritic, elongate appendage impressions with repeated bifurcations. These appendage impressions were likely flexible, as the trackway is often asymmetrical, with one side preserving appendage impressions that are medially curved backwards. Similar to the other large arthropod trackways of *K. aspodon* and *K. minkinensis*, these tracks are interpreted to represent underprint fallout due to the detailed and clear impressions seen in other examples of both invertebrate and vertebrate trackways where both surface and underprints are preserved in taphoseries. By comparison, these trackways are interpreted to be made below the water-surface interface and not in the water-saturated surface sediment. This ichnospecies currently has not been discovered with a medial telson impression, which suggests either that this is an underprint and a medial telson was not preserved in the underprint fallout, or that the trace maker did not have a telson.

Kouphichnium atkinsoni is not likely produced by a limulid due to its size being orders of magnitude larger than that of the known limulids of the Upper Carboniferous. The bifurcating impressions suggests a chelicerate arthropod, but some of the bifurcations may have been produced by other segmentations or spines along the jointed appendages. Similar to both *K. aspodon* and *K. minkinensis*, this trace may have been produced by a eurypterid or some other unknown chelicerate arthropod. The brackish conditions limit possible trace maker candidates for *K. atkinsoni*, and limulids are apparently excluded based

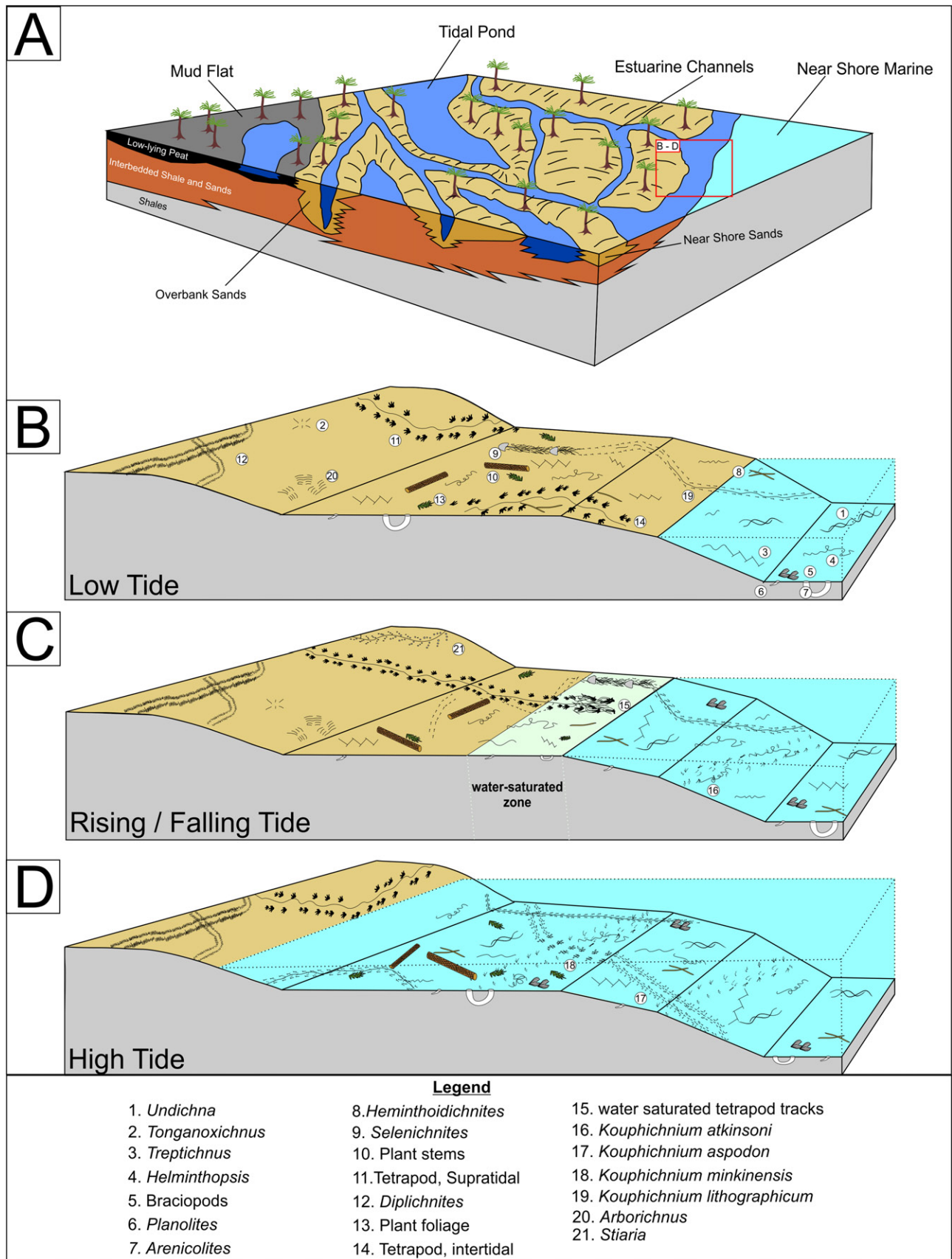


Figure 20. Paleoenvironmental reconstruction and interpretation of the ichnofaunal assemblages: A) paleoenvironmental reconstruction (modified from Pashin 2005) B) Low tide ichnofossil assemblage C) Rising and falling tide ichnofossil assemblage D) High tide ichnofossil assemblage (based on original work by Minkin 2005).

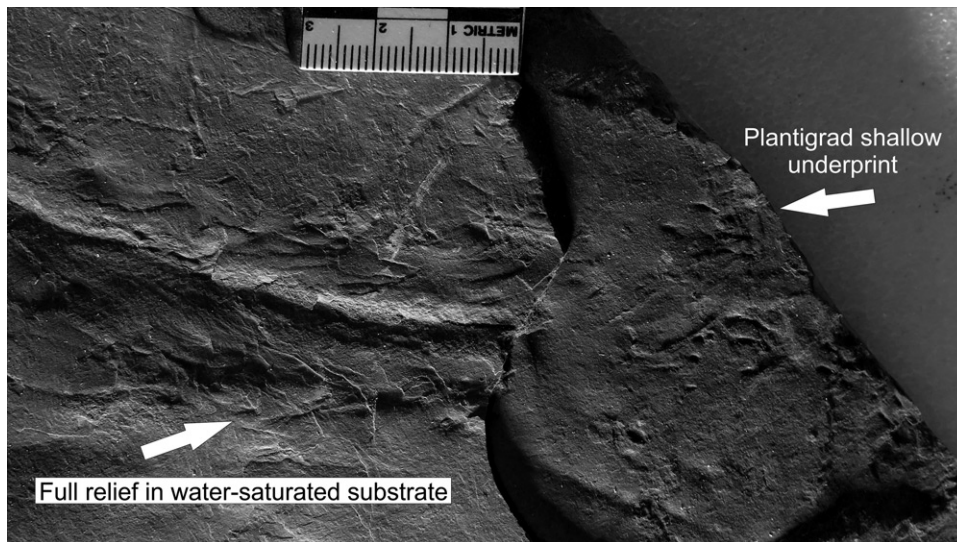


Figure 21. Underprint fallout of a *Cincosaurus* trackway, UCM 1708 (NMMNH P-43509).

on trackway size. Eurypterids and synxiphosurans remain the most likely candidates.

The unique morphology of *Kouphichnium atkinsoni* adheres to the broad ichnogenus concept of *Kouphichnium*, justifying a new ichnospecies. However, the dendritic nature of this trace has not been seen before in any known arthropod trackways and could be segregated in the future with more discoveries and novel specimens, perhaps in full relief, to justify a new ichnogenus. We take a conservative ichnotaxonomic approach here, given that only two specimens of *K. atkinsoni* have been found at the UCM.

Other xiphosuran traces

Although *Kouphichnium* is typically associated with xiphosuran activity, other examples of xiphosurid ichnofossils are also present at the UCM. The ichnogenus *Selenichnites* was first described by Hardy (1970) as semi-lunate impressions associated with *Kouphichnium* walking traces. These traces were interpreted as being the result of the prosoma (head shield) of the horseshoe crab plowing into the sediment in a digging fashion. Similar traces (*Limulicubichnus rossendalensis*) were also noted by Miller (1982), although more teardrop shaped rather than semi-lunate, that were also interpreted as the digging activity of limulids. These cubichnia resemble traces noted in the Solnhofen limestones associated with *Kouphichnium* tracks and *Mesolimulou*s body fossils at the ends of the trackways as mortichnia. *Selenichnites* traces at the UCM are rare and are only described from five known samples (Fig. 15; Supporting Information Appendix 5). Specimen UCM 007(2005.7.32) exhibits a unique co-occurrence

of *Cruziana* terminating in a *Selenichnites* resting trace. *Cruziana* is typically attributed to the walking and plowing traces of trilobites, as mentioned in previous work at the UCM (Buta and Kopaska-Merkel 2016; Lucas and Lerner 2005) but are here associated with a resting trace typically attributed to limulids. This suggests that with varying taphonomic conditions, *Cruziana* may be produced by various arthropods that include trilobites but may be produced by other invertebrates, apparently including xiphosurans, or that *Selenichnites* may be produced by other arthropods in addition to limulids, such as trilobites or eurypterids.

Additional specimens of *Selenichnites* from the UCM are larger and associated with *Dendroidichnites*-like trackways. Although typically preserved at other localities as either isolated impressions (underprints) or associated with *Kouphichnium* traces (Lerner and Lucas 2015; Buhler and Grey 2017), this is the first association of *Selenichnites* with *Dendroidichnites*. *Dendroidichnites* has been discussed by Davis et al. (2007) as being the result of a water-saturated substrate where details of trackways are not preserved and can thus be the product of a range of animals rather than attributed to a single biotaxon. It is thus not beyond possibility that these *Dendroidichnites* traces, where they are associated with *Selenichnites*, may be the soupy substrate product of xiphosuran, trilobite, synxiphosuran or eurypterid activity.

Arborichnus is a common trace fossil in the upper strata of the UCM mine and is typical of the sandy facies (Fig. 19). First described by Romano and Melendez (1985), *Arborichnus* was interpreted as being the product of limulid activity. *Arborichnus* typically has four to five linear impressions interpreted as leg impressions on either side of the bilaterally

symmetrical medial impression. Previous workers at the UCM have attributed these to limulids. Buta et al. (2013) suggested that *Arborichnus* is a resting or feeding trace produced by an invertebrate. Recent work by Buta et al. (2013) and Buta and Kopaska-Merkel (2016) has suggested this was not likely made by a limulid, as previously thought. They suggested that the *Arborichnus* specimens at the Crescent Valley Mine were likely produced by a decapod crustacean, although they also concluded that the trace maker is unknown. Regardless, the traces were imprinted on the tops of a sandy substrate that was deposited under high energy conditions, such as storm deposits (Buta and Kopaska-Merkel 2016). Given the reinterpretation of *Kouphichnium aspodon* as potentially being made by eurypterids, and *Selenichnites* associated with *Cruziana* traces that may be of trilobite origin, any of the decapods may be the trace maker of *Arborichnus*. Additional body fossils of a spider-like insect have been found at the UCM (Buta and Kopaska-Merkel 2005) that are also plausible candidates.

Paleoecological interpretation

The paleoenvironment at the UCM was interpreted by Pashin (2005) to be an estuarine tidal flat, thought to have been deposited within a deltaic system at the mouth of a large river that was tidally dominated (Figs. 4C and D). The paleoecology of the animals that inhabited this tidal flat are inferred almost entirely from ichnofossils, as invertebrate body fossils are rare at UCM (Atkinson 2005; Minkin 2005; Buta and Kopaska-Merkel 2016). All of the known ichnofossils are preserved within the finely interbedded tidal rhythmites and are interpreted to represent alternating subaquatic and subaerial ichnofossil assemblages (Pashin 2005; Fig. 20). A lack of rain impressions and desiccation features suggest that the substrate was permanently wet or submerged (Rindsberg 2005). Estuary conditions are typically hostile environments for most life, as the mix of fresh and salt water excludes many groups of animals except those euryhaline taxa tolerant of both salinity extremes. As discussed above, a number of invertebrate taxa are tolerant of these conditions, in addition to terrestrial taxa that may occupy this niche during subaerial exposure.

Observations in this study suggest that at the UCM many invertebrate and vertebrate traces were being made contemporaneously. Terrestrial trace fossils (tetrapod trackways: Haubold et al. 2005; and terrestrial arthropod trackways: Lucas and Lerner 2005) were produced under subaerial conditions on emergent muddy

freshwater-dominated estuarine tidal flats during falling or low tides (Minkin 2005; Dilcher et al. 2005). Previous workers inferred that tetrapods were feeding on intertidal invertebrate faunas that may have sustained populations of juvenile amphibians and amniotes (Rindsburg et al. 2004; Martin and Pyenson 2005), as invertebrate traces are common within the *Cincosaurus* beds (Martin and Pyenson 2005). Abundant infaunal burrows (*Treptichnus*, *Planolites*, *Cochlichnus*, *Helminthoidichnites*, *Heminthopsis* and *Gordia*) are present in both ichnofossil assemblages, and represent an intertidal invertebrate fauna (Rindsberg and Kopaska-Merkel 2005a,b; Fig. 20). Subaquatic traces such as *Undichna* were made during high tides (Fig. 20). Subaquatic and subaerial traces are separated stratigraphically at millimeter scale, with the exception of underprint fallout of larger, often tetrapod trackways and infaunal burrows that penetrate through multiple strata. The tetrapod tracks do not show evidence of swimming, suggesting that they were deposited during low tides under subaerial or near subaerial conditions. *Undichna* (fish trails) are found on bedding planes that lack tetrapod footprints, suggesting that fish and tetrapod traces were made under different depositional conditions (i.e. subaerial vs subaqueous; Pashin 2005). The *Undichna* traces were deposited during high tide as well as during rising or falling tidal cycles (Martin and Pyenson 2005; Minkin 2005). It has been interpreted that fish traces (*Undichna*) were made during falling tides, while tetrapod and some invertebrate trackways were made on emergent mudflats (Rindsburg et al. 2004; Haubold et al. 2005; Lucas and Lerner 2005; Martin and Pyenson 2005; Pashin 2005). The *Undichna* represent distal faunal elements that ephemerally occupied the tidal flat niche during subaquatic times. Similarly, tetrapod and terrestrial invertebrate traces represent proximal faunal elements that only occupied the tidal flat niche during times of subaerial exposure. The infaunal burrows are present in all strata and represent interstitial dwelling animals, while many euryhaline invertebrates interpreted from *Kouphichnium* trackways are also present under all tidal conditions when present.

Conclusions

The importance of paleoichnology to the understanding of paleoecology and paleo-communities is reinforced by studies at the UCM within transitional marine-freshwater environments. The UCM habitat was a biologically diverse ecosystem, and continued research will shed more light on the intricate interplay of paleoecologies at a marginal terrestrial-aquatic estuarine paleoenvironment. The paleoecology of the

animals that inhabited this paleoenvironment is inferred almost entirely from ichnofossils. Sites preserving both body fossils and tracks are rare, likely due to taphonomic differences, making understanding the tracemakers at fossil sites dominated by ichnofossils, such as the UCM, important.

Although a comprehensive revision of the ichnogenus *Kouphichnium* is in dire need (Buatois et al. 1998), this article assesses the ichnospecies assigned to *Kouphichnium* at the UCM. Previous to this study, only *Kouphichnium* isp. and *Kouphichnium aspodon* were noted, and the ichnogenus was used liberally, encompassing a wide range of morphologies and a number of specimens that were erroneously assigned to this ichnogenus (See Supporting Information Appendix 7). These previously unassigned xiphosurid traces are here noted and are excluded from the ichnogenus *Kouphichnium*, leaving them in open nomenclature, pending further investigation.

In part, the ambiguity surrounding *Kouphichnium aspodon* has been derived from an incomplete holotype specimen. Subsequently collected examples from the UCM have shed new light on and allowed for a better ichnological diagnosis of the ichnospecies here assessed to be valid ichnotaxa. *K. lithographicum* has been assigned to specimens previously misinterpreted as *Paleohelcura* trackways. Consequently, from this detailed study of *K. aspodon*, two new ichnospecies of *Kouphichnium* are described (*K. atkinsoni* and *K. minkinensis*). *K. atkinsoni* loosely fits the ichnogenetic concept of *Kouphichnium*, but additional specimens may reveal that it is unique enough, with its dendritic bifurcating tracks, that it should be segregated as a separate ichnogenus. With only two specimens encountered in this study, we conservatively assign the new ichnospecies to *Kouphichnium* (Fig. 14).

The wide range of morphological variation preserved at the UCM allows a better understanding of the underprint fallout. Sediment water-saturation affects the overall morphology and taphonomy of some *Kouphichnium* ichnospecies and has wider implications for the taphonomy of the ichnology at UCM (Fig. 11). In this study, *K. aspodon*, *K. minkinensis* and *K. atkinsoni* are interpreted to not have been made by xiphosurans based on the lack of pusher appendage impressions. Eurypterids appear to be the most likely candidates given the paleoecological conditions and similarities in both size and morphology of the imprints to the chelicerate anatomy of known Carboniferous eurypterid groups. Furthermore, they follow an ethology similar to known eurypterid ecologies from older strata (Braddy 2001; Tetlie 2007;

Vrazo and Braddy 2011). Through this study, we have suggested that some *Kouphichnium* ichnospecies may be produced by more than just limulids, and that other chelicerates should be considered as potential trace makers. This has broader implications for paleoenvironmental studies when ichnofossils are heavily relied on for paleoenvironmental and paleoecological interpretations.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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