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

Neil S. Davies1*, Russell J. Garwood2-3, William J. McMahon1, Joerg W. Schneider4,5 and Anthony P. Shillito1

1Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK
2Department of Earth and Environmental Sciences, University of Manchester, Manchester M13 9PL, UK
3Earth Sciences Department, Natural History Museum, London SW7 5BD, UK
4Department of Palaeontology/Stratigraphy, Technical University Bergakademie Freiberg, Institute of Geology, Bernhard-von-Cotta-Straße 2, D-09596 Freiberg, Germany
5Kazan Federal University, Institute of Geology and Petroleum Technologies, Kremlyovskaya Street 18, Kazan, Russia

Present address: APS, Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, UK.

* Correspondence: nsd27@cam.ac.uk

**Received** 17 September 2021; **revised** 9 November 2021; **accepted** 18 November 2021

**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 cuithensis*. 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

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. André 1913; Pruvost 1930; Waterlot 1934; Rolfe and Ingham 1967; Rößler and Schneider 1997; Schneider and Wernerburg 1998; Wilson 1999; Pacyna *et al.* 2012; Pillola and Zoboli 2021) and wide *Diplichnites cuithensis* 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 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 February 2020).
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 (CAMSM 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.
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). 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 Visean 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 foraminiferal 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).
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 Stigmaria. 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 Stigmaria 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...
**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 (*Baropezia*) (individual footprints arrowed). Located at 4.6 m on stratigraphic log in Figure 3d. Scale bar 10 cm. (b) Detail of *Baropezia* 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 *Archaonassa* (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.
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; Cózar 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.

Fig. 7. Schematic diagram showing taphonomic context and relationship between key attributes of the specimen.
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 arthrodial 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 arthrodial 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.
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 B); (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. (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).

**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.

**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...
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 un lithified 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 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 263 cm in length (Schneider and Barthel 1997, their fig. 6C) – assume 23 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 Boehner 1994).
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 350–550 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 cm $\times$ 55 cm $\times$ 263 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 cm$^3$, suggesting substantial weights of c. 55–87 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 cm$^3$, equivalent to c. 32–50 kg based on the densities of extant giant millipedes. This range of estimates converges at an approximate weight of c. 50 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 kg).

With a surface area of c. 2.7 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, *Isoetulus rex* (Rudkin et al. 2003). It may also record the largest arthropod 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 fossils in depositional settings with significant transport histories (Proctor 1998).

**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). Ichnological evidence shows that the lower delta plain also hosted 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 more recalcitrant than other arthropods in depositional settings with significant transport histories (Proctor 1998).

**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). Ichnological evidence shows that the lower delta plain also hosted 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 more recalcitrant than other arthropods in depositional settings with significant transport histories (Proctor 1998).

**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). Ichnological evidence shows that the lower delta plain also hosted eurypterid previously suggested to be the largest arthropod ever to have evolved (Braddy et al. 2008).
### 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      | Guthötl (1934, 1935), Hahn et al. (1986), Kraus and Brauckmann (2003), Kraus (2005) |
| 3      | Gzhelian–Asselian | Döhlen Formation               | Döhlen Basin, Saxony, Germany         | Giant partial      | Schneider and Barthel (1997), Schneider et al. (2010) |
| 4      | Gzhelian–Asselian | 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 et al. (1986)              |
| 6      | Visean         | Bertholdsfeld Formation          | Hainichen Basin, Saxony, Germany      | Fragmentary remains| Rößler and Schneider (1997), Schneider et al. (2010)  |
| 7      | Serpukhovian   | Lower Silesian Basin             | Przygorze – KWK Boleslaw, Poland     | Fragmentary remains| Pavela (2018)                                  |
| 8      | Serpukhovian   | Upper Silesian Basin             | Chlebovice – Dil 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 et al. (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 et al. (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     | Žaclč Formation                  | Nowa Ruda, Lower Silesia, Poland      | Fragmentary remains| Pacyna et al. (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      | Kittanning Formation             | Cannelton, Pennsylvania, USA          | Fragmentary remains| Hannibal (1997)                                |
| 26     | Moscovian      | Lorraine Basin                   | St. Avoold, Grand Est, France        | Fragmentary remains| Waterlot (1934)                                |
| 27     | Moscovian      | Pennine Middle Coal Measures Formation | Salford, Lancashire, UK              | Fragmentary remains| Salter (1863), Pruvost (1930), Hahn et al. (1986) |
| 28     | Moscovian      | Plzeň Basin                      | Zbíč - Dlůr Austria, Czech Republic  | Fragmentary remains| Pavela (2018)                                  |
| 29     | Bashkirian     | Ruda Beds                       | Chwalowice, Lower Silesia, Poland     | Fragmentary remains| Andrée (1913)                                 |
| 30     | Moscovian      | Saarbricker 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     | Comenauh Formation               | Columbiana County, Ohio, USA          | Fragmentary remains| Hannibal (1997)                                |
| 34     | Kasimovian     | Katěrina Coal Mine               | Radvance, Ostrava, Czech Republic    | Fragmentary remains| Štamberk and Zajíc (2008)                      |

(continued)
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 et al. 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* trackways (Schneider et al. 2010). A wealth of more recent ichnological evidence is aligned to the setting recorded by the Howick example, namely sparsely absolute autochthonous remains (e.g. Lucas et al. 2005; Schroeder and Werneburg 2010), contrary to the traditional view that the latter would have outcompeted them (e.g. Martino and Greb 2009; Walter and Gaitzsch 1988, Schneider and Werneburg 2010). 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. 2010; Getty et al. 2017; Pearson 2010; Minter et al. 2013). Thus, the available ichnological evidence that has been attributed to arthropleurid remains includes the large trackways (e.g. Diplichnites cuithensis).
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 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 *Stigmarralia*, 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. Stormer 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 Bohner 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...
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 $10^\circ$N or $10^\circ$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 $10^\circ$ 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 undisturbed 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 et al. 2004; 2019; 2021). 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).
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 (Berner 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 (Berner 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 to a favourable environment with a limited number of competitors (e.g. the anthracosaur tetrapods recorded by Baropezita), 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 arthropoderia. The fossil is also notable taphonomically as the individual is partially three-dimensionally preserved, interred in sand and deformed by syndepositional 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 Visean 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.

Acknowledgements

Greg Edgecombe, an anonymous reviewer and subject editor Xiaoya Ma are thanked for their reviews of this paper. The Howick Estate Office Katy Barrett and Jonathan Larwood (Natural Environment Research Council (NE)/T000813/1). APS was funded by a studentship from the Natural Environment Research Council (NE/L002507/1). JWS gratefully acknowledges the Russian Government for a subsidy allocated to Kazan Federal University for the state assignment no. 5.2192.2017/4.6.

Data availability

All data generated or analysed during this study are included in this published article (and its Supplementary Information files).

Scientific editing by Xiaoya Ma

References

Allport, H.A., Davies, N.S., Shillito, A.P., Mitchell, E.G. and Herron, S.T. 2021. Non-palimpsested crowded Skolithos ichnofabrics in a Carboniferous tidal rhythmites: disentangling ecological signatures from the spatio-temporal bias of outcrop. Sedimentology, https://doi.org/10.1111/sed.12947

Almond, J.E. 1985. Les Arthropleurides du Stéphanien de Montceau-les-Mines, France. Bulletin de la Société d’Histoire Naturelle d’Autun, 115, 59–60.

Anderson, L.I., Dunlop, J.A., Horrocks, C.A., Winkelmann, H.M. and Eagar, R.M.C. 1997. Exceptionally preserved fossils from Bickershaw, Lancashire UK (Upper Carboniferous, Westphalian A (Langsettian)). Geological Journal, 32, 197–210, https://doi.org/10.1002/(SICI)1099-1349(199709)32:3<197::AID-GJ739>3.0.CO;2-6

Andrieu, K. 1913. Weitere über das carbonisize Arthrostraken-Genus Arthropleura Jordaan. Palaeontographica, 60, 295–310.

Bailey, L.W. 1902. Report Upon the Carboniferous System of New Brunswick with Special Reference to Workable Coal. Geological Survey of Canada, No. 799; in Annual Report, Volume XIII, 1900 Geological Survey of Canada, No. 830 (1903), 1M–38M.

Bashforth, A.R., DiMichele, W., Eble, C.F., Falcon-Lang, H., Looy, C. and Lucas, S.G. 2021. The environmental implications of upper Paleozoic plant-fossil assemblages with mixtures of wetland and drought-tolerant taxa in tropical Pangea. Geobios, 68, 1–15, https://doi.org/10.1016/j.geobios.2021.04.002

Bercovitz, K. and Warburg, M.R. 1985 Developmental patterns in two populations of the millipede Archispirostreptus syriacus (De Saussure) in Israel (Diplodopa). Bijdragen tot de Dierkunde, 55, 37–46.

Berner, R.A. 2006. GEOCARBSULF: a combined model for Phanerozoic atmospheric O2 and CO2. Geochimica et Cosmochimica Acta, 70, 5635–5664, https://doi.org/10.1016/j.gca.2005.11.032

Booth, M.G., Underhill, J.R., Gardiner, A. and McLean, D. 2020. Sedimentary and tectonic controls on Lower Carboniferous (Visean) mixed carbonate–siliciclastic deposition in NE England and the Southern North Sea: implications for reservoir architecture. Petroleum Geoscience, 26, 204–231, https://doi.org/10.1144/petgeo2019-101

Boule M. 1893. Sur les débris d’Arthropleure trouvés en France. Bulletin de la Societe de l’Industrie Minérale, 7, 619–638.

Boyd, C. and McIlroy, D. 2016. Three-dimensional morphology and palaeobiology of the trace fossil Dactyloptus jordesi nov. isp. from the Carboniferous of England. Geobios, 49, 257–264, https://doi.org/10.1016/j.geobios.2016.05.004

Boyd, C. and McIlroy, D. 2017. Three-dimensional morphology of Beaconites capronus from Northeast England. Ichnos, 24, 250–258, https://doi.org/10.1080/10420409.2017.1282862

Boyd, C. and McIlroy, D. 2018. The morphology and mode of formation of Neurotonia, a new species from the Carboniferous of northern England. Paläontologische Zeitschrift, 92, 179–190, https://doi.org/10.1002/ps.12542-017-0379-7

Braddy, S.J., Poschmann, M. and Tettie O.E. 2008. Giant claw reveals the largest everarthropod. Biology Letters, 4, 106–109, https://doi.org/10.1098/rsbl.2007.0491

Mississippian Arthropleura from Northumberland
