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# Invertebrate trace fossils from the Alveley Member, Salop Formation (Pennsylvanian, Carboniferous), Shropshire, UK

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ABSTRACT

The late Carboniferous–early Permian was a period of major environmental change, with the rainforests that covered the equatorial zone during the Carboniferous disappearing due to increasing aridification. This environmental transition had significant impacts on the terrestrial biota, including a major extinction event among plant and vertebrate groups. A rich and unique ichnofauna from the Alveley Member (Moscovian: Westphalian D) of the Salop Formation at Alveley in Shropshire (England) has yielded important insights into late Carboniferous terrestrial communities. However, research to date has focused entirely on the vertebrate footprints. Abundant invertebrate ichnofossils also occur at Alveley, typically on the rippled upper surfaces of beds assigned to a floodplain facies that preserve the vertebrate tracks in hyporelief on their base. We provide the first detailed examination of the invertebrate ichnofauna from Alveley, identifying six ichnospecies within five ichnogenera (*Diplichnites*, *Gordia*, *Paleohelcura*, *Palmichnium*, *Protichnites*), including a new species of the common arthropod ichnogenus *Diplichnites*. This moderately diverse invertebrate ichnofauna is dominated by arthropod repichnia. There is no evidence of infaunal bioturbation and the single example of *Gordia* indicates limited sediment grazing activity. The Alveley ichnofauna is typical of Euramerican continental ichnoassemblages from the very latest Carboniferous, and

indicates a moderate diversity of arthropods (crustaceans, arachnids and chelicerates) living alongside the marginal freshwater to terrestrial assemblage of temnospondyl amphibians, and basal synapsid, diadectomorph and captorhinomorph amniotes.

KEYWORDS: Carboniferous, arthropods, trace fossils, terrestrialisation, taxonomy

## 1. INTRODUCTION

The late Carboniferous to early Permian time represents an interval of prominent change within terrestrial biota, with Euramerican strata from this interval documenting the transition from a rainforest biome through to the aridification of the New Red Sandstone continent (DiMichele et al*.* 2006; DiMichele 2013; Yang et al*.* 2014). This transition corresponds with the 'Carboniferous Rainforest Collapse', and is proposed to have led to dramatic changes in terrestrial tetrapod communities (Sahney et al*.* 2010; Dunne et al*.* 2018). Dating from this interval, late Carboniferous non-marine strata from the Alveley area, Shropshire, UK, have yielded a globally-significant vertebrate ichnofauna that is stratigraphically unique in Europe; extending the known ranges of several vertebrate ichnogenera from the early Permian into the late Carboniferous (Tucker and Smith 2004). Although this vertebrate ichnofauna has received relatively detailed study, other components of the ichnoassemblage from Alveley have been almost entirely neglected. We describe here the accompanying invertebrate ichnofauna, in order to further document the biotic composition of this unique window into late Carboniferous terrestrial environments.

### 1.1. Previous work

The importance of the Alveley sites (Fig. 1) was recognised in 1914 by Frank Raw, a lecturer in the geology department at the University of Birmingham. Initial collections were made from Butts Quarry (SO 7556 8298) and Hall Close Quarry (SO 7605 8375); both of which are now largely overgrown and inaccessible. It was not until after the First World War that the bulk of the material was excavated and deposited within the Lapworth Museum of Geology collections at the University.

The Raw Archive, held by the Lapworth Museum, includes an extensive lantern slide collection and scripts of public talks that indicate that the tracks were presented to a wider audience by Raw, but it took six decades before the first formal publication of a description of the Alveley trackways (Haubold and Sarjeant, 1973, 1974). Subsequently, there was a significant hiatus before these vertebrate trackways were later revised by Tucker and Smith (2004) and six ichnospecies were recognised, i.e.: *Limnopus* (*Limnopus*) *vagus* Marsh, 1894*; Limnopus* (*Batrachichnus*) *plainvillensis* Woodworth, 1900; *Limnopus* (*Batrachichnus*) *salamandroides* (Geinitz, 1861); *Dimetropus leiserianus* (Geinitz, 1863); *Hyloidichnus*? *bifurcates* Gilmore, 1927; and *Ichniotherium willsi* Haubold and Sarjeant, 1973. The only previous (unfigured) attempts at assigning ichnotaxa to invertebrate traces from Alveley were undertaken by Pollard (1988), who suggested the presence of "*Acripes* (*Diplichnites*?)" and *Paleohelcura*, and Tucker and Smith (2004) who noted the presence of *Diplichnites gouldi*. The collected material has been re-examined for this study and five ichnogenera are now identified, comprising four named ichnospecies and two unnamed ichnospecies.

## 2. GEOLOGICAL BACKGROUND

### 2.1 Stratigraphy

The Alveley Member (formerly the Keele Formation; Besly and Cleal 1997) is the lower of two members (the other being the Enville Member) of the Salop Formation, which crops out in Shropshire, Staffordshire and Warwickshire. Lithostratigraphically, the Salop Formation falls within the Warwickshire Group (formerly the 'Barren Coal Measures') (Powell et al*.* 2000) (Fig. 2). Largely based on regional context and correlation, the Salop Formation is considered as late Carboniferous (Pennsylvanian), with its stratigraphically lower Alveley Member dating from the Moscovian (Westphalian D) Stage and the overlying Enville Member ranging into the Kasimovian (Stephanian in the European context; Powell et al*.* 2000). The thickness of the unit within the type area varies between 152 and 247 metres (Johnson et al*.* 1997). The Enville Member has also yielded vertebrate and invertebrate ichnofossils (e.g. Hardaker 1912; Meade et al. 2016).

2.2 Sedimentary context

The Alveley Member is dominated by oxidised red-beds deposited after the shift from coal swamps to well-drained alluvial floodplains within the Pennine Basin; a forced response to the developing Variscan Orogeny to the south (Johnson et al. 1997). There are two principal facies represented by the Alveley Member, seemingly reflecting deposition under alternate states of fluctuating water levels (Glover and Powell 1996). The first is dominated by fine- to medium-grained red or grey sandstones, with sheet-like or channelized architectures, intercalated with rain-pitted mudstone horizons and ferruginous and gley palaeosols. This facies has previously been interpreted as reflecting a floodplain environment with a persistently high water table (Tucker and Smith 2004). The second facies consists of thin sheets of sandstones separated by calcrete-rich palaeosols, suggested to record lower water table levels and low rates of sedimentation, punctuated by alluvial flood deposits (Tucker and Smith 2004). The unit lacks distinct marker beds or biostratigraphic components (Powell et al. 2000).

Within the Alveley area, the Alveley Member is only 8 metres thick at outcrop (the greater thickness for the unit quoted above coming from boreholes), and records the first facies described above (Glover and Powell 1996). The ichnofossil material described here occurs in samples from both the mudrock and sandstone lithologies, in association with sedimentary structures including tool marks, flute casts, rain pits and desiccation cracks.

3. SYSTEMATIC PALAEONTOLOGY

Trace fossils are assigned to the ichnogenera *Diplichnites, Gordia, Paleohelcura, Palmichnium* and *Protichnites*. The majority of specimens described below come from Butts Quarry. Raw (1919, Lapworth Museum Archive, Miscellaneous Collection 60) indicated that the quarry contained two horizons, 3 cm apart, from which arthropod tracks were recovered: although the exact level for individual specimens is undocumented. The specimens of *Paleohelcura* and *Palmichnium* illustrated here come from the nearby Hall Close Quarry. The specimens of *Gordia* from Alveley occur in hyporelief on the base of the sandstone bed from Butts Quarry that hosts the majority of the Alveley vertebrate traces (Tucker and Smith 2004). Conversely, the arthropod traces from the same locality are all found on the rippled upper surfaces of the same bed and the overlying mud drapes. Specimens of *Diplichnites* (Figures 3 & 4), the commonest identifiable trace fossil, occur in both negative and positive epirelief on the same sedimentary lamination; in some specimens (e.g. Figure 4 b, d) this variation is seen within a single trackway, with the positive components potentially indicating where the tracemaker left the imprint by withdrawing their limbs from the substrate. This indicates variation in the cohesiveness of the depositional surface, probably due to variation in moisture content of the sediment on a highly localised scale.

All material is deposited in the Lapworth Museum of Geology, University of Birmingham, UK, with the prefix BU referring to specimens housed in the type and figured collection and those prefixed BIRUG residing in the general collection.

*Diplichnites* Dawson, 1873

Discussion: *Diplichnites* is the most frequently reported invertebrate trackway ichnogenus in the global stratigraphic record, but its ichnotaxonomy is in need of revision (Buatois et al., 1998; Keighley and Pickerill, 1998). However, the holotype of the ichnogenus has not been located and a full review is beyond the scope of this paper. *Diplichnites* is thought to have numerous different possible trace makers; whilst originally the ichnogenus was intended to be reserved for tracks produced by arthropods other than trilobites (Dawson, 1873) this was expanded by Seilacher (1955) to include trilobite traces. Eight ichnospecies of *Diplichnites* are currently taxonomically valid (Keighley and Pickerill, 1998), and a new ninth ichnospecies is reported herein. *Diplichnites* ichnospecies are generally diagnosed on the basis of the morphology of individual impressions, although *D. cuithensis* is defined as having 23 pairs of tracks in a natural cycle (Briggs et al., 1979).

*Diplichnites gouldi* Gevers (in Gevers et al., 1971)

Fig. 3

Material: Five specimens with four from Butts quarry (BU 5341, BIRUG 22063, BIRUG 22074, BIRUG 114104) and one from Hall Close (BIRUG 22100).

Description: All five specimens of *D. gouldi* are preserved as negative epirelief trackways. The trackways comprise two parallel rows of imprints without any medial groove or ridge and the general course of the track is slightly meandering. The number of tracks in a natural cycle is indeterminate for these specimens. The width of the trackways varies from 9-13 mm and the spacing between individual prints varies from 2 to 4 mm.

Discussion: *D. gouldi* is the most frequently reported ichnospecies of *Diplichnites* in the fossil record (Keighley and Pickerill, 1998). Due to the indeterminate track cycles in the Alveley specimens it is difficult to interpret a specific arthropod trace maker.

*Diplichnites rawi* (n. isp.)

Fig. 4

2003 *Merostomichnites* cf. *strandi* Størmer, 1934; Weber and Braddy, p. 10, fig. 12.

2007 *Diplichnites gouldi* Bradshaw, 1981; Minter et al., p. 403, fig. 7B, D.

2017 *Diplichnites gouldi* Gevers in Gevers et al. 1971; Getty et al., p. 190, fig. 4C.

Etymology: Named for the original collector of the material from Alveley, Frank Raw.

Material: At least nineteen slabs with fifty trackways, all from Butts Quarry, including the holotype BU 3727, figured specimen BU 5342, and additional unfigured specimens BIRUG 22056, BIRUG 11405, BIRUG 114106, BIRUG 21959, BIRUG 22006, BIRUG 22050, BIRUG 22059, BIRUG 22060, BIRUG 22061, BIRUG 22062, BIRUG 22067, BIRUG 22071, BIRUG 22072, BIRUG 22077, BIRUG 22079, BIRUG 22082 and BIRUG 22088.

Diagnosis: Trackways lacking a medial groove, symmetrical across the midline. Individual footfall marks can present in a variety of shapes (arcuate, elongate, or sub-circular) within a single trackway. Impressions are regularly spaced and arranged in series of 5-10 impressions. The final impression of any given series is commonly adjacent to the first of the subsequent series, creating the impression of en-echelon track cycles. Series form broad V shapes, with the medial angle upwards of 15 degrees.

Description: 50 trackways are preserved on 19 slabs in a mixture of negative and positive epirelief. The maximum external width ranges from 15-26 mm, the minimum internal width ranges from 6-11 mm and the distance between individual prints varies between 2.5 and 5 mm within a series depending upon size. Tracks occur in series of 5-7 distinct impressions and the general course of the trackways is predominately straight with some specimens demonstrating a slightly curved aspect.

Discussion: Examples of similar trackways have been previously reported on several occasions and assigned to a variety of ichnotaxa, including *Diplichnites gouldi* (Minter et al., 2007; Getty et al., 2017) and *Merostomichnites* (Weber and Braddy, 2003). The multiple possible secondary ichnotaxobases that can be used to distinguish these traces from other *Diplichnites* ichnospecies warrants the formal erection of a new ichnospecies to describe these distinct traces. The trackway bears similarities with *Protichnites* isp. (see below), but none of the 50 trackways in the Alveley collection exhibit the medial furrow necessary to assign them to that ichnogenus. Whilst a range of trace makers are possible, as tracks occur in series of 5-7 impressions it is likely that these traces were produced by an isopod.

*Gordia marina* Emmons, 1844

Fig. 5

Material: A single specimen from Butts Quarry (BU 5343).

Description: A single self-overcrossing trail, preserved in hyporelief. Trail is approximately 1 mm wide, unbranched, and non-ornamented, forming a single wide loop (c. 95mm at maximum dimension).

Discussion: *Gordia* is a facies-crossing form, known from a wide range of subaqueous environments from the Ediacaran onwards, and likely produced by a variety of mobile, non-specialized deposit feeders (Fillion and Pickerill, 1990; Buatois and Mángano, 2016).

*Paleohelcura tridactyla* Gilmore, 1926

Fig. 6

Material: Three specimens from Hall Close quarry including the figured specimen BU 5344 and unfigured slabs BIRUG 21967 and BIRUG 22096.

Description: Three trackways are observed in a combination of positive and negative epirelief. Footfalls occur in series of three, alternate asymmetry oblique to the midline. A discontinuous medial ridge or furrow is commonly observed. The trackways have internal width 23-57 mm and external width 29-63 mm. The individual footfall impressions are all approximately the same size, with diameter 6 mm, separated by c. 2 cm in a single series and 7 cm between series. Trackways are observed on rippled surfaces and their general course is straight as far as can be determined.

Discussion: From the arrangement of track series, *Paleohelcura* is thought to be produced by a hexapod with an asymmetric gait such as a scorpionid (Sadler, 1993). The body fossils of potential scorpionid tracemakers are known from Carboniferous strata, contemporaneous with the Alveley succession, from elsewhere in the UK (Anderson et al., 1997).

*Palmichnium* isp. Richter 1954

Fig. 7

Material: A single specimen from Hall Close quarry (BU5345).

Description: A single trackway preserved in positive relief. Footfalls occur in series of three, opposite symmetry oblique to the midline. Individual impressions are 11 mm in diameter, the internal width of the trackway 21-56 mm and external width 32-67 mm and the distance between individual prints varies between 1.5 and 2 cm within a series. The general course of the trackway appears to be straight. A weakly-developed medial ridge is intermittently evident.

Occurrence: Found in collections from Hall Close quarry.

Discussion: *Palmichnium* shares many similarities in form with *Paleohelcura* but is distinguished by its different symmetry, suggesting distinct trace makers for the ichnogenera. Although originally considered to have a trilobite tracemaker (Gevers et al., 1971), *Palmichnium* is now commonly accepted as having been formed by a eurypterid (Braddy and Milner, 1998).

*Protichnites* isp. Owen 1852

Fig. 8

Material: A single specimen from Butts Quarry (BU 5346).

Description: A single example of a trackway preserved in negative epirelief and traversing a rippled surface. Towards the crest of each ripple mark a medial furrow becomes apparent. Otherwise the trackway is near identical in form to *Diplichnites rawi*, with footfall impressions arranged symmetrically about the midline in oblique series of 5-7. The outer width of a series ranges from 22 mm at its widest point to 10 mm at its narrowest and the distance between individual prints varies between 1.5 and 2.5 mm within a series.

Occurrence: Found in collections from Butts quarry.

Discussion: The presence of a medial furrow is the key diagnostic criterion that permits the identification of this trace as *Protichnites* (Keighley and Pickerill, 1998). It is probable that this *Protichnites* specimen shares a common trace maker with *Diplichnites rawi* in the Alveley specimens, likely a crustacean such as an isopod, with the medial groove the result of the body of the animal dragging along the ground as it moved over the crest of a ripple.

## 4. COMPARISON WITH OTHER CARBONIFEROUS–PERMIAN CONTINENTAL ICHNOFAUNAS OF EURAMERICA

The Alveley collections exhibit a moderately diverse invertebrate ichnofauna of arthropod repichnia, with no evidence of infaunal bioturbation and a singular instance of *Gordia* indicating sediment grazing activity. The co-occurrence of such an invertebrate ichnofauna with vertebrate trackways can be contextualized with other mid to late Palaeozoic continental successions from Euramerica. Most studies of Carboniferous and Permian strata have considered either invertebrate or vertebrate traces in isolation (Minter et al., 2016). However, where holistic studies have been undertaken, archetypal trends in ichnoassemblage composition can be identified that stratigraphically correlate with sedimentological and palaeobotanical changes associated with Pangean supercontinental assembly; specifically, the Kasimovian collapse of "coal age" equatorial rainforests and the accelerated Permian expansion of dryland sedimentary environments (Davies and Gibling, 2013; DiMichele, 2013). In such a context, the Alveley ichnofauna is typical of Euramerican continental ichnoassemblages from the very latest Carboniferous ("Stephanian", or post–Kasimovian), but with notable dissimilarities from older late Carboniferous (Pennsylvanian) or younger Permian ichnoassemblages.

The oldest instances of non-marine late Carboniferous tetrapod trackways (Bashkirian and Moscovian) are often seen in association with *Diplichnites*, but in addition these ichnoassemblages typically also contain a variety of meniscate or U-shaped burrows (e.g., *Beaconites*, *Taenidium*, *Arenicolites*) and arthropod trackways directly attributable to xiphosaurids (*Kouphichnium*). Such ichnoassemblages typically occur in strata that contain sedimentological indicators of more persistent subaqueous or wetland conditions, and examples include the ichnofaunas of the Moscovian Warwickshire Group of the Somerset Coalfield, UK (Pollard and Hardy, 1991) and the various formations of the Bashkirian–Moscovian Cumberland Group in eastern Canada (Falcon-Lang et al., 2006, 2015). Younger, Permian assemblages are typified by a greater abundance and diversity of tetrapod trackways and the frequent association with insect or larval traces (e.g., *Tonganoxichnus*, *Cochlichnus*): examples include the early Permian Abo Formation of New Mexico (Lucas et al., 2005) and the early to middle Standenbühl Formation of Germany (Minter et al., 2016 and references therein).

The ichnological signature of a moderately diverse assemblage of tetrapod and arthropod epifaunal trackways appears to be archetypal of a transitional continental ichnoassemblage between a "coal age" signature of low diversity vertebrate tetrapod tracks in strata with arthropod (including xiphosaurid) trackways and abundant infaunal burrows, and a Permian signature of higher diversity tetrapod tracks with multiple arthropod (including insect) trackways and resting traces. Stratigraphically, such transitional ichnoassemblages appear to be commonly associated with the Kasimovian onset of the shift towards more arid non-marine alluvial sedimentary environments in Euramerica (Davies and Gibling, 2013). In addition to the Alveley ichnoassemblage reported here, similar assemblages have been recognised in the Kasimovian–Permian Pictou Group of eastern Canada (Ryan, 1986; Brink et al., 2012) and the "Stephanian" strata of Montceau-les-Mines, France (Pollard, 1988).

## 5. CONCLUSIONS

The Alveley Member of the Salop Formation provides a unique window into the composition of late Carboniferous ecosystems with a rich and diverse vertebrate ichnofauna accompanied by the invertebrate traces documented herein. The presence of crustaceans, arachnids and chelicerates as putative track makers indicates a moderate diversity of arthropods co-existing with the marginal freshwater-terrestrial assemblage of stem-lissamphibians, and basal synapsid, diadectomorph and captorhinomorph amniote ichnotaxa recognised by Tucker and Smith (2004).

Competing interests. The authors declare no competing interests.

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FIGURE CAPTIONS

Fig. 1. Location of Alveley (red star) within the English Midlands. Major motorway network in black, 'A' roads in dark grey.

Fig. 2. Stratigraphy of the Alveley Member, Salop Formation in a regional and global context (modified from Powell et al. 2000).

Fig. 3. a) photographic illustration and b) interpreted line drawing of *Diplichnites gouldi* (BU 5341) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Butts quarry , Alveley, Shropshire, U.K.

Fig. 4 a) photographic illustration and c) interpreted line drawing of *Diplichnites rawi* (BU 3727 holotype) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Butts quarry , Alveley, Shropshire, U.K.; b) photographic illustration and d) interpreted line drawing of *Diplichnites rawi* (BU 5342) illustrating preservation in negative and positive epirelief due to variable substrate from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Butts quarry, Alveley, Shropshire, U.K..

Fig. 5 a) photographic illustration and b) interpreted line drawing of *Gordia marina* Emmons 1844 (BU 5343) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Butts quarry, Alveley, Shropshire, U.K..

Fig. 6 a) photographic illustration and b) interpreted line drawing of *Paleohelcura tridactyla* Gilmore 1926 (BU 5344) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Hall Close quarry, Alveley, Shropshire, U.K..

Fig. 7 a) photographic illustration and b) interpreted line drawing of *Palmichnium* isp. Richter 1954 (BU 5345) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Hall Close quarry, Alveley, Shropshire, U.K..

Fig. 8 a) photographic illustration and b) interpreted line drawing of *Protichnites* isp. Owen 1852 (BU 5346) from the Alveley Member, Salop Formation, Warwickshire Group (Moscovian, Westphalian D) from Butts quarry , Alveley, Shropshire, U.K..

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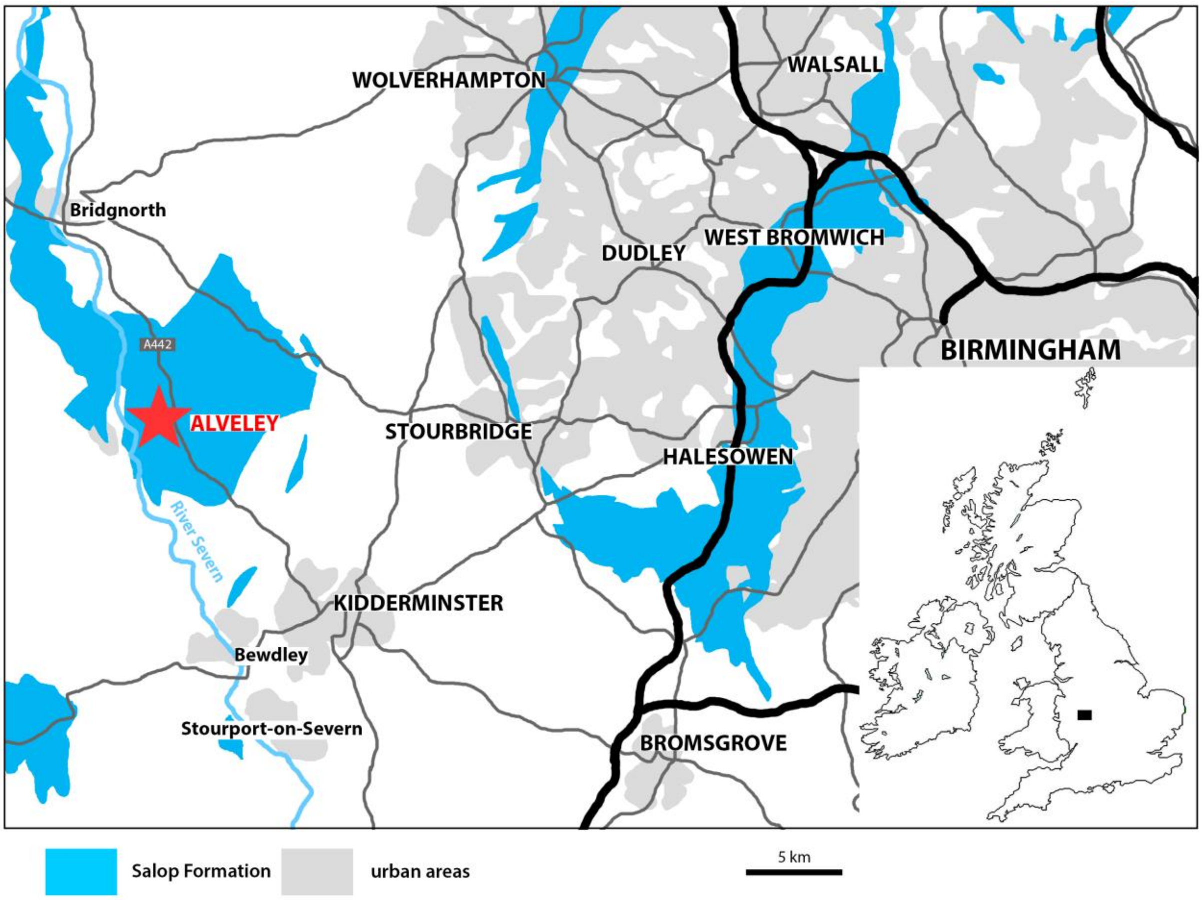
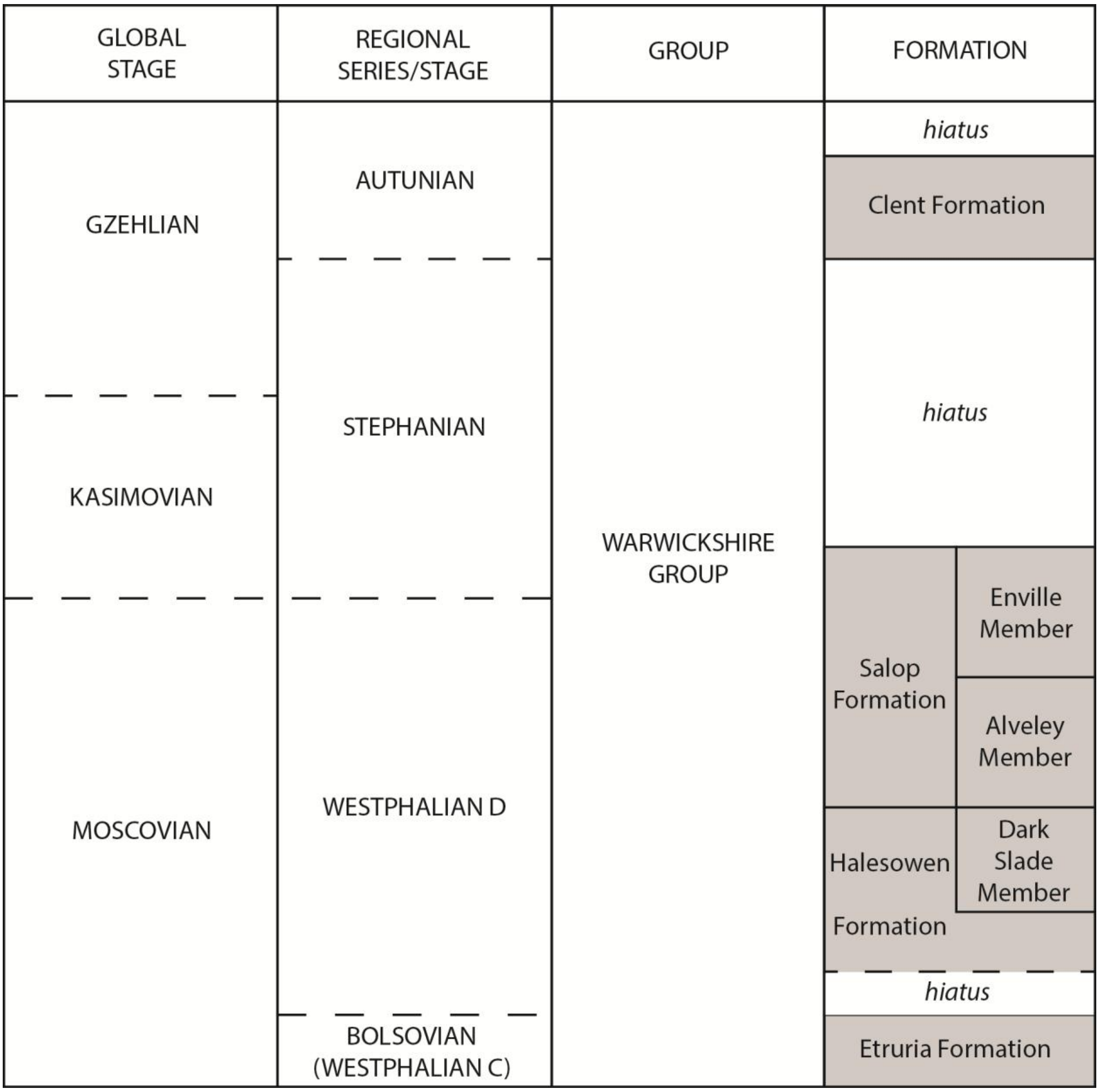



Figure 1 Colour online, greyscale in print

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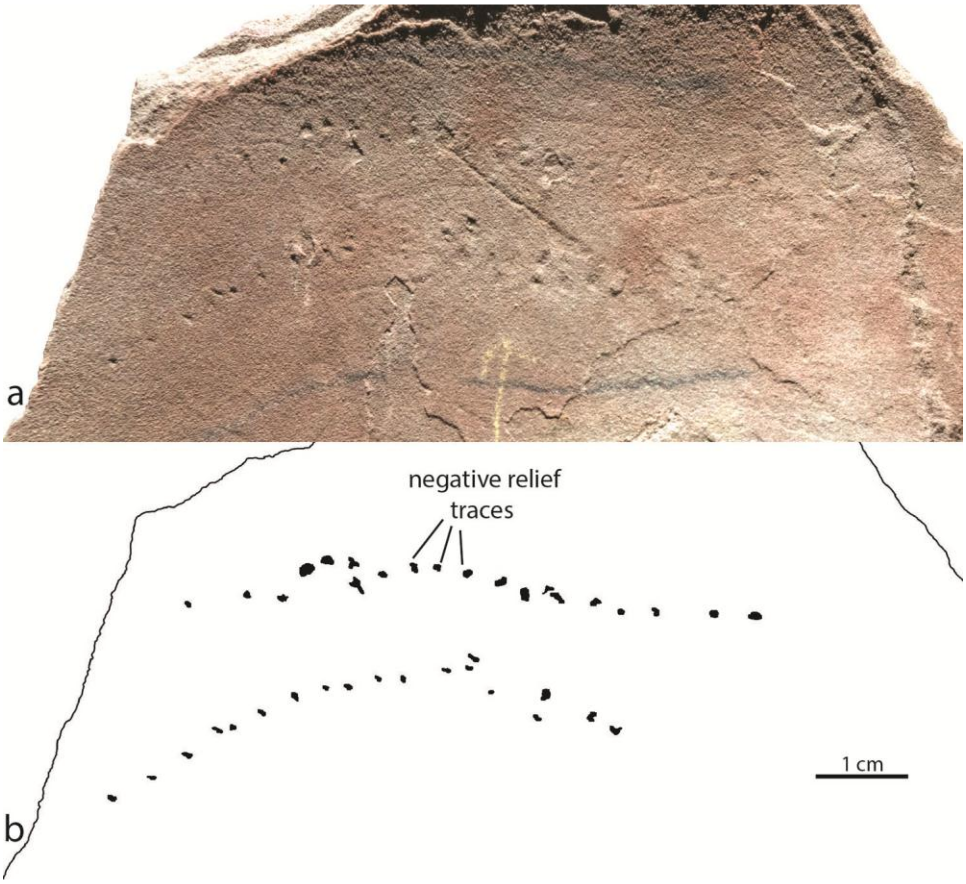


Figure 3 - *Diplichnites gouldi* Colour online, greyscale in print

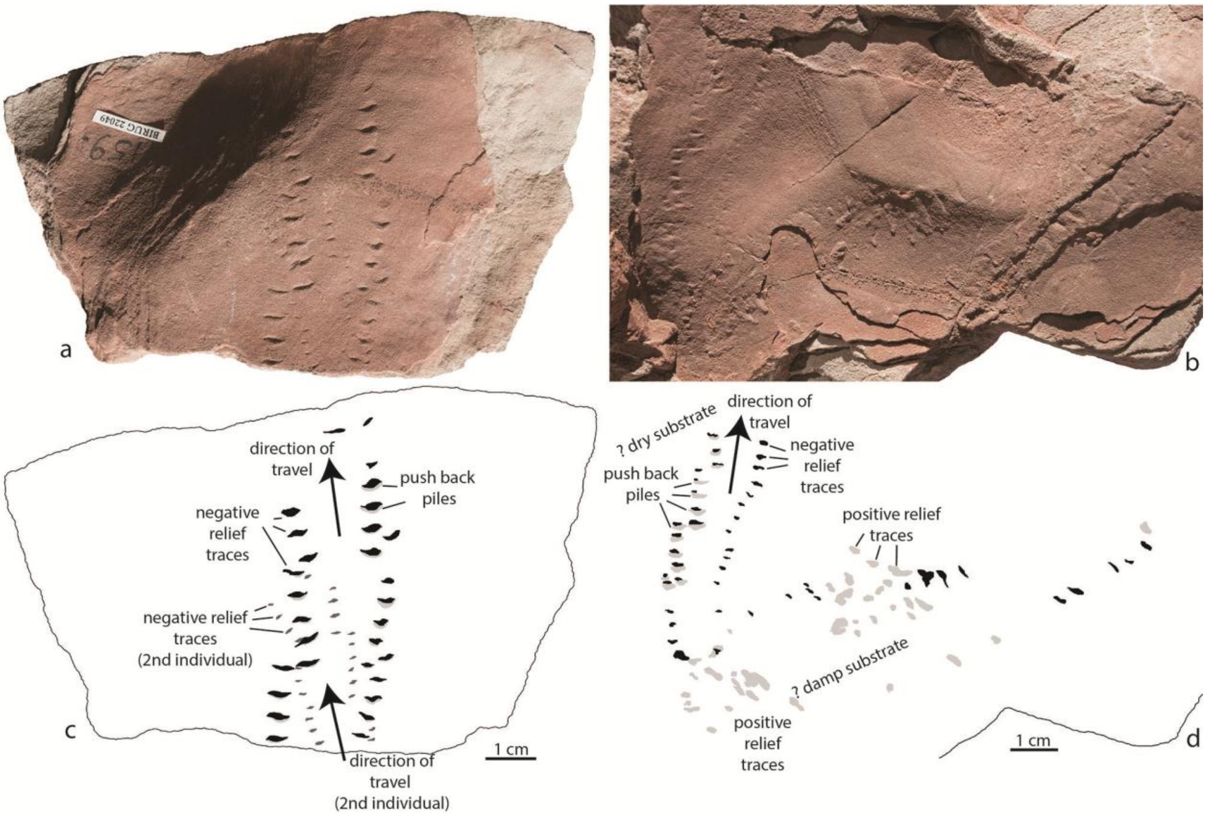


Figure 4 - *Diplichnites rawi* Colour online, greyscale in print

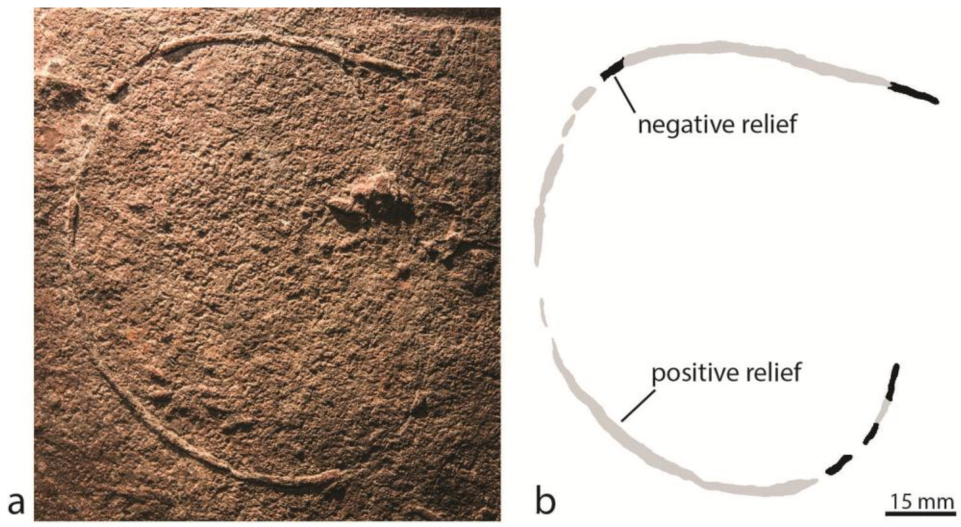


Figure 5 – *Gordia* Colour online, greyscale in print

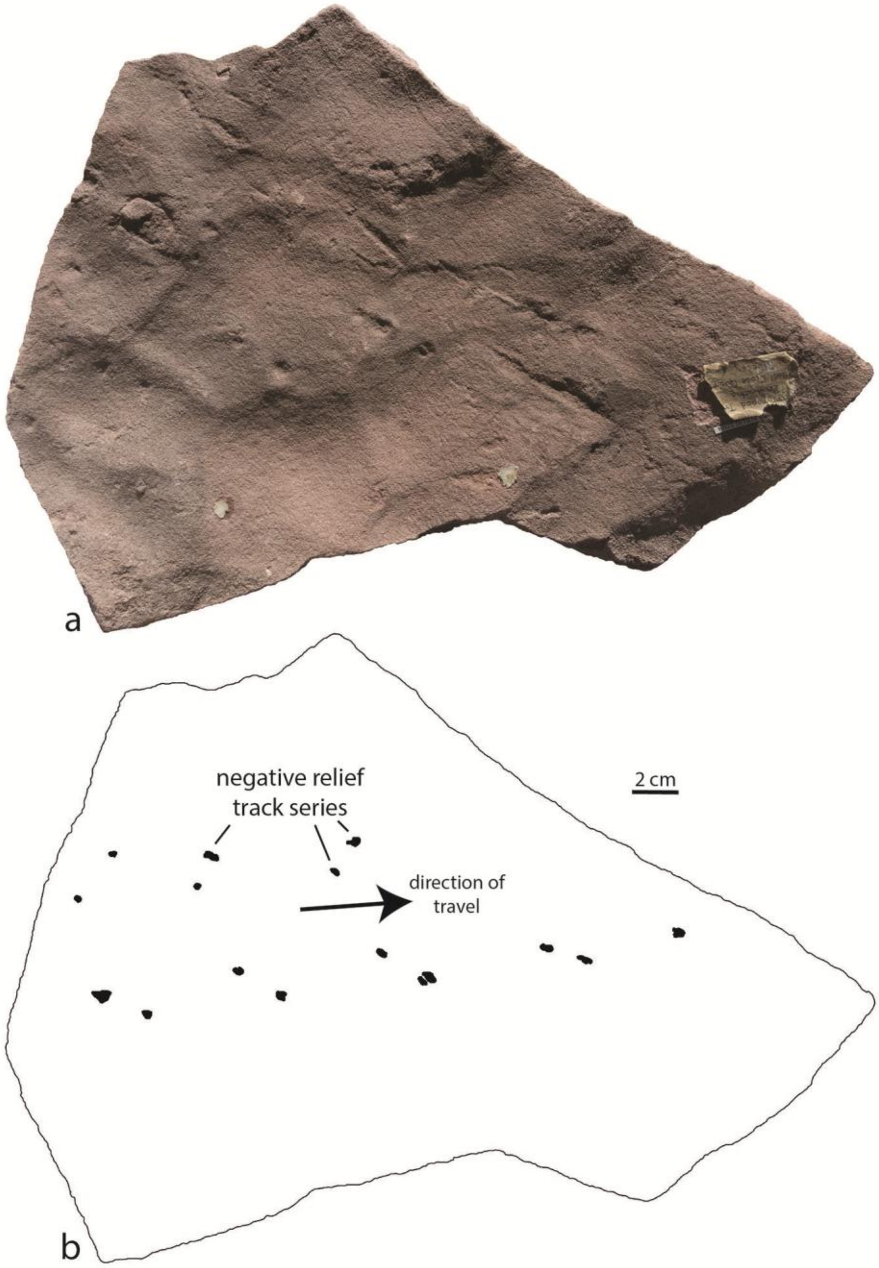


Figure 6 - *Paleohelcura tridactyla* Colour online, greyscale in print

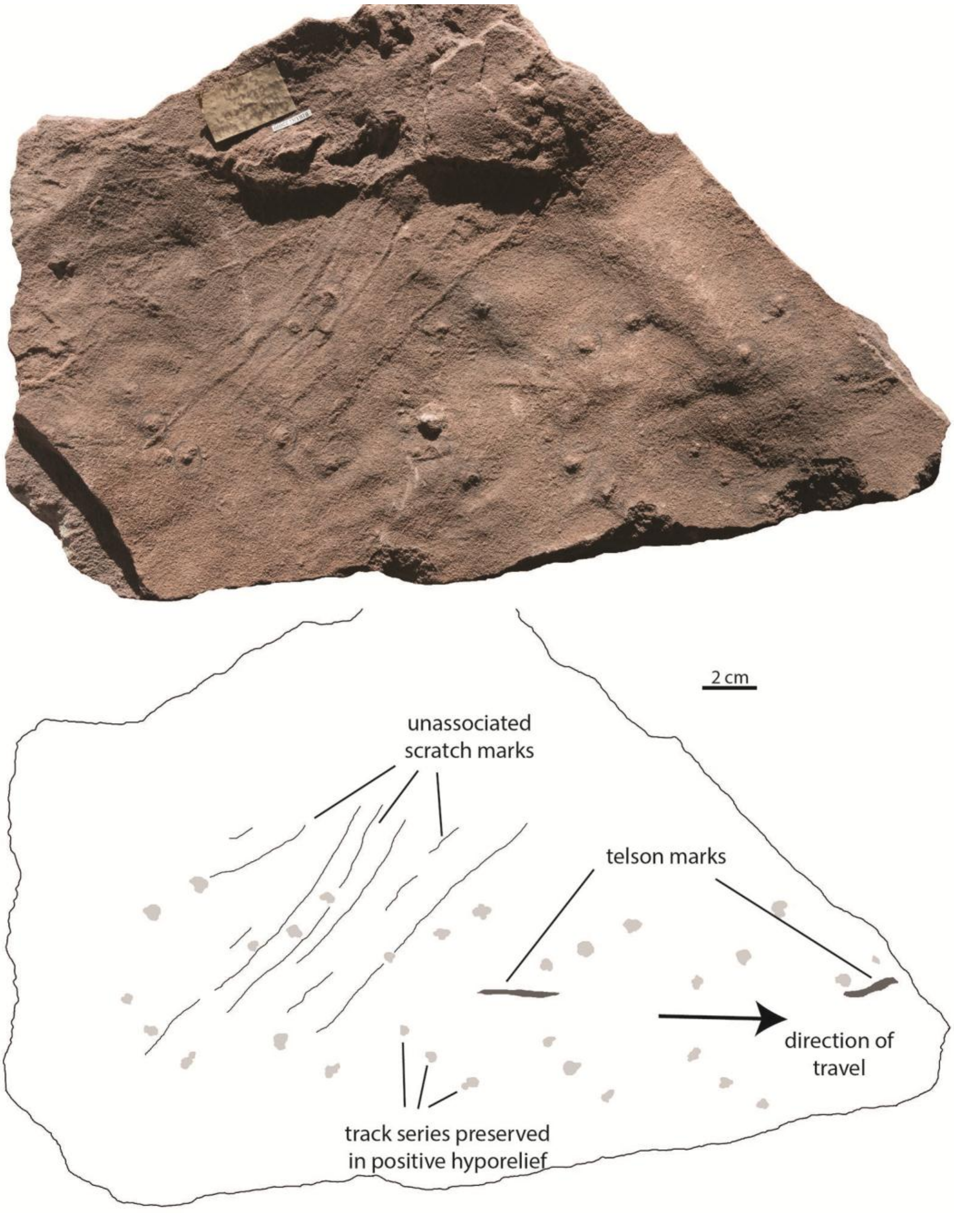


Figure 7 – *Palmichnium* Colour online, greyscale in print

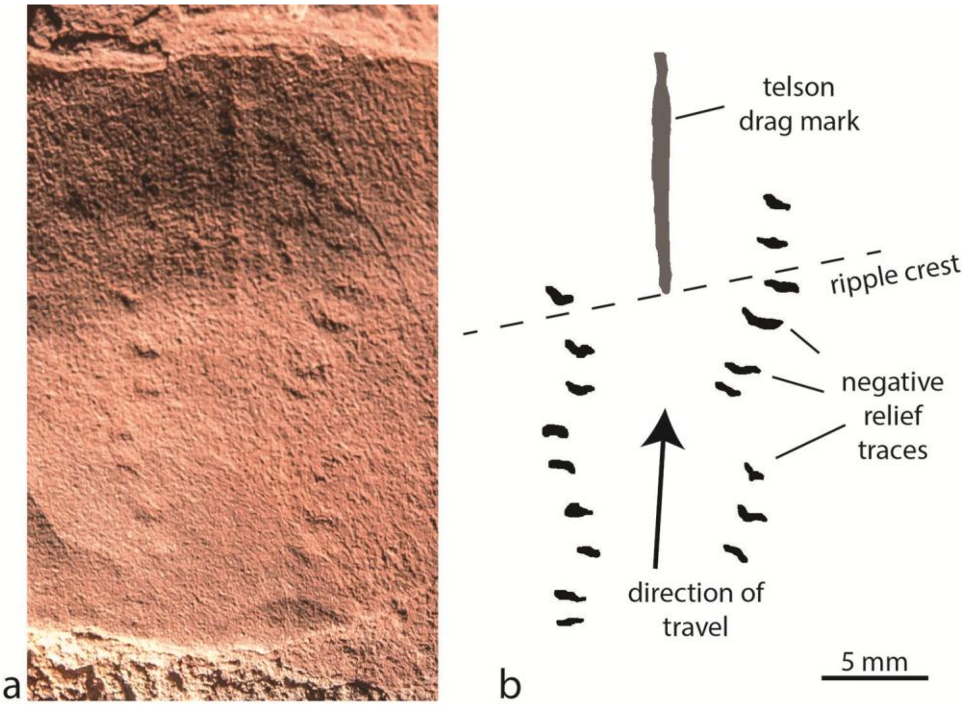


Figure 8 – *Protichnites* Colour online, greyscale in print