



The largest arthropod in Earth history: insights from newly discovered *Arthropleura* remains (Serpukhovian Stainmore Formation, Northumberland, England)

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Abstract: *Arthropleura* is a genus of giant myriapods that ranged from the early Carboniferous to Early Permian, with some individuals attaining lengths >2 m. Although most of the known fossils of the genus are disarticulated and occur primarily in late Carboniferous (Pennsylvanian) strata, we report here partially articulated *Arthropleura* remains from the early Carboniferous Stainmore Formation (Serpukhovian; Pendleian) in the Northumberland Basin of northern England. This 76 × 36 cm specimen represents part of an exuvium and is notable because only two comparably articulated giant *Arthropleura* fossils are previously known. It represents one of the largest known arthropod fossils and the largest arthropleurid recovered to date, the earliest (Mississippian) body fossil evidence for gigantism in *Arthropleura*, and the first instance of a giant arthropleurid body fossil within the same regional sedimentary succession as the large arthropod trackway *Diplichnites cuihensis*. The remains represent 12–14 anterior *Arthropleura* tergites in the form of a partially sand-filled dorsal exoskeleton. The original organism is estimated to have been 55 cm in width and up to 2.63 m in length, weighing c. 50 kg. The specimen is preserved partially in three dimensions within fine sandstone and has been moderately deformed by synsedimentary tectonics. Despite imperfect preservation, the specimen corroborates the hypothesis that *Arthropleura* had a tough, sclerotized exoskeleton. Sedimentological evidence for a lower delta plain depositional environment supports the contention that *Arthropleura* preferentially occupied open woody habitats, rather than swampy environments, and that it shared such habitats with tetrapods. When viewed in the context of all the other global evidence for *Arthropleura*, the specimen contributes to a dataset that shows the genus had an equatorially restricted palaeogeographical range, achieved gigantism prior to late Paleozoic peaks in atmospheric oxygen, and was relatively unaffected by climatic events in the late Carboniferous, prior to its extinction in the early Permian.

Supplementary material: Images of 3D mesh model of *Arthropleura* are available at <https://doi.org/10.6084/m9.figshare.c.5715450>

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The ancient giant myriapod *Arthropleura* is an instantly recognizable constituent of artistic reconstructions and museum dioramas illustrating the ‘coal age’ Carboniferous Period (359–299 Ma). Yet, despite the relative fame of these extinct animals, only two partially complete fossils of giant *Arthropleura* are presently known, both from Pennsylvanian (323–299 Ma) strata in Germany (Guthörl 1934, 1935; Hahn *et al.* 1986; Schneider and Barthel 1997; Schneider *et al.* 2010). Our understanding of *Arthropleura* otherwise draws on evidence from rare presumed juveniles (Calman 1914; Almond 1985; Briggs and Almond 1994), disarticulated cuticular fragments (e.g. Andrée 1913; Pruvost 1930; Waterlot 1934; Rolfe and Ingham 1967; Rößler and Schneider 1997; Schneider and Werneburg 1998; Wilson 1999; Pacyna *et al.* 2012; Pillola and Zoboli 2021) and wide *Diplichnites cuihensis* trackways in contemporaneous strata (e.g. Briggs *et al.* 1979, 1984; Ryan 1986; Pearson 1992; Lucas *et al.* 2005; Schneider *et al.* 2010; Moreau *et al.* 2019).

The specimen described here is a 76 × 36 cm three-dimensional fossil and represents the largest partially articulated *Arthropleura*

fossil known thus far (Figs 1 and 2). It is from Late Mississippian strata in northern England, making the specimen the earliest body fossil evidence for arthropleurid gigantism. The unusual taphonomy, and the potential significance and implications of the fossil, necessitate an understanding of its stratigraphic, palaeoenvironmental and tectonic context. We summarize these aspects here, offer a detailed description of the fossil’s morphology, discuss its synapomorphies, and thus taxonomic placement, and place it into a global context of other known giant arthropleurids and the Carboniferous world.

Geological context

The fossil was discovered in January 2018 in a large (c. 2 m × 3 m × 8 m) fallen block of sandstone in coastal cliff outcrops at Howick Bay, c. 10 km NE of Alnwick, Northumberland (55° 27′ 19.2″ N, 01° 35′ 32.4″ W) (Fig. 3). Based on repeat visits to the locality, it is likely that the block fell from the cliff between April 2017 and January 2018 and has been gradually eroding since then (the most recent visit was made in

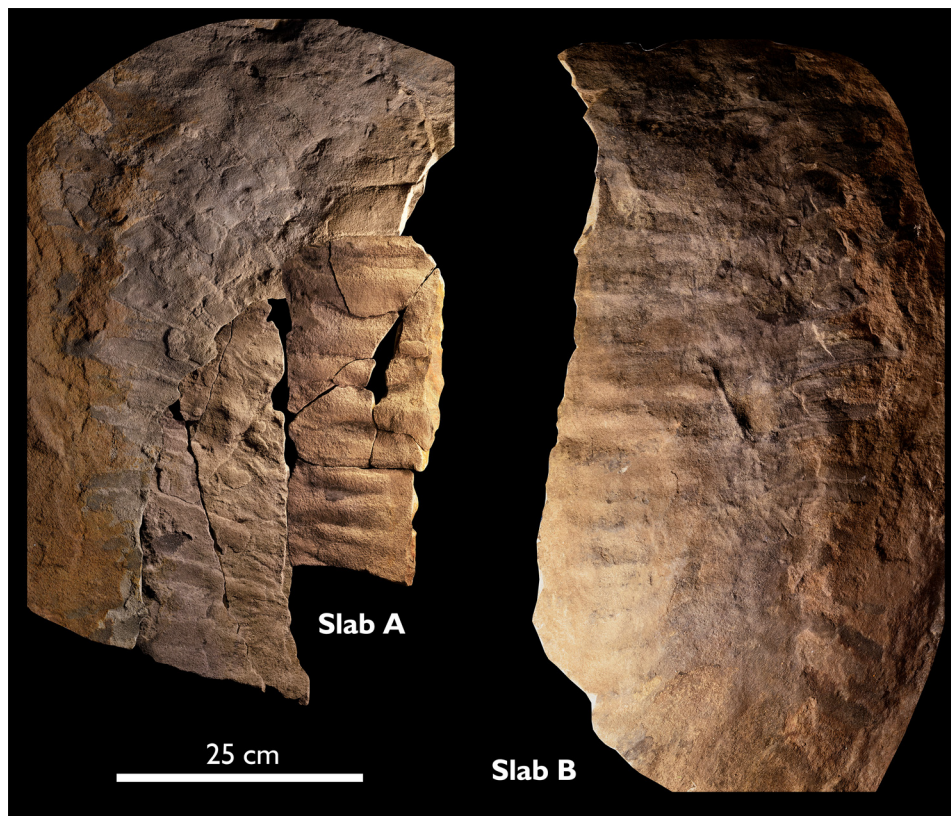


Fig. 1. Specimen of partial remains of a giant *Arthropleura* (anterior 12–14 tergites) after excavation from the Serpukhovian Stainmore Formation, Howick Bay, Northumberland, England (CAMS X.50355). Slab A and slab B are not true part and counterpart, but rather a split through the middle of a three-dimensional dorsal exoskeleton (see Fig. 7 and discussion in text).

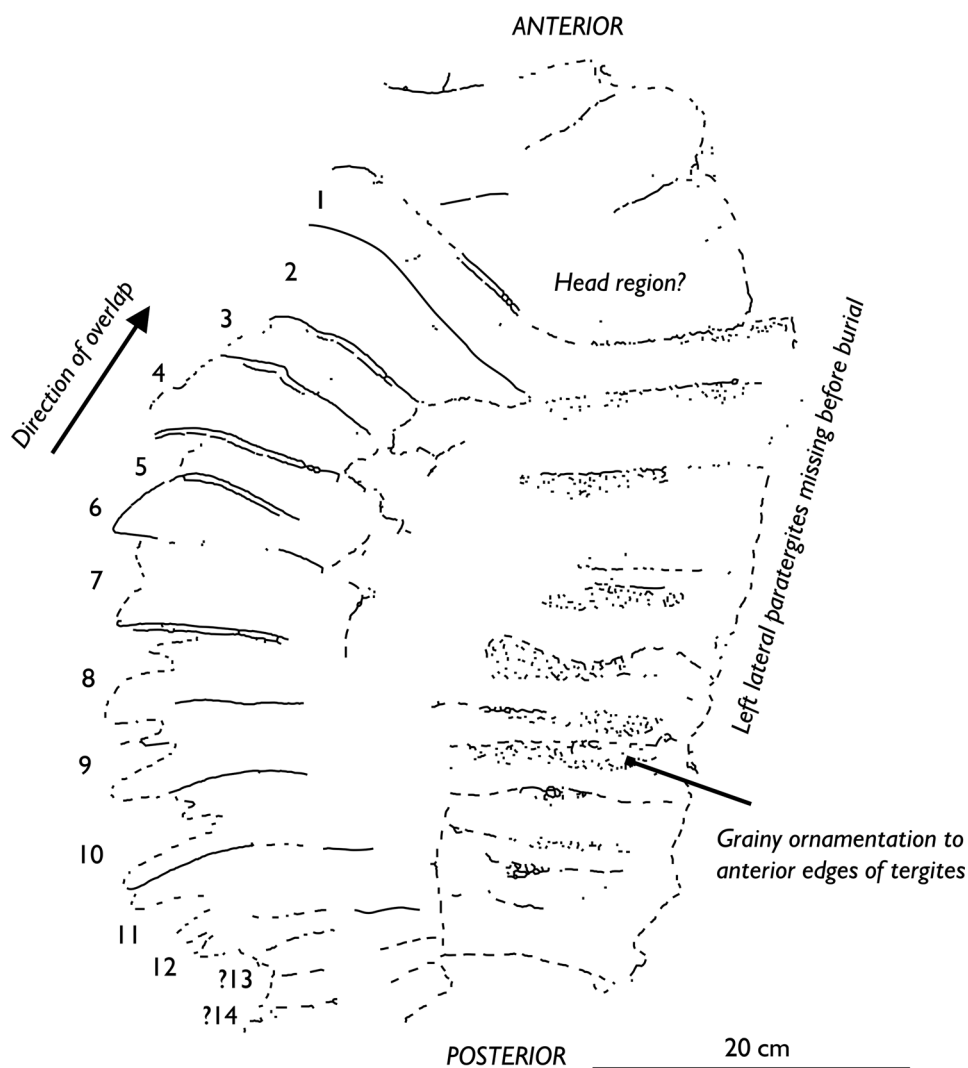


Fig. 2. Interpreted sketch of the fossil, as preserved in slab A, while still intact in fallen block of host sandstone prior to excavation. The overlap pattern of the paratergites on the left indicates that this is the ventral site of the dorsal exoskeleton. The typical ornamentation of the dorsal site of *Arthropleura* tergites and paratergites is therefore not visible.

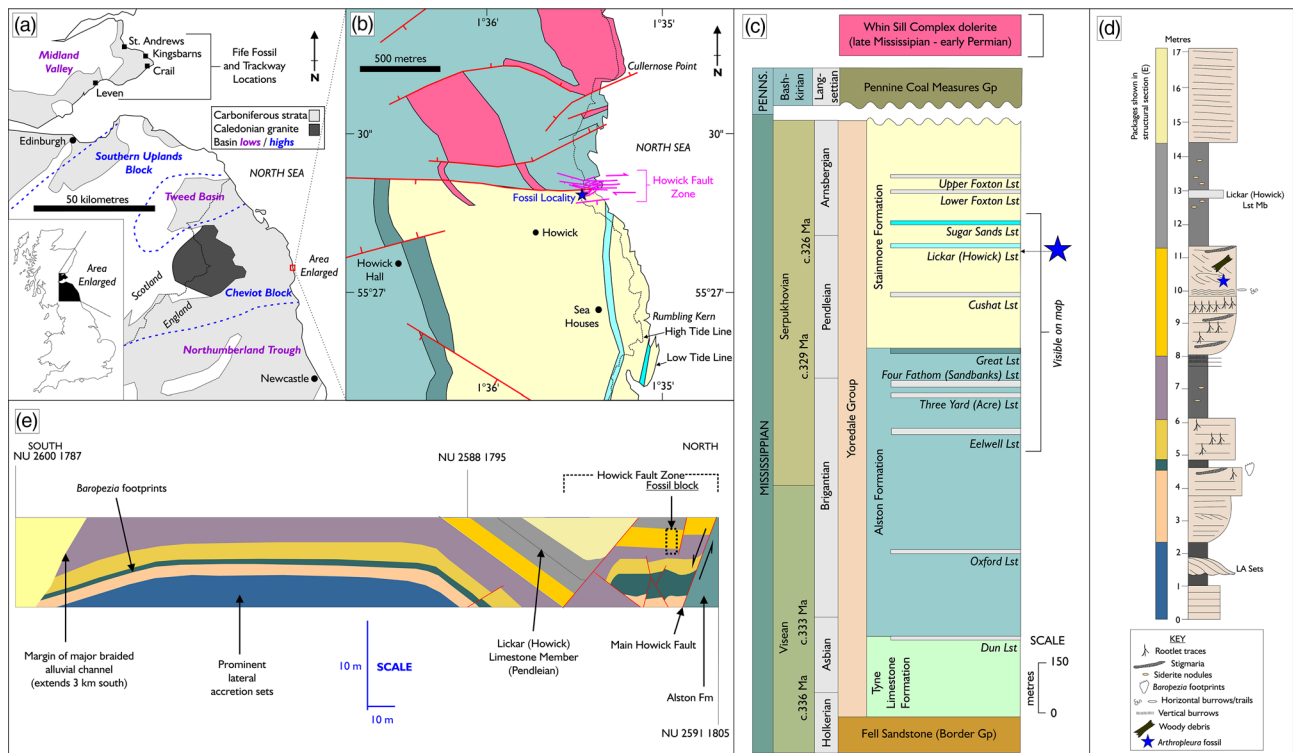
Mississippian *Arthropleura* from Northumberland

Fig. 3. Geological context of the site. (a) Locality within the Northumberland Basin. (b) Geological map of the fossil locality. (c) Regional stratigraphy. (d) Sedimentary log of the fossil site. LA sets, lateral accretion sets. (e) Structural profile along cliffs at the southern end of Howick Bay showing fossil site within damage zone of the Howick Fault (location of section denoted with British National Grid references).

September 2021). The bed from which the block fell is *c.* 6 m above beach level (Fig. 4). The locality occurs within a Site of Special Scientific Interest and the fossil was extracted in May 2018 with permission from Natural England and the landowners, the Howick Estate. It has been accessioned by the Sedgwick Museum of Earth Sciences (specimen number CAMSM X.50355).

Basin setting

The fossil bed occurs within the Stainmore Formation, deposited in the Northumberland Basin during the mid-Carboniferous (Fig. 3c). At this time, northern Britain was in the foreland region of the Variscan orogenic belt and had a basement topography characterized by a suite of small subsiding sub-basins separated by structural highs. The Northumberland Basin consists of the basinal lows of the Tweed Sub-Basin to the north and Northumberland Trough to the south, separated in the middle by the structural high of the fault-bounded and granite-cored Cheviot Block (Leeder *et al.* 1989; Chadwick *et al.* 1995; Fraser and Gawthorpe 2003) (Fig. 3b). As the Howick locality sits on the Cheviot Block, the Stainmore Formation reaches only 228 m thickness locally (Elliott 1976), compared with 500 m in the basinal lows (Dean *et al.* 2011).

Age

The Stainmore Formation is the youngest constituent unit of the Viséan Yoredale Group, overlying the Alston Formation and, below this, the Tyne Limestone Formation (Dean *et al.* 2011) (Fig. 3c). The formations of the Yoredale Group consist of repeating cyclothems of sandstones, shales, coals and limestones, but are differentiated by an upwards-decreasing frequency of carbonates as the units become increasingly dominated by terrigenous strata (Reynolds 1992; Frank and Tyson 1995; Dean *et al.* 2011; Booth *et al.* 2020).

Transgressive limestone marker horizons (with local lithostratigraphic names) occur throughout the Yoredale Group (Tucker *et al.* 2009; Waters *et al.* 2014; Booth *et al.* 2020) and can be biostratigraphically correlated to regional substage level throughout northern England and Scotland using miospore and foram assemblages (Turner and Spinner 1992; Cózar and Somerville 2012, 2020, 2021; Ingrams *et al.* 2020). The fossil-bearing bed occurs 2 m stratigraphically below the Lickar Limestone (formerly the 'Howick Limestone'; Farmer *et al.* 1970; Elliott 1976) and above the Cushat Limestone. Although these marker beds are dolomitized and lack biostratigraphically useful taxa, they both occur above the Great Limestone (early Pendleian) and below the Sugar Sands Limestone (earliest Arnsbergian) (Cózar and Somerville 2020). The Lickar Limestone is thus considered to mark the base of the late Serpukhovian (Cózar and Somerville 2021). Accordingly, the fossil-bearing bed can be confidently determined to have been deposited during the Pendleian regional substage, dating it to *c.* 326 Ma, within the latest early Serpukhovian (Heckel and Clayton 2006; Richards 2013; Cohen *et al.* 2021).

Local structure

The fossil and its host bed are strongly influenced by the adjacent Howick Fault, a major east-west-directed normal fault extending inland from the coast for 10 km with a vertical stratigraphic displacement of 200 m, downthrown to the south (Westoll *et al.* 1955; Farmer and Jones 1969; Kjemperud 2011; Burt and Tucker 2020). At Howick Bay, the fault directly juxtaposes the Stainmore Formation against the Alston Formation and 20 m of the total vertical displacement is accommodated within a 100 m-wide damage zone, where both the hanging wall and footwall are dissected by multiple small antithetic and synthetic faults. The fossil bed itself is sandwiched between several such faults in the hanging wall (Fig. 3e).

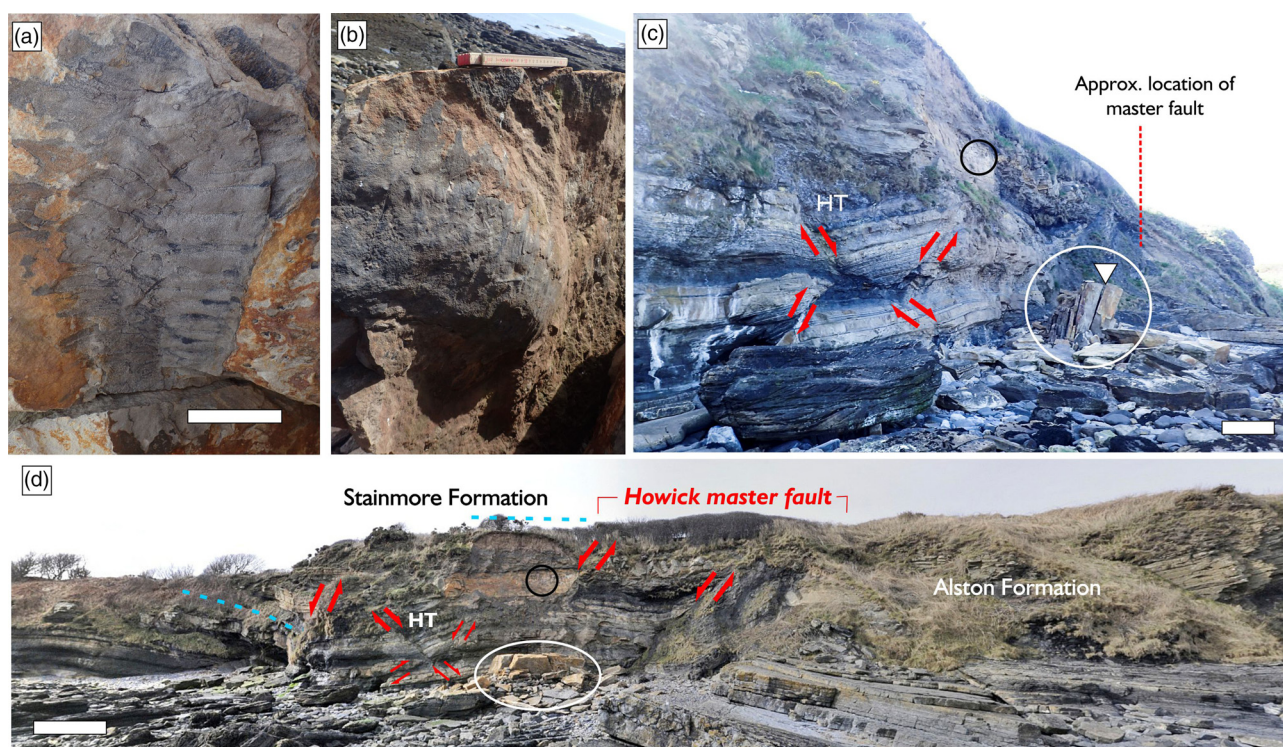


Fig. 4. Context of the specimen prior to extraction. (a) Slab A of the fossil (facing stratigraphically upwards). Note convex-down doming of the host sediment. Scale bar 20 cm. (b) Slab B of the fossil (facing stratigraphically downwards). (c) Fallen block in which the fossil was discovered in January 2018 (white circle), showing split in rock where fossil was exposed (white triangle). Black circle denotes position in cliff profile from where the block fell. Listric faults in hanging wall of Howick Fault are highlighted, showing hanging wall thickening of mudrock (HT), attesting to synsedimentary origin (red arrows indicate sense of fault movement). Scale bar 2 m. (d) View of the fallen block (white circle) and original position (black circle) in the context of the Howick Fault damage zone and master fault separating the Alston and Stainmore formations; HT is at same position as in part (c). Host bed is immediately adjacent to one of two syndimentary (Mississippian) normal faults that were later reactivated as strike-slip faults during the latest Carboniferous to Permian emplacement of the Whin Sill dolerite intrusion (De Paola *et al.* 2005). This structural context attests to strain in the fossil-bearing sandstone bed prior to full lithification and may explain certain features of the fossil (see main text). Blue dashed line show approximate stratigraphic position of the Lickar Limestone, marking the onset of the late Serpukhovian (Cózár and Somerville 2021). Scale bar 5 m. Photograph in part (d) courtesy of Geospatial Research Limited.

Sedimentological and palaeoenvironmental context

Most of the strata exposed at Howick Bay belong to the Visean Alston Formation (Fig. 3) and are typified by marine limestones and storm- and tide-deposited siliciclastic strata (Reynolds 1992; Booth *et al.* 2020; Allport *et al.* 2021). At the southern end of the bay, the Howick Fault juxtaposes these against the younger strata of the Stainmore Formation, in which the fossil was discovered, which yield a greater abundance of signatures of non-marine deposition among less frequent limestones and tidally influenced siliciclastic strata.

The section has been well studied from a sedimentological perspective (Farmer and Jones 1969; Elliott 1976; Scarboro and Tucker 1995) and the Stainmore Formation can confidently be interpreted as being deposited in a littoral deltaic setting. Although it has been purported to contain a fairweather- to storm-wave-base ichnofauna (Boyd and McIlroy 2016, 2017, 2018), the locality details in these papers show that the described trace fossils occur north of the Howick Fault, within the Alston Formation.

The Stainmore strata that immediately underlie the fossil horizon contain signatures of tidally influenced sedimentation, including possible tidal rhythmites burrowed with *Skolithos*, *Teichichnus* and *Taenidium* (Figs 5 and 6), siderite nodules and a prominent heterolithic lateral accretion set that likely records a small tidal channel (Scarboro and Tucker 1995; Davies and Gibling 2013). These strata are interbedded with sandstones and thin coals deposited in a lower delta plain setting, revealed by signatures including plant root traces, wave ripple marks, mud cracks and a

bedding plane that exposes a *Baropezia* trackway (Scarboro and Tucker 1995; since degraded by wave erosion; Fig. 6a, b) attributable to an anthracosaur tetrapod (Falcon-Lang *et al.* 2006).

The fossil bed itself is a gently channelized coarsening-up package of amalgamated sandstones, 3.2 m in thickness, and most easily studied in the recently fallen block. The lower half of the package consists of horizontally bedded fine-grained sandstone laminae that are disrupted by plant root traces, including *Stigmara*. These are succeeded by sandstone laminae that are notably wave ripple-marked and colonized with horizontal burrows (*Planolites*) and meandering grazing trace fossils (*Archaeonassa*) before the appearance of the 1 m thick package of trough cross-bedded medium-grained sandstone within which the fossil was fully interred.

In addition to the giant arthropod fossil, the cross-bedded package also hosts abundant plant debris from multiple different taxa (Fig. 6) including: (1) a thin axis that bifurcates at an acute angle distally (possibly being the proximal part of a pteridosperm frond) (Fig. 6f); (2) *Lepidodendron* (*sensu lato*) bark fragments (Fig. 6f); and (3) large seeds, possibly *Samaropsis*, which were produced by cordaitaleans (Fig. 6g). Both the top and base of the cross-bedded package are mantled with *Stigmara* roots (Fig. 6h). The bed has previously been interpreted (without access to the fallen block) as recording a crevasse channel deposit (Elliott 1976) or a small delta infilling a shallow embayment on the lower delta plain (Scarboro and Tucker 1995). However, here we favour the interpretation of deposition by a minor fluvial channel. This interpretation is based on the abundance of non-marine biological detritus within the cross-bedded sands and the fact that it is

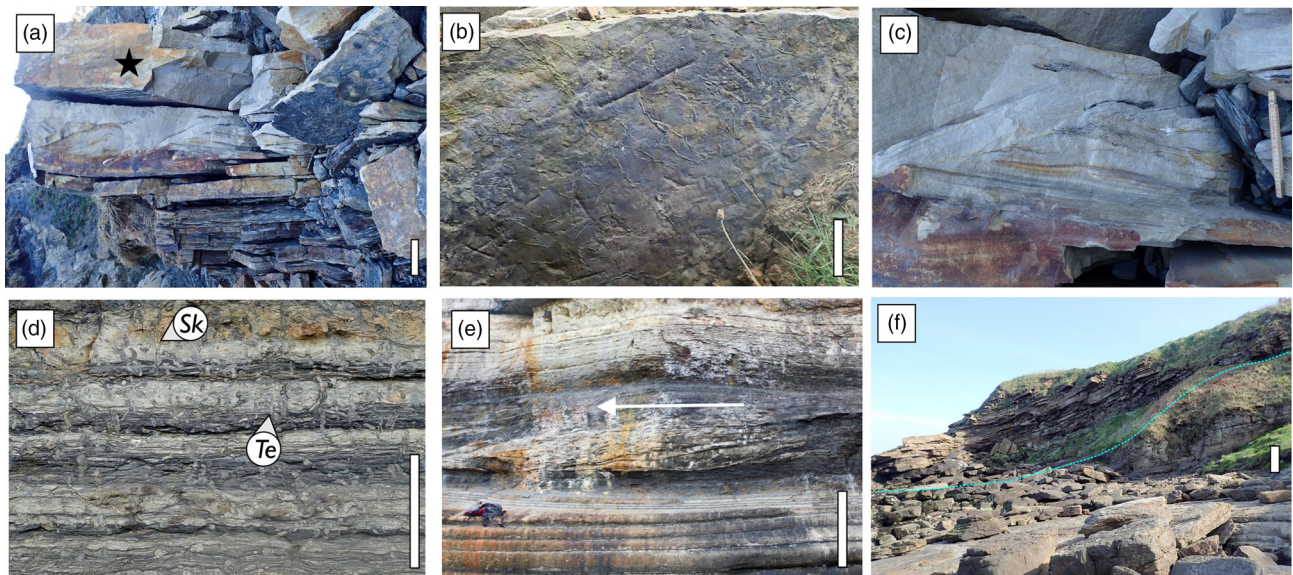
Mississippian *Arthropleura* from Northumberland

Fig. 5. Sedimentological characteristics of the Stainmore Formation at the southern end of Howick Bay, attesting to lower delta plain deposition. (a) Rotated view of fallen block hosting fossil at starred horizon, showing lithology of amalgamated trough cross-beds of fine sandstone, coarsening upwards from laminated very fine sandstone and siltstone. Located at c. 8–10 m on stratigraphic log in Figure 3d. Scale bar 20 cm. (b) Casts of syneresis cracks on underside of fallen block. Located at 8 m on stratigraphic log in Figure 3d. Scale bar 10 cm. (c) Detail of cross-bedded sets in which *Arthropleura* fossil was interred. Note clasts of coaly debris. Located at 9.5 m on stratigraphic log in Figure 3d. Ruler 20 cm. (d) Crudely developed rhythmites of probable tidal origin, colonized with *Skolithos* (Sk) and *Teichichnus* (Te) burrows. Located at 6 m on stratigraphic log in Figure 3d. Scale bar 15 cm. (e) Inclined heterolithic stratification in form of lateral accretion set of small tidal channel; northwards direction of migration arrowed. Located at 1.5 m on stratigraphic log in Figure 3d. Scale bar 70 cm. (f) Incised channel filled with braided alluvium and cutting into underlying sequence at far southern end of Howick Bay. Approximate channel base highlighted. The channel truncates the sequence illustrated in Figure 3d. Scale bar 2 m.

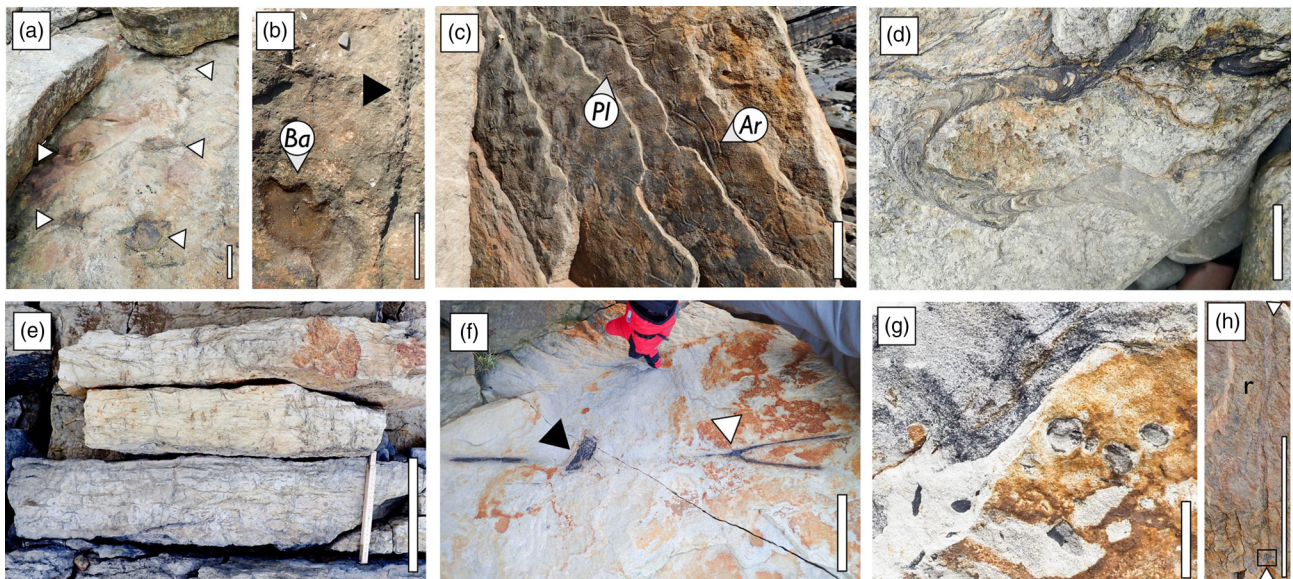


Fig. 6. Ichnological and palaeobotanical features associated with the *Arthropleura* fossil. (a) Trackway of an anthracosaur tetrapod (*Baroepiza*) (individual footprints arrowed). Located at 4.6 m on stratigraphic log in Figure 3d. Scale bar 10 cm. (b) Detail of *Baroepiza* footprint (Ba) adjacent to *Stigmaria* root (black arrow). For details of vertebrate tracks prior to recent erosional degradation, see Scarboro and Tucker (1995). Located at 4.6 m on stratigraphic log in Figure 3d. Scale bar 20 cm. (c) Thinly bedded wave-rippled facies immediately below fossil horizon showing horizontal invertebrate burrows *Planolites* (Pl) and *Archaeonassa* (Ar). Located at 10.6 m on stratigraphic log in Figure 3d. Scale bar 10 cm. (d) Tightly curved invertebrate burrow identified as *Taenidium* on basis of meniscate fill and absence of lining. Fallen block of same lithology adjacent to fossil-bearing block. Scale bar 10 cm. (e) Ripple-laminated sandstone beds colonized with coalified, downwards-branching plant rootlets. Located at 9.0 m on stratigraphic log in Figure 3d. Scale bar 20 cm. (f) Plant remains in same bed as *Arthropleura* fossil, including fragment of branch or bark belonging to *Lepidodendron sensu lato* (black arrow) and thin axis that acutely bifurcates distally, possibly the proximal part of a medullosalean pteridosperm frond (white arrow). Located at 10.0 m on stratigraphic log in Figure 3d. Scale bar 20 cm. (g) Seed fossils, possibly *Samaropsis*, as produced by cordaitaleans. Note seeds occur immediately adjacent to the *Arthropleura* remains in the part, seen at top left of image. Located at 10.2 m on stratigraphic log in Figure 3d. Scale bar 5 cm. (h) *Stigmaria* on stratigraphic top of fallen block hosting the *Arthropleura* remains. Preserved fraction of main rhizomorph axis extends between white arrows and shows ornamentation in boxed area. Adjacent part of bedding plane contains traces of rootlets (r) branching from the main rhizomorph. Located at 9.8 m on stratigraphic log in Figure 3d. Scale bar 1 m.

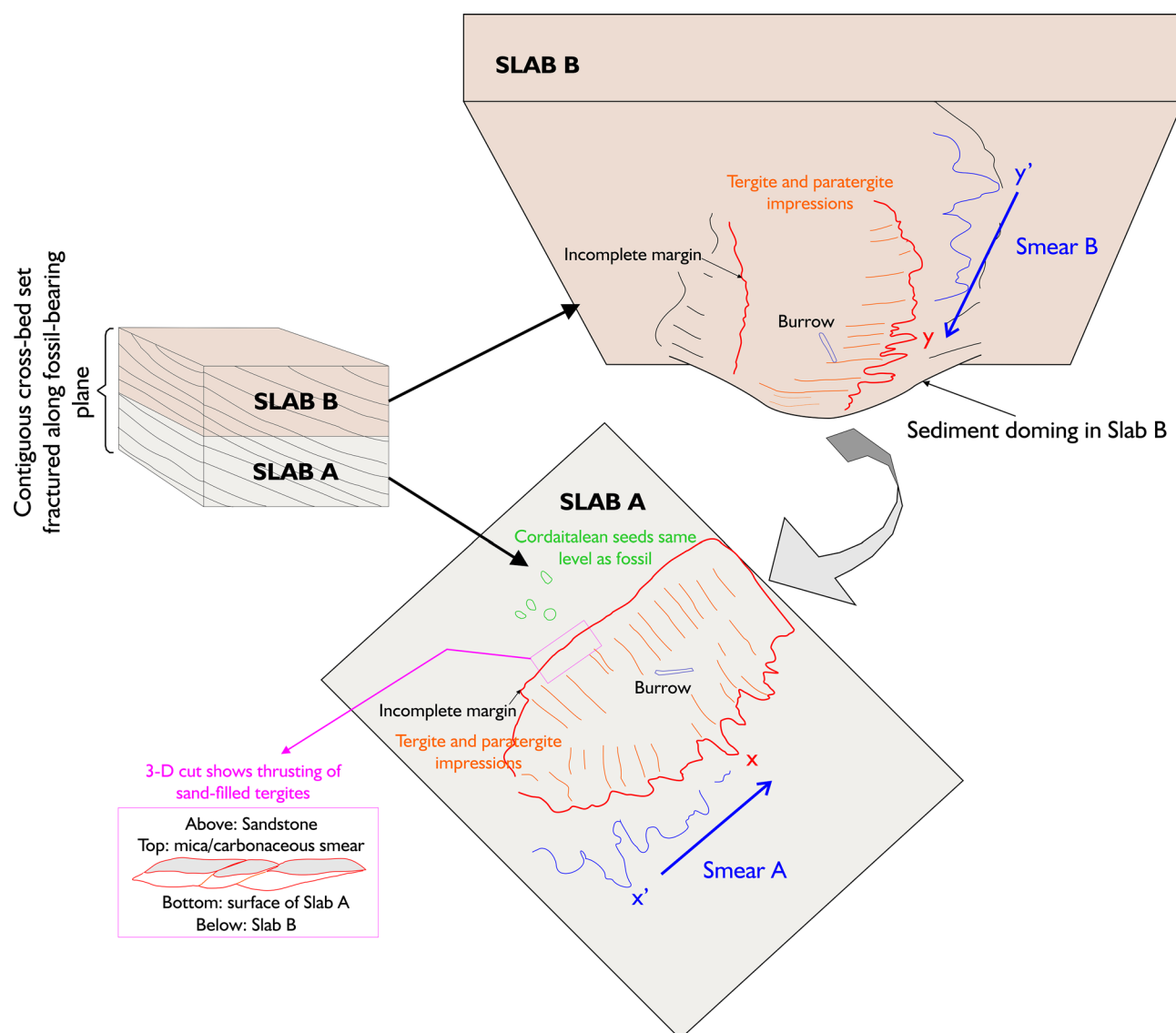


Fig. 7. Schematic diagram showing taphonomic context and relationship between key attributes of the specimen.

stratigraphically sandwiched between surfaces that were stabilized by lycopsid tree roots.

The strata that immediately overlie the fossil bed are less readily studied in the field. At the precise fossil locality they either occur in the inaccessible upper part of the cliff face, or are faulted out, whereas in the southernmost part of Howick Bay they are eroded out at an incised channel-bounding surface. Midway between these points, the overlying strata crop out at beach level as nondescript carbonaceous shales with siderite nodules, which yield bryozoans, brachiopods, crinoids and marine forams (Scarboro and Tucker 1995; C  zar and Somerville 2020). Above this transgressive package, the stratigraphic top of the Howick Bay section is characterized by 8 m of fully non-marine braided fluvial sandstones, which can be traced for 3 km south of Howick Bay, and which have incised a channelized base at least 4 m into the underlying strata (Farmer and Jones 1969; Elliott 1976). The sedimentological context of the fossil-bearing bed is thus diagnostic of a non-marine fluvial channel in immediate proximity to the marine shoreline.

Systematic palaeontology

Phylum ARTHROPODA Von Siebold, 1848
Subphylum MYRIAPODA Latreille, 1802
Order ARTHROPLEURIDA Waterlot, 1934

Family ARTHROPLEURIDAE Von Zittel, 1885

Genus *Arthropleura* Jordan in Jordan and von Meyer, 1854

Type species *Arthropleura armata* Jordan, 1854, plates 13–15, plate 2, figs 4–5 in Jordan and von Meyer, 1854, *Arthropleura* sp. Jordan in Jordan and von Meyer, 1854

(Figs 1 and 2)

Material: CAMSM X.50355, partial remains comprising articulated anterior 12–14 tergites in two slabs.

Locality: Howick Bay (55  27' 19.2" N, 01  35' 32.4" W), Northumberland, England.

Age and formation: Early Serpukhovian, Stainmore Formation (Yoredale Group).

Description: specimen identified as the partial anterior dorsal exoskeleton of *Arthropleura* because of the trilobate tergites, coupled with the large dimensions. Remains consist of 12–14 tergites and paratergites, 76 cm in maximum length from the anterior to posterior, and 36 cm at the greatest width. Preserved as a three-dimensional cuticular infill by sand, with limited cuticular material. Ornamentation limited: some longitudinal striae are visible on the paratergites and there is a granular or verrucose texture on the anterior margins of the medial tergites. The specimen has an irregular morphology as a result of the taphonomy of a large three-dimensional exoskeleton interred within sand in a tectonically active setting.

Mississippian *Arthropleura* from Northumberland

Description of the specimen

The three-dimensional preservation of this large fossil is summarized in Figure 7. The fossil is visible on a fracture surface within a block of cross-bedded fine-grained sandstone. The fracture splitting the well-indurated host lithology is recent and presumably formed when the host block fell from the cliff. The fossil is preserved on surfaces either side of this fracture. As the fracture may run through the middle of the three-dimensional fossil (see later discussion), it is inappropriate to refer to these as part and counterpart (Fig. 1) and they are here referred to as slab A and slab B. Slab A is the lower stratum and hosts the bulk of the fossil. Slab B is the upper stratum and preserves an impression that domes downward to a relief of c. 10 cm, creating a three-dimensional semi-cylindrical form.

The fossil consists of 12–14 sub-rectangular medial tergites, flanked on one side by right paratergites. The left paratergites are missing and the medial tergites terminate against a serrated edge. The right paratergites have frayed and irregular lateral margins and so are also imperfectly preserved (Figs 2 and 8). The anterior five to six paratergites are increasingly recurved (Figs 1 and 2).

Slab A broke into several pieces during extraction from the host block; these fragments reveal the three-dimensional form of the tergites. Each is filled with the host sediment, forming three-dimensional imbricated pillows. The tergite sand infills are 4 mm

thick in the medial tergites, thinning to 1 mm or less towards the paratergites (Fig. 9).

The fossil is underlain in slab A, and overlain in slab B, by a carbonaceous smear that exactly mirrors the form of the frayed right paratergites (Fig. 10). The offset between recognizable frayed paratergites and their displaced form in smears can be measured. The offset is consistent along the length of the fossil at 40 cm. Excluding the smear repetition, the total length of the fossil is 76 cm and its maximum preserved width from the right lateral paratergite to the termination of the left medial tergite is 36 cm.

In addition to this smear, remnants of carbonaceous material can be seen in patches on both slabs, most notably in the tergal margins in slab A (Fig. 9), where the arthrodistal membrane would have been present in life. The dorsal side of the tergites in slab A can be seen, in broken fragments, to be carbon-rich and flecked with abundant mica, which possibly adhered to a sticky surface prior to burial (Fig. 8). The majority of the fossil, however, has no organic material and its form is revealed by impression, or sand infill, alone.

As a result of the lack of well-preserved cuticle and the granular nature of the host sediment, ornamentation is not consistently visible on the specimen. However, the anterior margins of the medial tergites, where the segments would have been joined by a softer arthrodistal membrane, have a rough, grainy appearance on the surfaces of both slabs. The absence of this texture across the remainder of the fossil and host sediment implies either that it is an original texture or that it is a taphonomic difference reflecting the contrasting nature of the exoskeleton between these regions (Fig. 8). In addition, striae can be seen on some of the paratergites, some of

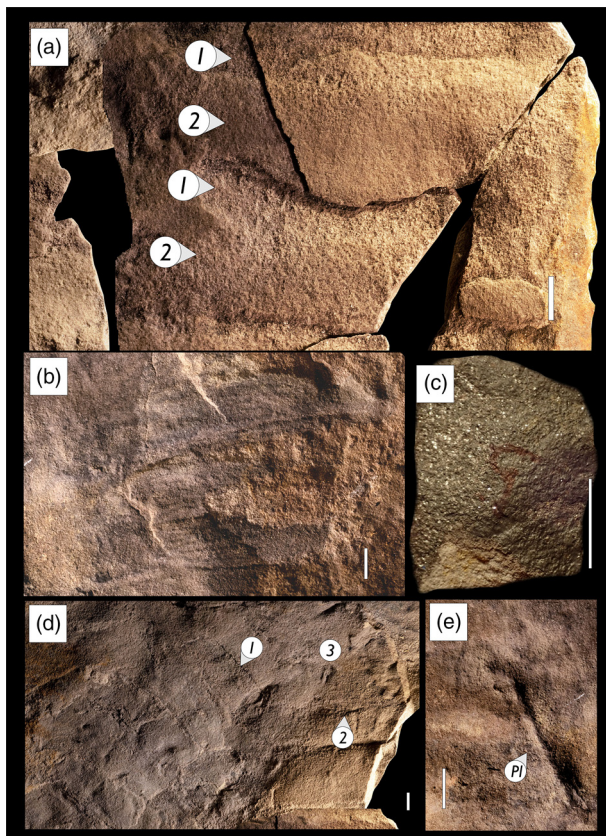


Fig. 8. Details of the *Arthropleura* specimen. (a) Alternation of granular (1) and smooth (2) texture on medial tergites. Granular texture interpreted to reflect degraded verrucose texture to anterior part of each tergite. View of underside of dorsal exoskeleton preserved on surface of slab A. Scale bar 1 cm. (b) Detail of right lateral paratergites seen on slab B showing striated patterning and frayed margins to the paratergites. Scale bar 1 cm. (c) Micaceous and carbonaceous smear on fragment of upper side of dorsal exoskeleton (slab A). Scale bar 1 cm. (d) Inflection of paratergites (1) relative to medial tergites (2) at anterior of specimen on the part. Head region seen at (3). Scale bar 1 cm. (e) Detail of invertebrate burrow (*Planolites*) seen in centre of slab B and likely exploiting remains shortly after interment. Scale bar 1 cm.

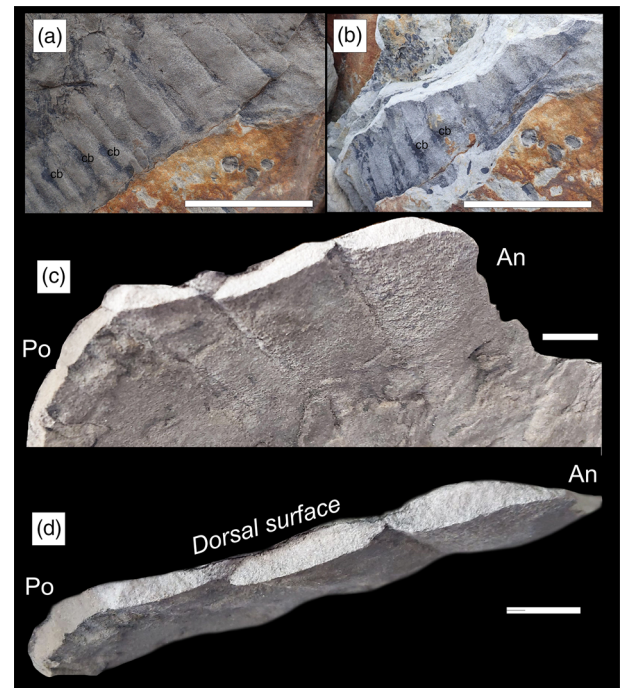


Fig. 9. Three-dimensional morphology of cuticular sand infill preserved in slab A. (a, b) Images of slab A before and after extraction of fossil. Part (a) shows a natural break in sandstone revealing the underside of the dorsal cuticle, notable for carbonaceous material (cb) between the paratergites and the presence of a granular texture. Part (b) shows slab A after extraction, revealing the cast of the dorsal exoskeleton, still yielding carbonaceous material, but with no granular texture. Scale bars 20 cm. (c, d) Images of partial fragment of cuticular sand infill between the underside and upper side of the dorsal cuticle, as extracted from slab A. Part (c) shows the exoskeleton underside with a granular texture and both images show cross-section through lenticular imbricated tergites, possibly compressed by synsedimentary tectonics. Scale bar 1 cm. An, anterior; Po, posterior.

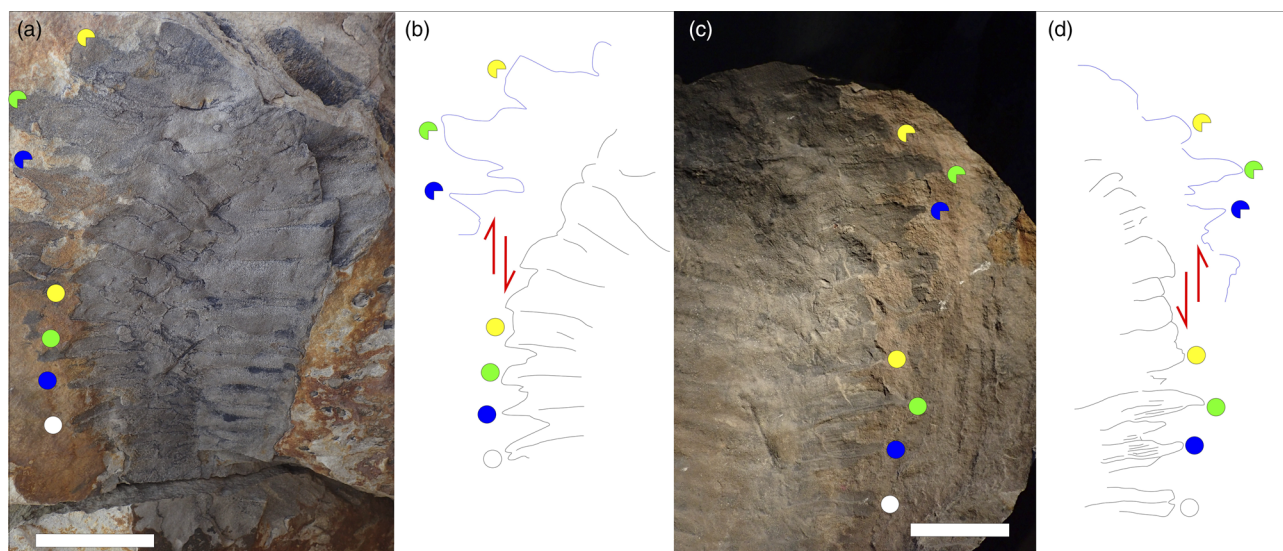


Fig. 10. Details of (a, b) slab A and (c, d) slab B with interpreted sketches of margins showing offset of three-dimensional sand infill from carbonaceous smear. Same tergites on each slab are colour-coded (with reference to prominent tergite shown in white). Cuticular interior shown as full circles with correspondingly shaped carbonaceous smear shown as colour-coded partial circles, indicating consistent 40 cm squeezed offset of infill from cuticle in direction of red bidirectional arrow, associated with synsedimentary deformation. Scale bars 20 cm.

which appear to form pronounced medial grooves that are parallel to the central axis of a paratergite (Fig. 8).

This information can be combined to describe a stratigraphic transect downwards through the fossil as follows: (1) 10 cm of domed fine-grained sand (slab B); (2) a negligible thickness, offset carbonaceous smear (slab B); (3) an impression fossil of tergites/paratergites, with grainy and striated surface textures (slab B); (4) remnant patches of organic material and the original form of the tergites, recording verrucose and striated surface textures (slab A); (5) 1–4 mm thickness of sand infill within three-dimensional tergites (slab A); (6) a highly micaceous and carbonaceous veneer on the surface of the tergites (slab A); (7) a negligible thickness, offset carbonaceous smear (slab A); and (8) underlying fine-grained sand (slab A).

Taphonomy of the specimen

The granular sandy host lithology of the specimen is remarkably coarse for preserved arthropleurid remains. All the other articulated remains are known from very fine-grained mudrocks, sandy siltstones or crystal tuffs (Guthörl 1934, 1935; Hahn *et al.* 1986; Schneider and Barthel 1997; Schneider *et al.* 2010), although several isolated remains from the late Visean Hainichen basin in Saxony are well preserved in silty fine-grained sandstones to fine- to medium-grained sandstones (Rößler and Schneider 1997). The well-sorted, granular nature of the host sediment created taphonomic conditions that were not conducive to preserving chitinous cuticles in high fidelity (Briggs *et al.* 1998) and the fossil is identifiable primarily because the cuticle was filled with sediment post-mortem. The only evidence of the original organic material is some carbonized material between the tergites in slab A (Fig. 9a) and the carbonaceous and micaceous material that appears offset and smeared across both the ventral and dorsal extremes of the fossil.

Missing body parts

The Howick specimen preserves only part of the dorsal exoskeleton of the organism, with no evidence of appendages. As is common to all other reports of giant *Arthropleura*, the head is also missing, but the lack of segmentation anterior to the first sizeable tergite suggests that the fossil may terminate where the head capsule was during life

(Fig. 2). No trace of appendage attachment points is present on either side of the specimen preserved in slab A, where both the ventral and dorsal surfaces of the dorsal exoskeleton can be observed. The most plausible explanation for these characteristics is that the specimen is an exuvium, potentially one in which the suture was located between the ventral edge of the paratergite and the body. This scenario would have resulted in a hollow mass of cuticle representing the dorsal and lateral exoskeleton, which was open to sediment infilling during an interval after moulting, but prior to ultimate internment in the sediment pile.

Despite missing key body parts, the remains are not fully disarticulated, which is unexpected given the sedimentological evidence for relatively high-energy deposition because arthropod exoskeletons rapidly disarticulate when tumbled in a fluid (McCoy and Brandt 2009). Considered alongside the fact that the fossil is preserved in three dimensions, fully enveloped and partially coiled (longitudinal doming of the sediment in part B) within a fine-grained cross-bedded sandstone, this suggests that the remains were instantaneously deposited with the host sediment. In a scenario where the fossil was parautochthonous, with the exuvium discarded and filled with sand away from the final resting location, this could feasibly have occurred as a pulse of bank margin debris (i.e. sand, exuvium and plant remains) that collapsed into a river channel and was subsequently sculpted by migrating bedforms.

Two further characteristics imply that the fossil represents an articulated exuvium that had already degraded prior to such collapse and internment: (1) the absence of any other fragments of arthropleurid material within the host bed (despite intensive searching), which implies that a complete organism was not disarticulated within the bedform in which it was ultimately preserved; and (2) the degradation recorded by the serrated left-lateral margin to the tergites and the irregular broken appearance of the majority of the right paratergites (Figs 1 and 2).

Post-burial deformation

Two key characteristics of the fossil imply that it has been deformed post-burial. First, the sand-filled tergites in slab A can be seen to buckle, suggesting that they experienced compressional stress within the sediment pile. Second, the repetition of form between the carbonaceous smears that sandwich the fossil and the sand infill

Mississippian *Arthropleura* from Northumberland

implies that the internal cast has been squeezed out and offset from the dorsal and ventral cuticles after partial lithification. Both characteristics are unusual, but can be readily explained through the tectonic taphonomy of the host bed.

The fossil-bearing bed occurs within the hanging wall damage zone of the Howick Fault (Fig. 4) and has previously been imaged, when still *in situ* in the cliff face, in earlier structural geology investigations of the locality (see De Paola *et al.* 2005, their fig. 8; Kjemperud 2011, their figs 14 and 17). The Stainmore Formation in the hanging wall damage zone contains several features – including small thrust faults, listric geometries, stratal thickening in the hanging wall, mudstone deformation and calcite veins – that together show that the master fault was syndepositional and occurred when the sediment was only partially lithified (De Paola *et al.* 2005; Kjemperud 2011). Normal faulting in the Howick Fault Zone was initiated during thermal subsidence after the earliest Carboniferous cessation of rifting in the Northumberland Basin and was contemporaneous with the deposition of the Yoredale Group (Kimbell *et al.* 1989; De Paola *et al.* 2005; Kjemperud 2011). Development continued when it was reactivated as a strike-slip fault during Variscan-induced shortening (Leeder *et al.* 1989; Chadwick *et al.* 1995; Fraser and Gawthorpe 2003; De Paola *et al.* 2005), as well as during the Carboniferous–Permian emplacement of the adjacent Whin Sill dolerite (De Paola *et al.* 2005; Kjemperud 2011).

Fault development at the precise fossil locality thus involved the near-continual deformation of the host sediment, prior to full lithification, throughout the Carboniferous and into the Permian. To accommodate the stress in the synsedimentary main fault, internal compressional strain in the fossil-hosting bed would have occurred. The arthropleurid fossil – as a significantly large material discontinuity within the unlithified to partly lithified sandstone bed – likely took up some of this strain, buckling the tergites and offsetting the internal sand moulds from the carbonized remains of the exuvium.

Interpretation of Arthropleurid identity

The partial preservation of cuticular material, the segmented nature of this fossil and the partial preservation of the lateral divisions of the segments into medial and paratergites strongly supports an arthropod identity for this fossil, even though no appendage is preserved. The morphology of the best-preserved paratergites (i.e. four to six; Fig. 2) indicates that the fossil records the anterior part of the animal.

The surface of slab A is interpreted as recording the ventral surface of the dorsal exoskeleton, with the surface of slab B recording a three-dimensional counter-print of this, and the pillow forms in slab A being sand infills of the tergites. The dorsal surface of the dorsal exoskeleton is visible in some fragments that have broken off from slab A (Fig. 8c).

No other Carboniferous arthropod with this morphology, or of this size, is known. Therefore, based on these observations, we propose that this fossil represents a giant arthropleurid. Although it is possible that other – yet unreported – arthropod taxa reached this size during the Carboniferous, an identity as *Arthropleura* sp. remains the most parsimonious explanation. In addition, two characteristics of the specimen bear notable resemblances to other specimens of *Arthropleura*: (1) the recurvature of the anterior paratergites is similar to that seen in other specimens (Hahn *et al.* 1986; Briggs and Almond 1994; Brauckmann *et al.* 1997; Kraus and Brauckmann 2003; Schneider and Werneburg 2010); and (2) the granular surface texture on the anterior border of the tergites bears a resemblance to that visible in partial specimens (Brauckmann *et al.* 1997).

Five morphospecies of *Arthropleura* have previously been described, mainly based on cuticular ornamentation: *A. armata*

and *A. mammata* are in common use (e.g. see Hahn *et al.* 1986) and there are less frequent or isolated reports of *A. cristata* (Hannibal 1997), *A. fayoli* (Boule 1893) and *A. maillieuxi* (Pruvost 1930). Comparable large arthropleurids have been assigned to the species *A. armata*, but the lack of preserved appendages or detailed ornamentation in the Howick specimen precludes confident species-level diagnosis.

Original size

Assuming that the missing left paratergites were the same size as those preserved on the right, the original carcass must have been at least 55 cm in width and considerably more than the 76 cm length that is preserved. A number of alternative width to length ratios for *Arthropleura* have been posited, calculated on the basis of trackways and partial giant, or complete juvenile, specimens with appendages. Estimates range between 3.47 (Martino and Greb 2009), 3.75 (Ryan 1986), 3.6–4.4 (Kraus 1993; Schneider and Werneburg 1998; Schneider *et al.* 2010) and 4.78 (Hahn *et al.* 1986). The Howick specimen is the widest arthropleurid fossil thus far discovered. Based on these ratios, it would also represent the largest individual discovered to date – being between 190 and 263 cm in length (Fig. 11). We contend that the true size is most likely to have been at the upper end of these estimates because the fossil has been tectonically compressed and only 12–14 tergites are preserved.

Estimates of the number of tergites in *Arthropleura* have improved with the discovery of new specimens, but all estimates are considerably greater than the 12–14 in the specimen described here. Early morphological details were based on the description of a c. 6.5 cm long, nearly complete, juvenile specimen (Calman 1914) from below the Top Hard Coal in Derbyshire, England (late Bashkirian; Duckmantian; Sheppard 2005). That specimen has an indistinct head region, a nearly complete trunk in dorsal aspect and an indistinct terminal segment, permitting the recognition that *Arthropleura* had at least 28 tergites (Calman 1914).

Several subsequent reconstructions (e.g. Rolfe and Ingham 1967, fig. 2; Briggs *et al.* 1984) were strongly influenced by the c. 90 cm long ‘Maybach specimen’ from the Moscovian Saarbrücker Schichten (Sulzbach Formation, Saarbrücken Subgroup) of the Saar Basin, Germany (Guthörl 1935; first described and figured in detail by Hahn *et al.* 1986, fig. 1 and plates 1 and 2). That specimen shows 23 tergites from a dorsal aspect, but the head and tail regions are missing (Hahn *et al.* 1986, plate 2). Hahn *et al.* (1986, fig. 2) suggested these represent the remains from a trunk of an estimated 30 tergites.

Other discoveries that inform on *Arthropleura* segment numbers include two associated remains of a distorted ventral exoskeleton from the Gzhelian–Asselian Döhlen Formation of Saxony, which preserve 25 articulated leg-bearing segments of an individual between 0.65 and 0.8 m in length (Schneider and Barthel 1997, p. 195, plates 5–7). The most recent reconstructions of *Arthropleura* – a 2.20 m long three-dimensional reconstruction, figured by Schneider and Werneburg (2010, fig. 6C) – assume 32 tergites for adult giant arthropleurids. All of these reconstructions imply that the Howick specimen comprises less than half the length of the original organism.

The Howick specimen is thus analogous in size to the very largest *Arthropleura* previously interpreted from indirect evidence: the 51 cm wide organism interpreted from fragmentary preserved appendages in the Gzhelian–Asselian Manebach Formation, Germany (Schneider and Werneburg 1998) and the organisms that left nearly 50 cm wide trackways in the Visean Strathclyde Group of Scotland (Pearson 1992; Pearson and Gooday 2019) and the Gzhelian Cape John Formation of Nova Scotia (Ryan 1986; Ryan and Bochner 1994).

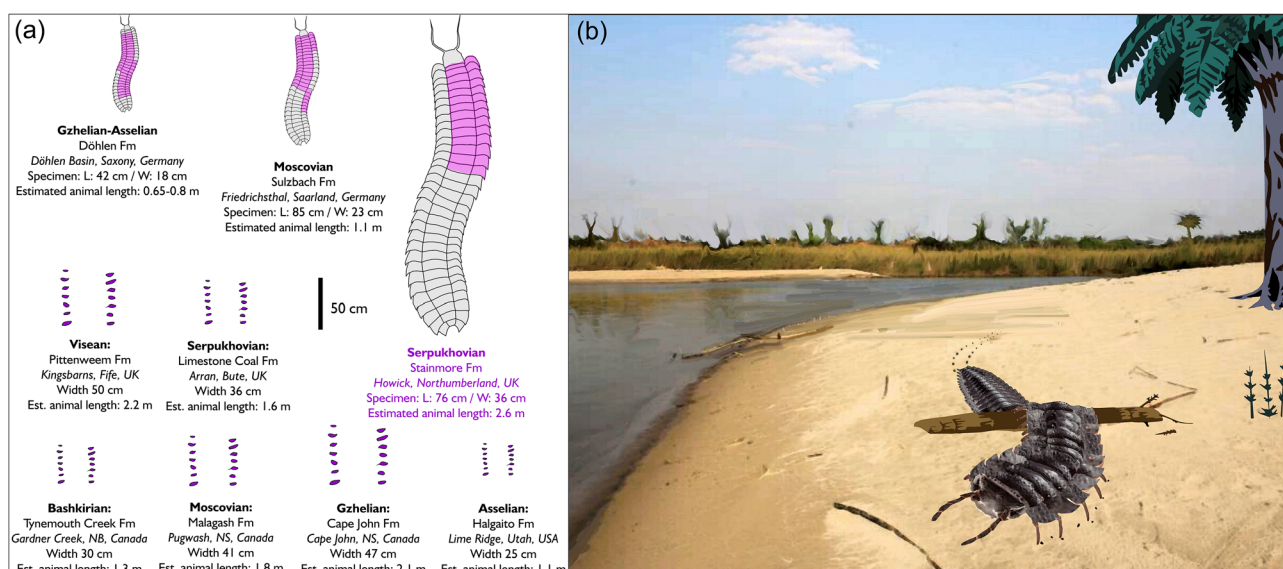


Fig. 11. Reconstruction of the Howick *Arthropleura*. (a) Scale of the Howick *Arthropleura* relative to other articulated giant specimens (preserved remains highlighted pink) and the largest *Diplichnites cuithensis* trackways known from each Carboniferous–Permian stage. Note that the previously known partially complete body fossils were both markedly smaller than the dimensions of *Arthropleura* revealed by trace fossil evidence. For references and details of localities mentioned, see Table 1. (b) Reconstruction of the Howick *Arthropleura* within its habitat of a lower delta plain with open woodland.

Weights of 8–10 kg have previously been calculated for giant *Arthropleura*, estimated from interpretations of a fraction of a simplified cylindrical volume and a density equivalent to that of water (Kraus and Brauckmann 2003). However, a cylinder is not representative of the true form of *Arthropleura*, which is better envisaged as a hemi-ellipsoid with a flat underside and raised topside tapering towards the lateral, anterior and posterior edges. In addition, the density of water (997 kg m^{-3}) is not representative of the densities of modern giant millipedes, which are typically $350\text{--}550 \text{ kg m}^{-3}$ (Bercovitz and Warburg 1985; Mwabvu *et al.* 2010; Horváthová *et al.* 2021).

We calculated two possible estimates for the weight of the Howick *Arthropleura* based on a reasonable estimate of 20 cm as the height and consequent dimensions of $20 \text{ cm} \times 55 \text{ cm} \times 263 \text{ cm}$. Calculating this volume as a hemi-ellipsoid (volume = $\frac{2}{3}\pi abc$, where a , b and c are the half-height, width and length) equates to $c. 158\,000 \text{ cm}^3$, suggesting substantial weights of $c. 55\text{--}87 \text{ kg}$ based on the densities of extant giant millipedes. This method provides a replicable estimate, but does not account for the true shape of the organism being a fraction of a complete hemi-ellipsoid. To account for the likely overestimate, we also purchased a commercially available three-dimensional mesh of a model *Arthropleura* from Turbosquid.com, loaded this into Blender (Garwood and Dunlop 2014) and scaled it to the dimensions derived from this fossil (see Supplementary Information). The 3D Print Toolbox in Blender provided a volume measurement for an *Arthropleura*-shaped object with the specified dimensions of $91\,509 \text{ cm}^3$, equivalent to $c. 32\text{--}50 \text{ kg}$ based on the densities of extant giant millipedes. This range of estimates converges at an approximate weight of $c. 50 \text{ kg}$, which is substantially larger than previous estimates, but inevitable due to the extreme size of this specimen (applying the calculation method of Kraus and Brauckmann (2003) would lead to an implausible weight estimate of $c. 205 \text{ kg}$).

With a surface area of $c. 2.7 \text{ m}^2$, the Howick specimen is one of the largest individual arthropod fossils found to date globally, comparable with the largest specimen of the Ordovician trilobite, *Isotelus rex* (Rudkin *et al.* 2003). It may also record the largest known arthropod in Earth history. The upper size estimate of a 2.63 m length and $c. 50 \text{ kg}$ weight exceeds the 2.5 m length interpreted for *Jaekelopterus rhenaniae*, the Early Devonian

eurypterid previously suggested to be the largest arthropod ever to have evolved (Braddy *et al.* 2008).

Implications for the understanding of *Arthropleura*

The Howick specimen provides limited new information on *Arthropleura* Bauplan, being primarily the ventral surface of the dorsal exoskeleton. The specimen lacks the ornamentation of arthropleurid remains that are found in more taphonomically favourable settings (indeed, these would not be expected on the ventral surface of the dorsal exoskeleton). Despite this limited detail, the curvature of the specimen supports assertions of arthropleurid manoeuvrability and refutes the suggestion that *Arthropleura* may have had a weak, unmineralized cuticle and was stabilized by musculature and antagonistic hydraulics, as in caterpillars (e.g. Kraus and Brauckmann 2003; Kraus 2005; McGhee 2018). The fractured margins and sand infill of the tergites in the Howick specimen imply a sclerotized exoskeleton in life, as does the survival of an exuvium. Further supporting evidence is provided by arguments based on trackways, where leg stance (Shear and Edgecombe 2010) and track depth (Lucas *et al.* 2005; Schneider *et al.* 2010) suggest that skeletal support was offered by more than just haemolymph pressure, and the observation that arthropleurid remains are more recalcitrant than other arthropod fragments in depositional settings with significant transport histories (Proctor 1998).

Arthropleurid habitat

The fossil-bearing bed was deposited in a minor fluvial distributary channel in direct proximity to the coast and the completeness of the arthropleurid fossil suggests that it has not been subject to a significant history of transport. Direct palaeobotanical evidence shows that the small river traversed a lower delta plain that was colonized by a mixed arborescent flora of lycopsids, medullosalean pteridosperms and cordaitaleans (Fig. 6). The presence of only thin, discontinuous and infrequent coals implies that the vegetation was relatively open at the coast, rather than forming dense coal forests (at 326 Ma old, the fossil also predates the widespread dominance of equatorial wetland coal forests in Euramerica; Greb *et al.* 2006). Ichological evidence shows that the lower delta plain also hosted

Mississippian *Arthropleura* from Northumberland**Table 1** Details of previously reported *Arthropleura* localities

Number	Age	Stratigraphic context	Location	Type	Reference
1	Serpukhovian	Stainmore Formation	Howick, Northumberland, UK	Giant partial	This study
2	Moscovian	Sulzbach Formation	Maybach mine, Saarland, Germany	Giant partial	Guthörl (1934, 1935), Hahn <i>et al.</i> (1986), Kraus and Brauckmann (2003), Kraus (2005)
3	Gzhelian–Asselian	Döhlen Formation	Döhlen Basin, Saxony, Germany	Giant partial	Schneider and Barthel (1997), Schneider <i>et al.</i> (2010)
4	Gzhelian–Asselain	Montceau-les-Mines lägerstätten	Montceau-les-Mines, Burgundy, France	Small complete	Briggs and Almond (1994), Almond (1985), Perrier and Charbonnier (2014)
5	Bashkirian	Pennine Middle Coal Measures Formation	Shipley, Derbyshire, UK	Small partial	Calman (1914), Hahn <i>et al.</i> (1986)
6	Visean	Berthelsdorf Formation	Hainichen Basin, Saxony, Germany	Fragmentary remains	Rößler and Schneider (1997), Schneider <i>et al.</i> (2010)
7	Serpukhovian	Lower Silesian Basin	Przygorze – KWK Bolesław, Poland	Fragmentary remains	Pavela (2018)
8	Serpukhovian	Upper Silesian Basin	Chlebovice – Důl Staříč, Czech Republic	Fragmentary remains	Pavela (2018)
9	Pennsylvanian	Karaganda Basin	Karaganda, Kazakhstan	Fragmentary remains	Novozhylov (1962), Dernov (2019)
10	Bashkirian	Charleroi Formation	Mariemont mine, Hainaut, Belgium	Fragmentary remains	Pruvost (1930)
11	Bashkirian	Grand Anse Formation	Maringouin, New Brunswick, Canada	Fragmentary remains	R. Miller (2021, pers. comm.: New Brunswick Museum specimen NBMG15084)
12	Bashkirian	Joggins Formation	Joggins, Nova Scotia, Canada	Fragmentary remains	Falcon-Lang <i>et al.</i> (2006)
13	Bashkirian	Lancaster Formation	Saint John, New Brunswick, Canada	Fragmentary remains	Falcon-Lang and Miller (2007)
14	Bashkirian	Mospinka Formation	Makedonovka, Donets Basin, Ukraine	Fragmentary remains	Dernov (2019)
15	Bashkirian	Nord-Pas-de-Calais Mining Basin	Anzin, Hauts-de-France, France	Fragmentary remains	Pruvost (1930)
16	Bashkirian	Pennine Lower Coal Measures Formation	Bickershaw, Lancashire, UK	Fragmentary remains	Anderson <i>et al.</i> (1997)
17	Bashkirian	Pennine Middle Coal Measures Formation	Barnsley, Yorkshire, UK	Fragmentary remains	Andrée (1913)
18	Bashkirian	Pennine Middle Coal Measures Formation	Baxterley, Warwickshire, UK	Fragmentary remains	Vernon (1912), Pruvost (1930)
19	Bashkirian	Upper Silesian Basin	Czerwionka - Ameryka, Poland	Fragmentary remains	Pavela (2018)
20	Bashkirian	Żaclę Formation	Nowa Ruda, Lower Silesia, Poland	Fragmentary remains	Pacyna <i>et al.</i> (2012), Pavela (2018)
21	Bashkirian–Moscovian	Emma mine	Brunssum, Limburg, Netherlands	Fragmentary remains	Pruvost (1930)
22	Moscovian	Francis Creek Shale	Mazon Creek, Illinois, USA	Fragmentary remains	Richardson (1959), Hannibal (1997)
23	Moscovian	Grovesend Formation	Camerton & Writhlington, Somerset, UK	Fragmentary remains	Woodward (1907), Andrée (1913), Proctor (1998)
24	Moscovian	Heiligenwald Formation	Friedrichsthal, Saarland, Germany	Fragmentary remains	Jordan and von Meyer (1854)
25	Moscovian	Kittaning Formation	Cannelton, Pennsylvania, USA	Fragmentary remains	Hannibal (1997)
26	Moscovian	Lorraine Basin	St. Avold, Grand Est, France	Fragmentary remains	Waterlot (1934)
27	Moscovian	Pennine Middle Coal Measures Formation	Salford, Lancashire, UK	Fragmentary remains	Salter (1863), Pruvost (1930), Hahn <i>et al.</i> (1986)
28	Moscovian	Plzeň Basin	Zbůch - Důl Austria, Czech Republic	Fragmentary remains	Pavela (2018)
29	Bashkirian	Ruda Beds	Chwałowice, Lower Silesia, Poland	Fragmentary remains	Andrée (1913)
30	Moscovian	Saarbrücker Subgroup	Saarbrücken region, Saarland, Germany	Fragmentary remains	Andrée (1913)
31	Moscovian	San Giorgio Formation	Rio San Giorgio, Sardinia, Italy	Fragmentary remains	Pillola and Zoboli (2021)
32	Moscovian	Scottish Upper Coal Measures Formation	Leven, Fife, UK	Fragmentary remains	Andrée (1913)
33	Kasimovian	Conemaugh Formation	Columbiana County, Ohio, USA	Fragmentary remains	Hannibal (1997)
34	Kasimovian	Kateřina Coal Mine	Radvanice, Ostrava, Czech Republic	Fragmentary remains	Štamberg and Zajíč (2008)

(continued)

Table 1 (*Continued*)

Number	Age	Stratigraphic context	Location	Type	Reference
35	Kasimovian	San José Formation	Ciñera, León, Spain	Fragmentary remains	Castro (1997)
36	Gzhelian	La Magdalena Coalfield	Carrocera, León, Spain	Fragmentary remains	Castro (1997)
37	Gzhelian	Stephanian strata	St. Etienne, Auvergne-Rhône-Alpes, France	Fragmentary remains	Boule (1893), Waterlot (1934)
38	Gzhelian	Stephanian strata	Commentry, Auvergne-Rhône-Alpes, France	Fragmentary remains	Boule (1893)
39	Gzhelian	Toledo Mountains	Puertollano, Ciudad Real, Spain	Fragmentary remains	Castro (1997)
40	Asselian	Manebach Formation	Manebach, Thuringia, Germany	Fragmentary remains	Schneider and Werneburg (1998)
41	Asselian	Autunian strata	Autun, Burgundy, France	Fragmentary remains	De La Comble (1963), Moreau <i>et al.</i> (2019)
42	Sakmarian	Leukersdorf Formation	Chemnitz, Saxony, Germany	Fragmentary remains	Rößler <i>et al.</i> (2012)
43	Visean	Anstruther and Pittenweem formations	Crail to St Andrews, Fife, UK	Multiple trackways	Pearson (1992), Whyte (2018)
44	Serpukhovian	Limestone Coal Formation	Isle of Arran, UK	Single trackway	Briggs <i>et al.</i> (1979)
45	Serpukhovian	Limestone Coal Formation	Glasgow, UK	Single trackway	J. Buckman (2021, pers. com.)
46	Pennsylvanian	Zhezkazgan Group	Zhezkazgan, Kazakhstan	Single trackway	Nelikhov (2010), Dernov (2019)
47	Bashkirian	Boss Point Formation	Alma, New Brunswick, Canada	Single trackway	Bailey (1902)
48	Bashkirian	Little River and Joggins formations	Joggins, Nova Scotia, Canada	Multiple trackways	Ferguson (1966), Calder <i>et al.</i> (2005), Falcon-Lang <i>et al.</i> (2006)
49	Bashkirian	Mospinka Formation	Makedonovka, Donets Basin, Ukraine	Multiple trackways	Dernov (2019)
50	Bashkirian	Tynemouth Creek Formation	Gardner Creek, New Brunswick, Canada	Multiple trackways	Briggs <i>et al.</i> (1984), Falcon-Lang <i>et al.</i> (2015)
51	Moscovian	Malagash Formation	Pugwash to Smith Point, Nova Scotia, Canada	Multiple trackways	Ryan (1986), Ryan and Boehner (1994)
52	Moscovian	Rhode Island Formation	Plainville, Massachusetts, USA	Multiple trackways	Getty <i>et al.</i> (2017)
53	Kasimovian	Cutler Group	El Cobre Canyon, New Mexico, USA	Single trackway	Lucas <i>et al.</i> (2005), Schneider <i>et al.</i> (2010)
54	Gzhelian	Cape John Formation	Cape John, Nova Scotia, Canada	Multiple trackways	Ryan (1986), Ryan and Boehner (1994)
55	Gzhelian	Conemaugh Formation	Boyd County, Kentucky, USA	Multiple trackways	Martino and Greb (2009)
56	Gzhelian	Eiche Member (Flechtingen Formation)	Flechtingen Volcanic Complex, Germany	Multiple trackways	Walter and Gaitzsch (1988), Schneider and Werneburg (2010)
57	Gzhelian	Graissessac Formation	Graissessac, Hérault, France	Multiple trackways	Moreau <i>et al.</i> (2019)
58	Gzhelian–Asselian	Montceau Formation	Montceau-les-Mines, Burgundy, France	Multiple trackways	Langiaux and Sotty (1977), Briggs (1986)
59	Gzhelian	Stull Shale Member (Kanwaka Formation)	Waverly, Kansas, USA	Multiple trackways	Mángano <i>et al.</i> (2002)
60	Asselian	Halgaito Formation	Lime Ridge, Utah, USA	Single trackway	Chaney <i>et al.</i> (2013)

communities of terrestrially adapted amphibians and small infaunal and surface-grazing invertebrates (Fig. 6), whereas the adjacent marine waters were populated by a normal salinity community of vertical burrowers, bryozoans, brachiopods, crinoids and marine forams.

This setting contrasts with the traditional view that arthropleurids predominantly occupied swampy environments (e.g. Donovan 2002; Kraus and Brauckmann 2003). Although even early investigations noted that *Arthropleura* was more common in fluvial sandstones that were intercalated with coals (Guthörl 1940), the common perception of an association of *Arthropleura* with coal swamp environments appears to have arisen as an artefact of the earliest fossil discoveries of the organism being made in working coal mine settings and excavation dumps (e.g. Guthörl 1936). The interpretation of tightly vegetated coal-forming swamps as the preferred habitat of *Arthropleura* is not supported by finds of

more or less allochthonous body remains and especially not by the absolutely autochthonous *Arthropleura* tracks (Schneider *et al.* 2010). A wealth of more recent ichnological evidence is aligned to the setting recorded by the Howick example, namely sparsely wooded, alluvial and littoral environments (e.g. Pearson 1992; Lucas *et al.* 2005; Schneider *et al.* 2010; Getty *et al.* 2017; Pearson and Gooday 2019). In addition, the close proximity of the fossil to the trackway *Baropezia* (Scarboro and Tucker 1995) provides direct evidence that confirms that arthropleurids shared an environmental niche with tetrapods, even by the end Mississippian (Falcon-Lang *et al.* 2006; Martino and Greb 2009; Schneider *et al.* 2010; Minter *et al.* 2016; Getty *et al.* 2017; Dernov 2019), contrary to the traditional view that the latter would have outcompeted them (e.g. DiMichele *et al.* 1992).

Ichnological evidence that has been attributed to arthropleurid activity includes the large trackways *Diplichnites cuithensis* (e.g.

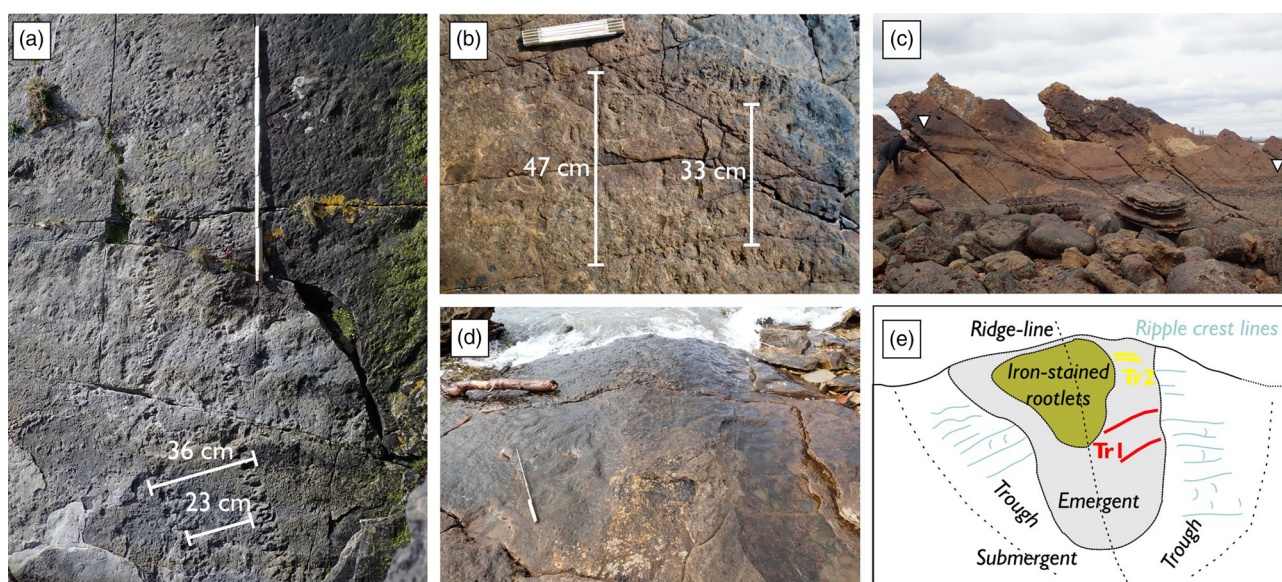
Mississippian *Arthropleura* from Northumberland

Fig. 12. Trace fossil evidence for *Arthropleura* from the trackway *Diplichnites cuithensis*, preserved in strata, near contemporaneous in age to the Howick specimen, from adjacent basins in northern Britain (see Fig. 3 for localities). (a) Trackway from which the *D. cuithensis* holotype was cast (Briggs *et al.* 1979) in the Serpukhovian Limestone Coal Formation of Laggan, Isle of Arran, Scotland. Stick is 1 m long, inner and outer width of trackway highlighted. (b) *D. cuithensis* trackway of near-analogous width to the Howick body fossil, Visean Pittenweem Formation, Crail, Fife, Scotland. (c) *D. cuithensis* trackway >10 m long (arrowed) in the Visean Pittenweem Formation, St Andrews, Fife, Scotland (see Whyte 2018). Geologist is 1.8 m tall. (d, e) Photograph and interpreted sketch of context of *D. cuithensis* on a true substrate (Davies and Shillito 2018, 2021) recording the passage of two animals between emergent and subaqueous substrates. Convex bedform, colonized with plants, provided small island surrounded by shallow water puddles in a delta-top setting. Trackways are well-defined on emergent substrate and less so on subaqueous parts of substrate. Visean Anstruther Formation, 3.5 km NW of Kingsbarns, Fife, Scotland. Measuring stick 60 cm long.

Briggs *et al.* 1979, 1984; Ryan 1986; Pearson 1992; Schneider *et al.* 2010; Moreau *et al.* 2019), possible large *Beaconites* aestivation burrows (Falcon-Lang *et al.* 2006; Falcon-Lang and Miller 2007; Pearson and Gooday 2019) and rare coprolites (Scott and Taylor 1983). The identification of an arthropleurid trace-maker for many of these ichnofossils is assumed primarily based on their size; sites that yield both trace and body fossils are thus far unknown (Table 1). Trace fossil localities have a different bias to body fossil localities, requiring the presence of true substrates (bedding planes that have archived ancient air–substrate interfaces), which are most favourably exposed in areas of extensive rock outcrop rather than abundant spoil debris (Davies and Shillito 2018, 2021; Shillito and Davies 2020).

Diplichnites cuithensis is thus far known from the Northumberland Basin, but the Stainmore Formation is directly contemporaneous in age, and comparable in facies, with the Upper Limestone Formation of the adjacent Midland Valley basin of southern Scotland. Despite different lithostratigraphic and basin names, the units were deposited within a linked deposystem during the Pendleian, connected by contiguous deltaic sedimentary environments in the present North Sea area, with upland and emergent areas in the region of the Southern Uplands Block (Fig. 2) (Kearsey *et al.* 2015, 2019). *Diplichnites cuithensis* trackways are common in the Upper Limestone Formation, recorded from both Glasgow city, 170 km WNW (Buckman 2021, pers. comm) and the Isle of Arran, 220 km WNW (Fig. 12; the type locality of *D. cuithensis*; Briggs *et al.* 1979).

The marginally older Visean strata of the Midland Valley basin in Fife (the Anstruther and Pittenweem formations) also have abundant reported *D. cuithensis* (Pearson 1992; Whyte 2018) and original fieldwork at these localities has yielded 26 individual instances of the track form, ranging in external width from 23 to 47 cm (mean 32 cm) and indented into sand to depths of up to 8 mm. These dimensions strongly suggest that the trackways were made by organisms of the same size and posited weight as recorded

by the Howick body fossil. The trackways all occur in similar sedimentary facies to the Howick body fossil: delta-top alluvial and littoral sandstone facies with patchy standing tree fossils and abundant *Stigmara*, but no evidence for extensive afforestation. They provide direct evidence for arthropleurid habitat preferences, with individual trackways traversing both submerged and emergent substrates (Fig. 12). This ichnological evidence supports physiological evidence that arthropleurids were suited to both subaerial and very shallow water locomotion (e.g. Størmer 1976; Shear and Selden 1995; Schneider and Barthel 1997) and would have been well-suited to the patchily wet lower delta plain environment recorded in the Howick section.

Palaeogeographical and stratigraphic range

The full known stratigraphic and palaeogeographical range of arthropleurids is shown in Figure 13 and Table 1. The organism is known from Visean to Sakmarian strata and has a tight palaeogeographical range in the narrow equatorial belt (Schneider and Werneburg 2010).

The earliest fossil evidence is known from a handful of Mississippian sites in Britain and Germany (including this study) and becomes widespread across equatorial Euramerica later in the Carboniferous. The peak geographical distribution of unequivocal body and trace fossils is known from the Early to Mid-Pennsylvanian. Post-Kasimovian body fossils are less common, with evidence primarily from a few sites in central and southern Europe (Table 1), despite a notably abundant trackway record from this interval across North America (Ryan 1986; Ryan and Bochner 1994; Mángano *et al.* 2002; Lucas *et al.* 2005; Martino and Greb 2009; Schneider *et al.* 2010; Chaney *et al.* 2013). Two secondary reports of fragmentary remains and trackways from Kazakhstan (Novozhylov 1962; Nelikhov 2010), cited by Dernov (2019), represent a higher latitude palaeogeographical outlier, but these instances remain anecdotal in the absence of published

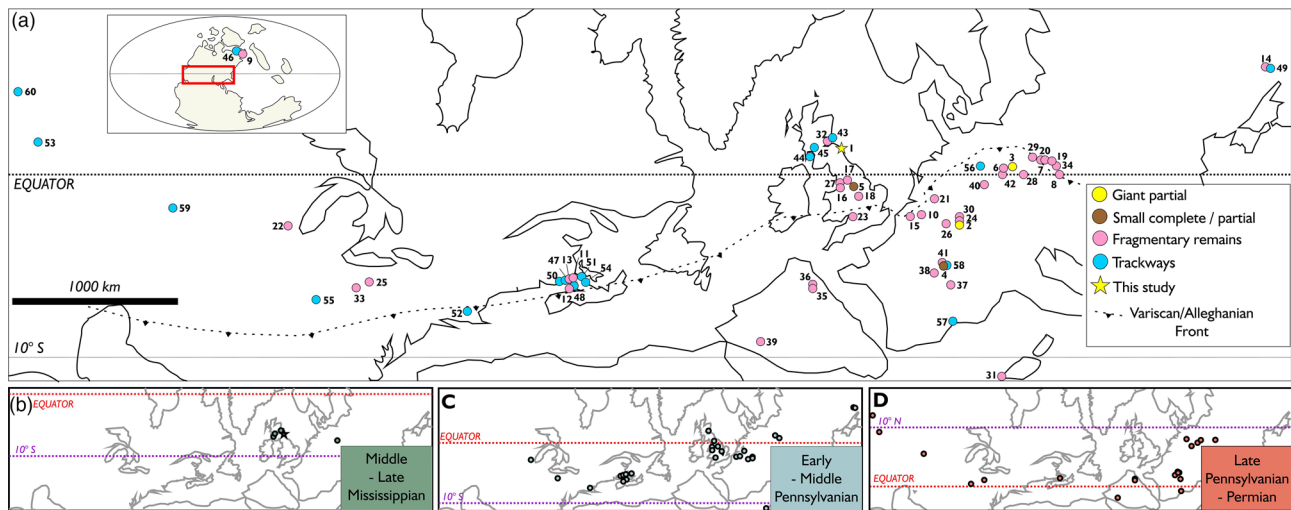


Fig. 13. Palaeogeographical range of *Arthropleura* body and trace fossils. (a) Known sites of evidence plotted on a palaeogeographical map of the late Carboniferous (c. 310 Ma; after Torsvik and Cocks 2016). Numbers refer to sites listed in Table 1. (b) Viséan to Serpukhovian sites (latitudinal parallels shown for c. 320 Ma; from Torsvik and Cocks 2016). (c) Bashkirian to Moscovian sites (latitudinal parallels shown for c. 310 Ma; from Torsvik and Cocks 2016). (d) Kasimovian to Sakmarian sites (latitudinal parallels shown for c. 290 Ma; from Torsvik and Cocks 2016).

illustration and the host strata are only coarsely dated to the Pennsylvanian.

The shifting distribution of both body and trace fossil evidence for *Arthropleura* (Fig. 13) may imply that the palaeogeographical range of arthropleurids expanded from a localized subequatorial crucible in the Mid- to Late Mississippian. The fossil described here, in addition to the Scottish trackways, indicates Mississippian gigantism in this group before arthropleurid fossils become widespread in the late Carboniferous. By the Pennsylvanian, *Arthropleura* had an extensive west–east palaeogeographical range across the entire continent of Laurussia/Pangaea, but no verified evidence for the organism is present from palaeolatitudes higher than 10° N or 10° S and most known instances tightly follow the palaeoequator (Schneider and Werneburg 2010, fig. 16). In the Late Pennsylvanian and early Permian, a transcontinental range was maintained, but almost all known arthropleurid and track instances remain within 10° of the palaeoequator. The Carboniferous–Permian northwards drift of Pangaea appears to be reflected by the increased abundance of younger *Arthropleura* remains from more southern modern latitudes because fossil evidence tracks the relative southwards migration of the palaeoequator during this interval.

The strong relationship between *Arthropleura* body fossils and the location of the palaeoequator could be counter-argued to be reflective of sampling biases, tracking the distribution of mined coal-bearing strata. However, the trend is also seen within the trace fossil record (Fig. 13), which is subject to a different and mutually exclusive suite of biases (i.e. extensive bedding plane outcrop instead of excavated spoil tips). For example, in Britain, multiple outcrops of strata with bedding plane exposures persist through the latest Carboniferous and early Permian and have been investigated for (vertebrate) trackways (e.g. Sarjeant 1974; Hedge *et al.* 2019). However, despite these directed ichnological surveys and the correct outcrop type, the youngest British trace fossil evidence for *D. cuithensis* is Serpukhovian (Briggs *et al.* 1979). By contrast, in Spain, the oldest worked coal measures are of Moscovian age (Piedad-Sánchez *et al.* 2004) and spoil from these measures has been intensively interrogated for plant and other fossil remains (e.g. Wagner and Álvarez-Vázquez 2010). However, despite these directed palaeontological surveys and the correct outcrop type, the earliest Spanish body fossil evidence for *Arthropleura* is not known until the Kasimovian (Castro 1997).

These examples illustrate that although different outcrop expressions can bias evidence for *Arthropleura*, the appearance and disappearance of suitable outcrop types is discordant with the appearance and disappearance of evidence for *Arthropleura*. The most parsimonious explanation for the southwards drift of evidence through the Carboniferous and Permian is that the affinity of *Arthropleura* for equatorial latitudes was robust and that the genus maintained its geographical range as the Carboniferous continents drifted northwards.

Response to Carboniferous–Permian climate change and oxygen

The undisrupted record of *Arthropleura* throughout the interval of the Kasimovian rainforest collapse (DiMichele *et al.* 2009, 2011; Sahney *et al.* 2010; Davies and Gibling 2011; Falcon-Lang *et al.* 2018; Bashforth *et al.* 2021) is testament to the fact that the organism was not reliant on wetland coal forests as a habitat. The increasing post-Kasimovian dominance of seasonally dry vegetation and open forests in equatorial Euramerica (DiMichele 2014) appears to have had little impact on the palaeogeographical range and abundance of evidence for *Arthropleura*. However, increasing aridity during Pangean assembly may explain changes in the evidence of arthropleurids. The post-Kasimovian record of *Arthropleura* shows a shift where trace fossil sites become almost as abundant as those yielding cuticular fossils. Although *Arthropleura* appears to have successfully weathered climate and habitat change around the Carboniferous–Permian boundary, the youngest evidence for the organism is known from the Sakmarian of Saxony, Germany (Rößler *et al.* 2012). The absence of records younger than c. 290 Ma, despite fossils of other terrestrial fauna, suggests that the early Permian disappearance of *Arthropleura* records the extinction of the organism. The reason for this extinction may be related to increasing supercontinental aridification near the equator, in addition to increased competition associated with the Permian rise of reptiles (Schneider *et al.* 2010).

The age of giant *Arthropleura* is frequently linked to atmospheric oxygen peaks, which are suggested to have facilitated gigantism (e.g. Harrison *et al.* 2010; Vermeij 2016; McGhee 2018). If atmospheric oxygen is not the primary constraint on arthropod body size, then ecological interactions with predators, environmental factors and Cope's rule are alternative potential drivers (e.g. Hone

Mississippian *Arthropleura* from Northumberland

and Benton 2005; Schneider and Werneburg 2010; Schachat *et al.* 2018). The known stratigraphic range of *Arthropleura* is discordant with the Paleozoic oxygen peaks predicted by the GEOCARBSULF model (Bernier 2006), with the first appearance of *Arthropleura* (and other giant aquatic and terrestrial arthropods; Carpenter 1939; Braddy *et al.* 2008) predating significant increases in atmospheric O₂ and the last appearance of trace or body fossil evidence for *Arthropleura* predating the oxygen peak of the mid-Permian). The Howick specimen dates from an interval when atmospheric O₂ was 23%, not significantly elevated above present day concentrations (Bernier 2006), and suggests that high atmospheric oxygen concentrations alone were not required for the evolution of a 2.63 m long myriapod, *c.* 50 kg in weight. Hence a more parsimonious explanation for the gigantism of this organism was that it evolved and sustained giant dimensions simply due a favourable environment with a limited number of competitors (e.g. the anthracosaur tetrapods recorded by Baropezia), few predators and an abundance of high-nutrition food (potentially including prey; Schneider *et al.* 2010; Schneider and Werneburg 2010).

Conclusions

Recently discovered giant arthropleurid remains in the Serpukhovian Stainmore Formation of the Northumberland Basin are notable because (1) they constitute one of the largest known arthropod fossils in the world, (2) are presently the remains of the largest individual arthropod known to have evolved and (3) are the oldest semi-complete body fossil evidence for gigantism in arthropleurids. The fossil is also notable taphonomically as the individual is partially three-dimensionally preserved, interred in sand and was deformed by synsedimentary tectonics prior to lithification. The specimen is interpreted as the anterior part of an exuvium, which sedimentological evidence suggests was discarded on the banks of a small coastal river channel, where it sat amongst plant detritus and filled with sand through open sutures, before being entrained and interred in the channel by bank collapse.

The fossil and its context lend weight to recent assertions about arthropleurids: they lived in open wooded habitats, instead of, or in preference to, the coal forests with which they have traditionally been associated; they occupied the same environmental niches as early tetrapods; they were highly manoeuvrable; and they had hardened sclerotized cuticle. The Northumberland specimen has much in common with the 59 other body and trace fossil records of *Arthropleura* from Viséan to Sakmarian strata from equatorial Euramerica. This fossil presents a rare example of the remains of this giant millipede, up to 2.63 m long and *c.* 50 kg in weight, the likes of which crawled throughout the Earth's equatorial region for a *c.* 45 myr interval during the late Paleozoic.

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Author contributions NSD: conceptualization (lead), formal analysis (equal), investigation (lead), methodology (lead), project administration (lead), writing – original draft (lead), writing – review & editing (lead); RJG: formal analysis (equal), funding acquisition (supporting), resources (supporting), software (lead), validation (supporting), writing – original draft (supporting), writing – review & editing (supporting); WJM: conceptualization (equal), formal analysis (supporting), investigation (equal), writing – review & editing (supporting); JWS: formal analysis (equal), investigation (supporting), validation (equal), writing – review & editing (equal); APS: formal analysis (equal), funding acquisition (supporting), investigation (equal), methodology (supporting), validation (supporting), writing – original draft (supporting), writing – review & editing (supporting).

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Mississippian *Arthropleura* from Northumberland

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