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1 **A lower Carboniferous (Visean) tetrapod trackway represents the earliest record of an**
2 **edopoid amphibian from the UK**

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10

11 **Abstract:** The ichnological fossil record has previously provided key evidence for the
12 diversification of land vertebrates (tetrapods) during the Carboniferous Period, following the
13 invasion of the land. Within the United Kingdom, tetrapod ichnofossils from the late
14 Carboniferous of the English Midlands are well documented, but few such fossils are known
15 from earlier in the period. We present a rare ichnological insight into early Carboniferous
16 tetrapod diversification in the United Kingdom based on a Visean-aged specimen collected
17 from an an intertributary trough palaeoenvironment at Hardraw Scar, Wensleydale, North
18 Yorkshire. This specimen represents the stratigraphically oldest known tetrapod trackway
19 from the UK. We refer this specimen to *Palaeosauropus* sp., providing the earliest known
20 occurrence of an edopoid temnospondyl. Supplementing the sparse record of contemporary
21 body fossils from the early Carboniferous, this provides further insights into the
22 diversification of temnospondyl amphibians across Euramerica.

23 **Supplementary material:** A 3D model of the plaster cast produced from the trackway
24 specimen is available at <https://doi.org/10.5519/0022377> and a lower resolution version is
25 available on Sketchfab (<https://skfb.ly/6OAxR>).

26 The Carboniferous Period was a key interval in the diversification of land vertebrates
27 (tetrapods). Following the appearance of the first tetrapods in the Late Devonian (Clack
28 2012), the group underwent a substantial diversification in the early part of the Carboniferous
29 and was well established across Euramerica by the Tournaisian–Visean on the basis of body
30 fossil remains of several tetrapods from Nova Scotia (Clack & Carroll 2000; Anderson *et al.*
31 2015) and Scotland (Smithson *et al.* 2012; Clack *et al.* 2016; Pardo *et al.* 2017; Otoo *et al.*
32 2018). Tetrapod trackways have been known for over a century from the Horton Bluff
33 Formation (Tournaisian) of Nova Scotia. The diversity of footprints and trackways from this
34 locality indicate a locally diverse population of terrestrial tetrapods of varying size, including
35 larger amphibians than are known from the very incomplete bone record (Sarjeant &
36 Mossman 1978; Clack & Carroll 2000; Mansky & Lucas 2013, and references therein). In the
37 UK, tetrapod ichnofossils (footprints and trackways) are relatively well known from the late
38 Carboniferous (Moscovian–Kasimovian) of the English Midlands (Haubold & Sarjeant 1973;
39 Tucker 2003; Tucker & Smith 2004; Meade *et al.* 2016), with isolated examples elsewhere
40 (Milner 1994), and have provided important insights into faunal turnover towards the end of
41 the Carboniferous. However, early Carboniferous tetrapod footprints are much scarcer, and
42 the only ones to receive detailed study are several poorly preserved examples from the
43 Serpukhovian of Northumberland (Scarboro & Tucker 1995).

44 Here, we describe a tetrapod trackway from the Visean stage of the early Carboniferous, the
45 stratigraphically oldest known tetrapod footprint occurrence from the UK. This trackway
46 provides a rare ichnological insight into tetrapod diversification in the early Carboniferous of
47 Europe. The presence of ‘*Megapezia*’ footprints in the Hardraw Sandstone of Yorkshire was
48 previously noted as a personal communication from G. A. L. Johnson in Scarboro & Tucker
49 (1995), but no further information has previously been published.

50

51 **Geological context**

52 Hardraw Scar (= Hardrow Scar), Wensleydale, North Yorkshire, is a limestone gorge through
53 which Hardraw Beck flows, with the Hardraw Force waterfall [SD 86959 91599] forming a
54 well-known landmark (Fig. 1). Hardraw Scar exposes the Hardraw Scar cyclothem
55 (cyclothem 3; Fig. 2), one of eight major cyclothem sequences comprising the Alston
56 Formation of the Yoredale Group. The Alston Formation is dated to the Brigantian regional
57 substage of the Visean stage (Waters *et al.* 2007), based on biostratigraphic data including
58 ammonoids, algae and foraminifera (Cózar & Somerville 2004). The Hardraw Scar
59 cyclothem sequence ranges in thickness from 6.4 m in Greenhow, North Yorkshire (36 km
60 southeast of Hardraw Scar), to a maximum of 28 m in a section at Birkett Cutting, Cumbria
61 (20 km northwest of Hardraw Scar; Dunham & Wilson 1985). Within this larger cyclothem,
62 four minor cyclothems are preserved, though only three are consistently present within the
63 Wensleydale vicinity (Moore 1959; Fig. 2).

64 The characteristic Yoredale cyclothem succession contains basal limestones (fine grained,
65 grey biosparite) occasionally displaying grain size gradation upwards, with coral beds

66 towards the base and algal limestones forming the tops of major units (Moore 1959). The
67 limestones transition upwards into calcareous shales and mudstones, the former being richly
68 fossiliferous at the base and the latter often alternates with thin sandstone units towards the
69 top. Succeeding these are flaggy sandstones divided into micaceous laminated units and
70 massive unidirectionally-rippled units, massive sandstones containing one or two foresets,
71 seatearths of ganister sandstone and fireclay, topped by thin and impersistent coals. The
72 sequence is interpreted as representing a mature river delta system entering a shallow
73 epicontinental sea (the Euramerican Seaway located north of the equator) with limestone
74 deposition, regressing through pro-delta shales, delta-front silts, and interdistributary trough
75 sandstones, before becoming emergent leading to the formation of seatearths and temporary
76 marshes (Tucker 2003). These sequences may be cut by thick channel sandstones, deposited
77 by freshwater rivers oriented from north to south.

78 The specimen was obtained from one of two micaceous sandstone units in the succession
79 (Fig. 2), comprised of fine-grained quartz containing thin laminae of muscovite mica, though
80 the collector did not note from which minor cyclothem it was acquired.

81 Fragmentary tetrapod body fossil material has also been briefly reported from the Yoredale
82 Series of Wensleydale, Yorkshire (Horne 1874), but has not been described. These specimens
83 are currently housed at the Yorkshire Museum, York, but their tetrapod affinities are unclear
84 (TR Smithson pers. comm. 2019). An undescribed fragment of tetrapod skull bone from
85 Wensleydale is present in the collections of the Museum of Natural Sciences in Brussels,
86 Belgium (TR Smithson pers. comm. 2019).

87

88 **Methods**

89 The original specimen is on permanent display in the Natural History Museum (NHMUK)
90 exhibition ‘*From the Beginning*’. As a result, a 3D model of a plaster cast was made using a
91 Faro Edge scanner and the data processed using Geomagnetic Wrap. This model has been
92 made available as an .obj file at <https://doi.org/10.5519/0022377>, and a lower resolution
93 version is available on Sketchfab (<https://skfb.ly/6OAxR>).

94

95 **Systematic ichnology**

96

Ichnogenus

97

***Palaeosauropus* sp.**

98

(=*Megapezia* sp.)

99 *Locality*: Hardraw Scar, near Hardraw, Hawes, Wensleydale, North Yorkshire, UK.

100

101 *Horizon*: Hardraw Scar Limestone, Alston Formation, Yoredale Group, Brigantian substage,
102 late Viséan, lower Carboniferous (Mississippian).

103

104 *Referred material:* NHMUK PV R 9372. A sandstone slab collected by S. J. Maude in 1977
105 from fallen material at the base of Hardraw Force waterfall and donated to the Natural
106 History Museum by the collector in 1978.

107

108 *Description:* The slab is a 3.5 cm thick bed of well-cemented, fine-grained, light grey
109 micaceous sandstone, weathered to a buff colour along the bedding plane, with dimensions of
110 45 cm by 40 cm. Faint ripple cross laminations are present on the uppermost part of the bed,
111 whilst the lower part is massive.

112

113 Five prints are preserved, all primarily as convex hyporelief (Figs. 3–5). They appear to
114 represent a left manus print ('a' in Fig. 3; Figs. 4A, 5A), left pes print ('b' in Fig. 3; Figs. 4B,
115 5B), right manus print ('d' in Fig. 3; Figs. 4D, 5D) and two right pes prints ('c' and 'e' in Fig.
116 3; Figs. 4C, E, 5C, E).

117

118 Manus prints are widely separated from the pes prints, being positioned closer to and inclined
119 towards the midline. Print 'a' is the best preserved of the two (Figs. 4A, 5A), and has a
120 maximum anteroposterior length of 61 mm from back of the sole impression to the tip of
121 preserved digit II. The width of the print rim immediately posterior to the bases of the digits
122 is 45 mm. Only four digits are discernible on manus print 'a', with I–III being similar in
123 length, whilst IV is the longest and characteristically curved along its length. Digit I is
124 directed slightly inwards whilst digits II–IV are directed laterally, away from the inferred
125 midline. Behind the digits, the sole is preserved as a concavity on the surface of the slab.
126 Print 'd' has three clearly impressed broad digits, interpreted as digits I–III (Figs. 4D, 5D).
127 By contrast with print 'a', digit IV is incompletely impressed and its curved distal portion is
128 not preserved. In this print the sole is a concavity. The length of print 'd' is 69 mm and the
129 width of the rim immediately posterior to the bases of the digits is 50 mm.

130

131 Pes prints are less well impressed than manus prints. In 'b' digits I–V are poorly impressed
132 and difficult to distinguish (Figs. 4B, 5B). Although digit V appears at first sight to be
133 characteristically curved like the outermost digit of manus print 'a', this seems to be an
134 artefact of another impression (potentially an invertebrate trace) being preserved adjacent to
135 the print, with digit V being relatively short. Print 'b' is 62 mm in length from back of the
136 sole to the tip of preserved digit II and the width of the footprint rim immediately posterior to
137 the bases of the digits is 48 mm (Figs. 4B, 5B). The least well-preserved pes is print 'c' (Figs.
138 4C, 5C), measuring a length of 67 mm, with only two digits well impressed (interpreted as
139 digits III and IV). Print 'e' is the best preserved with apparent impressions of five digits
140 (Figs. 4E, 5E); I and II are closely appressed and may only be subtly distinguished from one
141 another at their tips. These digits are directed anteromedially towards the midline, with digit
142 III also directed slightly medially, whereas digit IV is anterolaterally directed. The print has a
143 length of 67 mm and the width of the footprint rim immediately posterior to the bases of the
144 digits is 50 mm, with the sole preserved entirely as hyporelief. Stride for the pes (tip of digit
145 3 on print 'c' to tip of digit 3 on print 'e') is 108 mm.

146

147 The prints form a trackway consisting of manus-pes from the right side (prints ‘a’ and ‘b’)
148 and pes-manus-pes prints from the left side (prints ‘c’, ‘d’ and ‘e’). This reveals one distinct
149 manus-pes pair of ‘c’ and ‘d’, whilst the corresponding pes to ‘a’ is off the slab and matching
150 manus prints for pes prints ‘b’ and ‘e’ are also absent from the specimen. We therefore infer a
151 gently left-curving midline through the specimen.

152

153 **Invertebrate traces**

154 In association with the footprints is a high density, moderate diversity assemblage of
155 invertebrate trace fossils from 11 different ichnogenera (Fig. 6). These trace fossils evidence
156 a range of behaviours: surficial grazing (*Gordia*), locomotion (*Archaeonassa*, *Cruziana*,
157 *Didymaulichnus*, *Diplopodichnus*, *Herpystezoum*, *Planolites*), vertical burrowing
158 (*Cylindricum*, *Arenicolites*), and periods of stationary non-activity both at and below the
159 surface (*Rusophycus*, *Lockeia*). The causal invertebrate tracemaker community was
160 comprised dominantly of small arthropods, annelids and molluscs.

161 The most prominent invertebrate trace present, a 10 mm-wide ‘groove’, is a transitional form
162 between *Archaeonassa* and *Herpystezoum*, revealing that some of the invertebrate activity
163 predated the emplacement of the footprints, as one such footprint overprints this trail. This
164 apparent sequence of events precludes association of this trace with the footprints as a
165 vertebrate ‘tail drag’, and successive sections of the trace occurring in positive and negative
166 relief suggests instead that the trace is an invertebrate trail formed through a combination of
167 infaunal and epifaunal locomotion. The transitions in relief are obscured by small mounds of
168 sediment, recording the disturbance of the substrate at the entrances to the burrow, produced
169 through active excavation of the burrow rather than purely compaction, implying an
170 arthropod tracemaker (Dorgan 2015).

171 The remaining invertebrate ichnotaxa observed upon the Hardraw specimen are less laterally
172 extensive and, despite the overall abundance of traces upon the surface, each typically occurs
173 either once or twice within the specimen (Fig. 6). These are identified as follows:
174 *Arenicolites* – a transverse section through paired burrows with no intervening spreite;
175 *Cruziana* – an elongate bilobed trail with putative striations oblique to the midline;
176 *Cylindricum* – a sub-round section through a simple vertical burrow; *Didymaulichnus* – short,
177 closely spaced, parallel paired scratch marks; *Diplopodichnus* – elongate parallel paired
178 grooves with no disturbance to the intervening sediment; *Gordia* – narrow, meandering
179 grooves which self-cross-cut; *Lockeia* – an almond shaped horizontal burrow; *Planolites* – a
180 simple, cylindrical horizontal burrow with no evidence for a distinct lining; *Rusophycus* – a
181 short, symmetrical trace comprised of two kidney-shaped lobes.

182 The high density of invertebrate traces present on the bedding surface, with constituent
183 grazing trails and resting traces, implies an extended period of sedimentary stasis during
184 which the substrate was sporadically inhabited (Davies *et al.* 2017; Davies & Shillito, 2018).

185

186 **Discussion**

187 The Hardraw footprints were originally identified as cf. *Megapezia* sp., based on similarities
188 to the ichnotaxon *Megapezia pineoi* Matthew 1903, by one of the current authors (ACM) in
189 1978 when the specimen was accessioned at the Natural History Museum. *Megapezia pineoi*
190 was figured by Matthew (1903, p. 100, figs. 2a, b) and reviewed by Sarjeant & Mossman
191 (1978, p. 291, fig. 4) as bearing a four-digit pes and five-digit manus, although Matthew
192 expressed some doubts regarding his determinations of manus and pes prints. Sarjeant &
193 Mossman (1978) included these comments in a historical overview of the Carboniferous
194 Nova Scotia trackways that were first discovered in 1841. These authors also noted that
195 Matthew (1903) gave no precise locality or horizon in his original work but *Megapezia* was
196 demonstrably from the Tournaisian of Horton Bluff in Nova Scotia. This data contradicts
197 Haubold (1970), who documented the locality as Mabou Group Namurian A (=
198 Serpukhovian). Haubold classified the taxon formally in the temnospondyl amphibian
199 superfamily Edopoidea Romer 1945. He described the *Megapezia pineoi* prints on the basis
200 of outline scaled drawings (Haubold 1970, p. 94, fig. 4E) as having a step angle of 106°, a
201 tetradactyl hand with four sub-parallel toes where digit IV is strongly splayed laterally, and a
202 large sole. The five-toed pes bears slender digits arranged in a 105° arc and a small
203 proximolaterally-extended sole. Haubold (1970) also noted that *Megapezia* was generally
204 similar to *Palaeosauropus* sp. indet. from Horton Bluff, in which he included *Sauropus*
205 *antiquior* Dawson 1882 as a synonym, now suggested as a nomen dubium by Lucas *et al.*
206 (2010) since the track was not illustrated by Dawson and the type specimen is lost. The
207 specimen repository for the holotype of *Megapezia pineoi* was noted as the Geological
208 Survey of Canada (GSC) by Haubold (1970) but no record of the specimen is held in the
209 GSC collections.

210 Vertebrate ichnofossils from the Tournaisian Horton Bluff Formation have been well known
211 since their discovery by W. E. Logan in 1841 (Sarjeant & Mossman 1978) and have been
212 studied with increasing frequency since the 1970s. Abundant trackway discoveries from the
213 Blue Beach locality at Horton Bluff are currently recognised as representing the earliest
214 diverse community of pentadactyl tetrapods, and the first ones capable of fully terrestrial
215 locomotion (Mansky & Lucas 2013, and references therein).

216 The trackmaker of *Palaeosauropus* was considered to be a temnospondyl amphibian by
217 Lucas *et al.* (2010), with the Blue Beach vertebrate ichnological site preserving hundreds of
218 trackways extensively reviewed by Mansky & Lucas (2013). Ichnotaxon morphotypes from
219 Blue Beach include *Palaeosauropus* as the commonest track type, displaying relatively large
220 prints and a digital formula (four-digit manus and five-digit pes) matching the temnospondyl
221 skeleton and representing the basal condition of the clade (Ruta *et al.* 2003). Mansky &
222 Lucas (2013) noted that *Palaeosauropus* prints could be distinguished by several traits: (1)
223 tetradactyl manus and a larger pentadactyl pes; (2) digits are short and broad; (3) the sole of
224 the foot is wider than long; (4) the tracks are commonly overstepped; and (5) the trackways
225 are relatively wide and often show median drags. Furthermore, they regarded *Megapezia*
226 *pineoi* Matthew 1903 (*Sauropus antiquior* of Dawson 1882) as a probable synonym of

227 *Palaeosauropus* sp., a conclusion also reached by Haubold (1970). It follows that having
228 initially identified the Hardraw specimen as cf. *Megapezia* sp., we now consider it referable
229 to *Palaeosauropus* sp.

230 *Palaeosauropus* is also known from Visean trackways in the Mauch Chunk Formation near
231 Pottsville, Pennsylvania (Fillmore *et al.* 2009). Lucas *et al.* (2010) documented wide
232 variation in the print morphology of *Palaeosauropus primaevus* depending on epirelief and
233 substrate variation. On the basis of footprint length the trackmaker was estimated to have
234 been 500–750 mm long, half the length of *Eryops* from the Permian of Texas (Lucas *et al.*
235 2010). The Mauch Chunk tracks and footprints show a very similar morphology to those of
236 *Palaeosauropus* from the Tournaisian at Blue Beach, Nova Scotia (Mansky & Lucas 2013).

237 An edopoid temnospondyl is the suggested trackmaker, based on the morphological features
238 described in detail by Mansky & Lucas (2013) from the Tournaisian sites in Nova Scotia.
239 Edopoid body fossils first appear in the Bashkirian and the record extends to the late
240 Permian. They were large long-snouted crocodile-like animals up to two metres or more in
241 length and are known from both cranial and incomplete postcranial material (Schoch &
242 Milner 2014, and references therein). *Procochleosaurus jarrowensis* is the earliest record of
243 an edopoid body fossil taxon from the Bashkirian locality at Jarrow Colliery, Kilkenny,
244 Ireland (Sequeira 1996). However, a representative of a more derived clade, the
245 Eutemnospondyli Schoch 2013, is also known from the Visean in the UK. *Balanerpeton*
246 *woodi* was described from Visean freshwater limestones at East Kirkton Quarry near
247 Bathgate, West Lothian, Scotland (Milner & Sequeira 1994). A recent cladistic analysis of
248 temnospondyl evolution mapped on a gross stratigraphical scale predicted an evolutionary
249 origin of the basal radiation of temnospondyls in the Tournaisian (Schoch 2013). Tournaisian
250 trackway sites in Nova Scotia are evidence that the early radiation of temnospondyls was
251 well established. The Visean track from Hardraw represents the earliest British record of the
252 basal edopoid clade, and the occurrence of contemporary body fossils in the UK provides
253 further evidence of the earliest Carboniferous diversification of temnospondyls across
254 Euramerica.

255 A semi-terrestrial mode of life is likely for edopoids, walking terrestrially and probably
256 feeding on land but returning to water to breed. This is consistent with the trackway being
257 preserved underwater or in well-saturated sediment, these being micaceous sandstones
258 indicative of an interdistributary trough palaeoenvironment (Moore 1959). Within the
259 Hardraw Scar cyclothem, interdistributary areas are characterised by shallow waters being
260 quiet or even stagnant environments. This supports the period of sedimentary stasis identified
261 to facilitate the diversity of modes of life apparent for the invertebrate assemblage of
262 arthropods, annelids and molluscs. Evidence of surficial grazing and shallow burrows support
263 the oxygenated environment of low water depths, or partial exposure with moistening of
264 sediment within the interdistributary trough setting.

265

266 **Conclusion**

267 Offering an additional ichnological insight into tetrapod diversification across Euramerica in
268 the lower Carboniferous, this specimen establishes the earliest known occurrence of the
269 edopoid clade in Britain. The presence of semi-terrestrial forms aligns with the environmental
270 transitions occurring at this time as the palaeoenvironment in the region consisted of shallow
271 epicontinental seas and associated deltaic systems, depositing the sandstone within which the
272 Hardraw tracks are preserved. The ichnological record supplements body fossil data and
273 illustrates the contemporary Visean records of temnospondyls across Euramerica. Combining
274 both approaches contributes to a more comprehensive understanding of palaeoenvironments
275 and evolutionary patterns.

276

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282

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376 **Figure captions**

377 **Fig. 1.** (a) Geographic setting of Hardraw Force within Britain. (b) Location of Hardraw
378 Scar, site of specimen discovery, though the exact position is unknown.

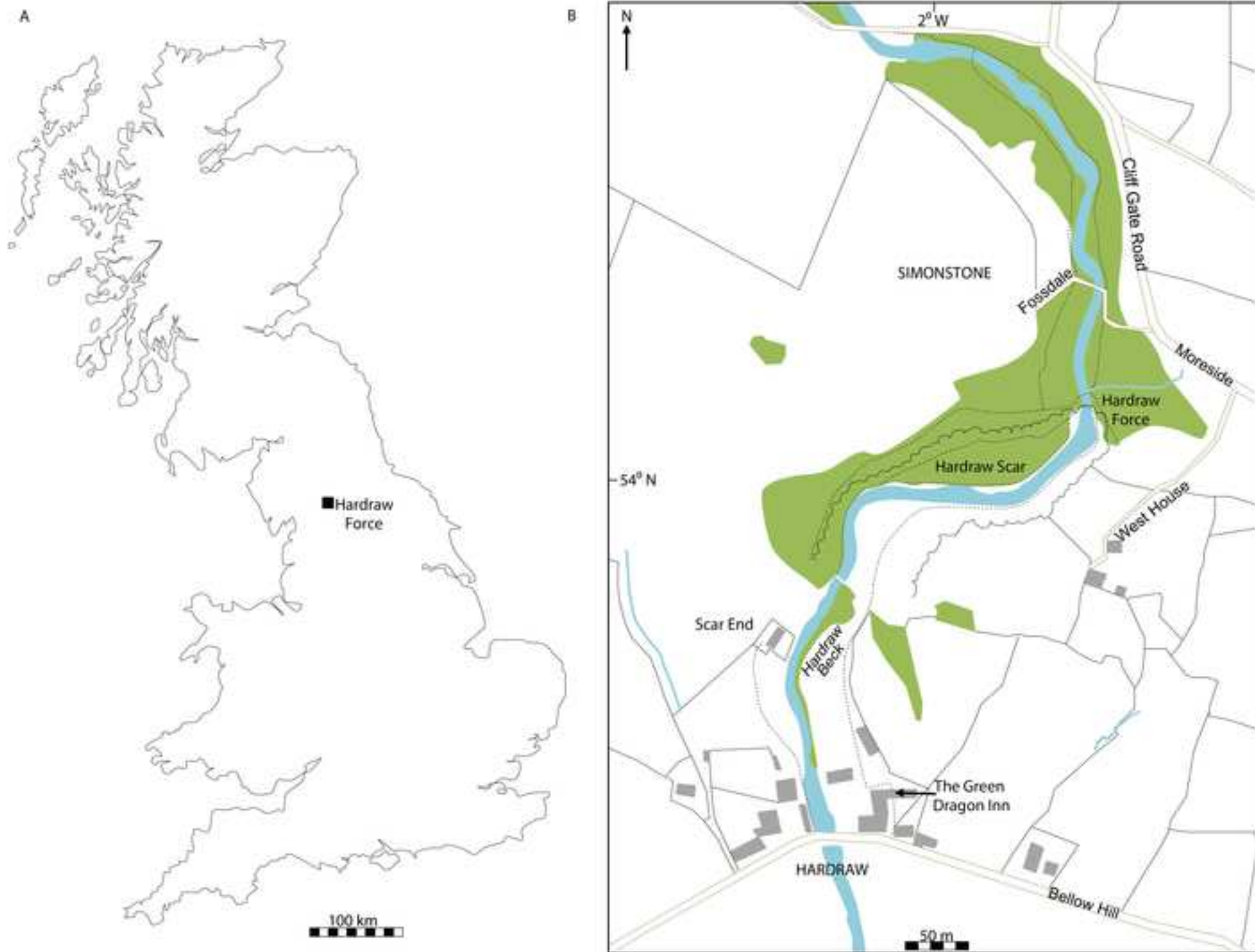
379 **Fig. 2.** Lithostratigraphy of the Hardraw Force area, with an expanded view of the Hardraw
380 Scar cyclothem (cyclothem 3 of the 8 comprising the Alston Formation). Three minor
381 cyclothems (i–iii) comprise the Hardraw Scar cyclothem in the Wensleydale area, within
382 which are two micaceous sandstone units as potential footprint-bearing horizons.

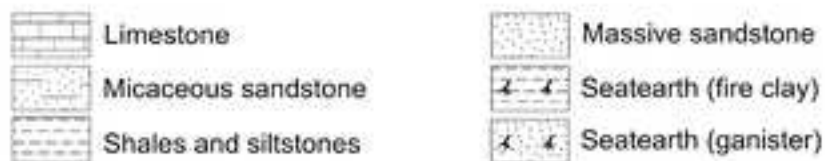
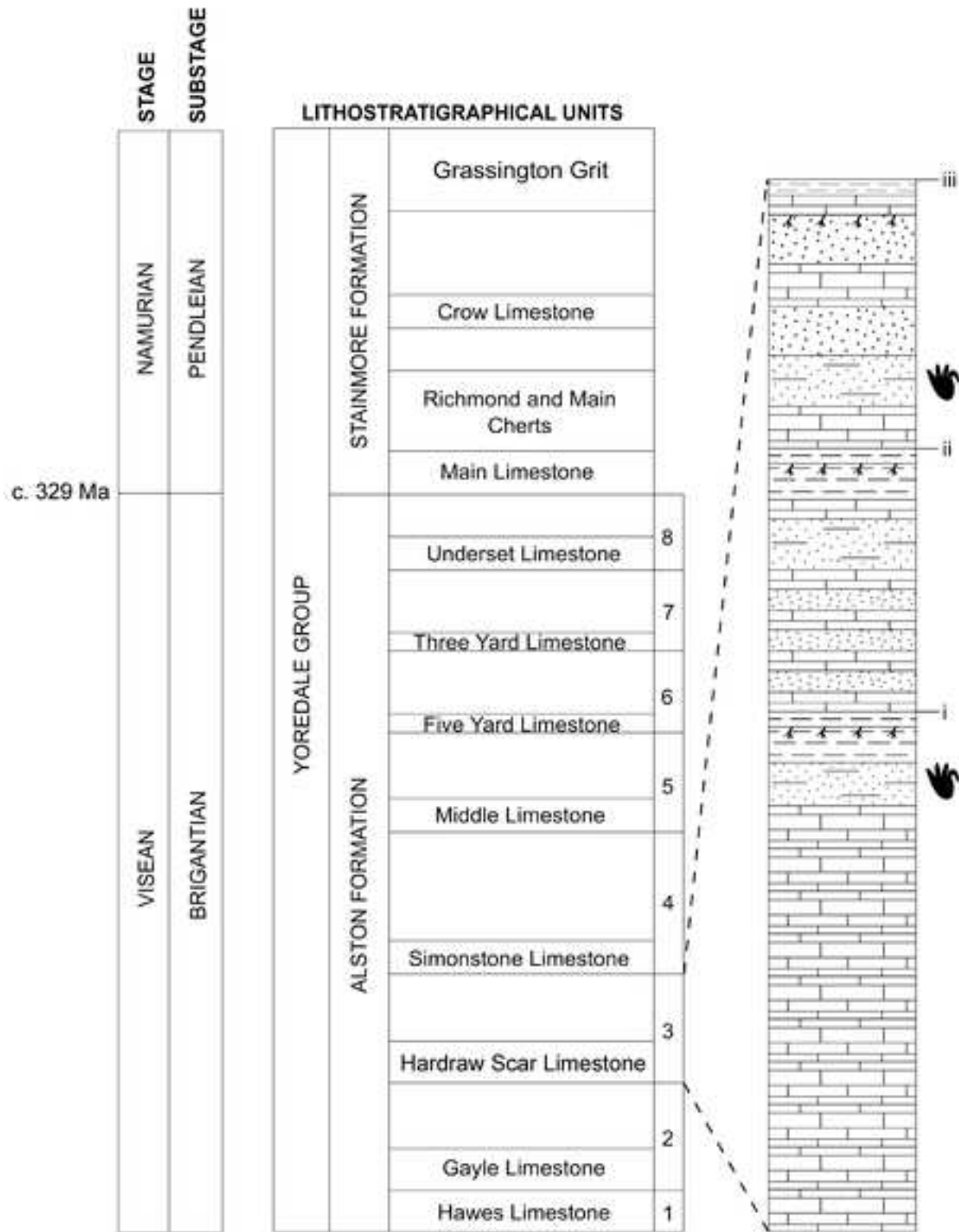
383 **Fig. 3.** NHMUK PV R 9372, *Palaeosauropus* sp. (a) Colour photograph of original
384 sandstone slab and tracks. (b) 3D digital render of the plaster cast of the sandstone slab and
385 tracks. (c) Black and white photograph of original sandstone slab and tracks. In (b), left
386 manus and pes prints are denoted a and b respectively, the right pes prints c and e, with print
387 d being the right manus. The indented area left of print e is identified as damage to the
388 specimen rather than a footprint impression.

389 **Fig. 4.** NHMUK PV R 9372, *Palaeosauropus* sp. Photographs of prints ‘a’ to ‘e’ (see Figure
390 3), representing one manus-pes pair (‘c’-‘d’) and three single manus (‘a’) or pes (‘b’ and ‘e’)
391 prints with their counterparts not preserved on the slab.

392 **Fig. 5.** NHMUK PV R 9372, *Palaeosauropus* sp. Line drawings of prints ‘a’ to ‘e’ (see
393 Figure 3).

394 **Fig. 6.** NHMUK PV R 9372. Positions of invertebrate traces associated with the specimen,
395 including eleven infaunal and epifaunal ichnogenera: 1) *Gordia*, 2) *Didymaulichnus*, 3)
396 *Cruziana*, 4) *Rusophycus*, 5) *Lockeia*, 6) *Diplopodichnus*, 7) *Arenicolites*, 8) *Cylindricum*, 9)
397 *Planolites*, 10) *Archaeonassa*, 11) *Herpystezoum*.





Potential footprint-bearing horizon

