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

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

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

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

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

Geological context

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

The characteristic Yoredale cyclothem succession contains basal limestones (fine grained, grey biosparite) occasionally displaying grain size gradation upwards, with coral beds towards the base and algal limestones forming the tops of major units (Moore 1959). The limestones transition upwards into calcareous shales and mudstones, the former being richly fossiliferous at the base and the latter often alternates with thin sandstone units towards the top. Succeeding these are flaggy sandstones divided into micaceous laminated units and massive unidirectionally-rippled units, massive sandstones containing one or two foresets, seatearths of ganister sandstone and fireclay, topped by thin and impersistent coals. The sequence is interpreted as representing a mature river delta system entering a shallow epicontinental sea (the Euramerican Seaway located north of the equator) with limestone deposition, regressing through pro-delta shales, delta-front silts, and interdistributary trough sandstones, before becoming emergent leading to the formation of seatearths and temporary marshes (Tucker 2003). These sequences may be cut by thick channel sandstones, deposited by freshwater rivers oriented from north to south.

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

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

Methods

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

Systematic ichnology

Ichnogenus
Palaeosauropus sp.
(=*Megapezia* sp.)

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

Horizon: Hardraw Scar Limestone, Alston Formation, Yoredale Group, Brigantian substage, late Visean, lower Carboniferous (Mississippian).

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

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

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

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

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

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

Invertebrate traces

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

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

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

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

Discussion

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

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

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

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

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

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

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

Conclusion

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

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Figure captions

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

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

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

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

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

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

figure 1

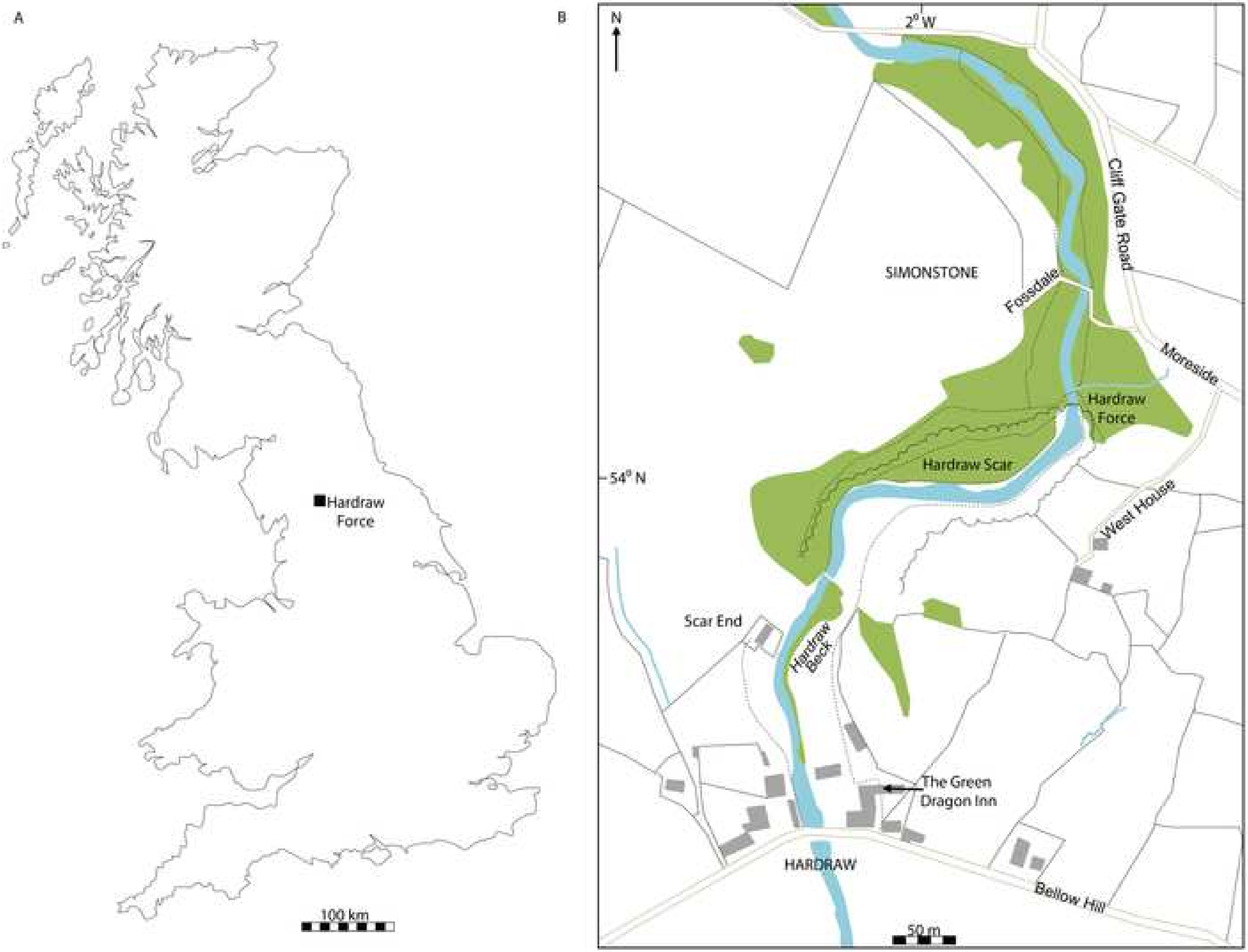

A
Hardraw Force
100 km
B
N
2° W
54° N
SIMONSTONE
Fossdale
Cliff Gate Road
Moreside
Hardraw Force
Hardraw Scar
West House
Scar End
Hardraw Beck
The Green Dragon Inn
HARDRAW
Bellow Hill
50 m

figure 2

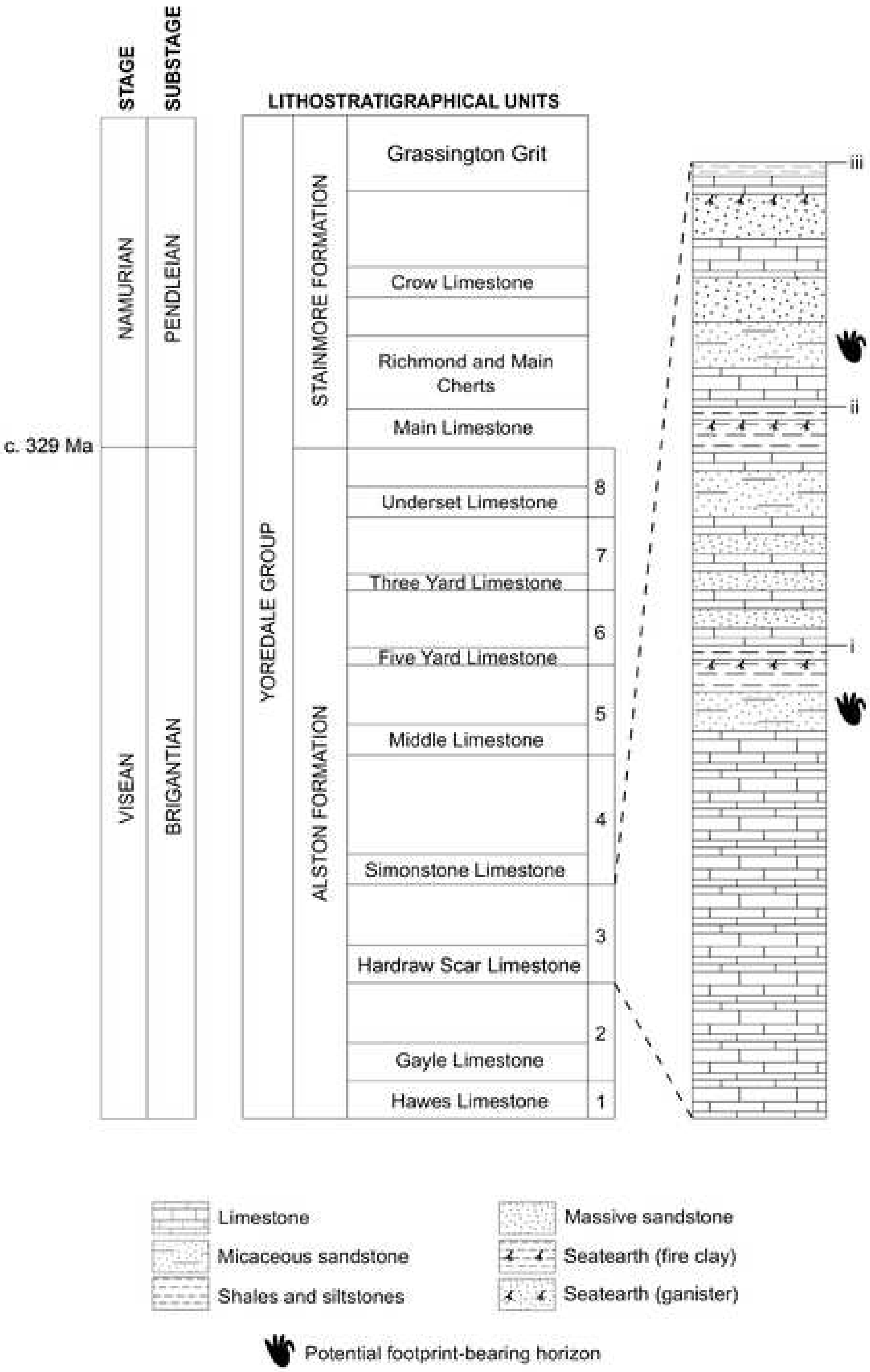
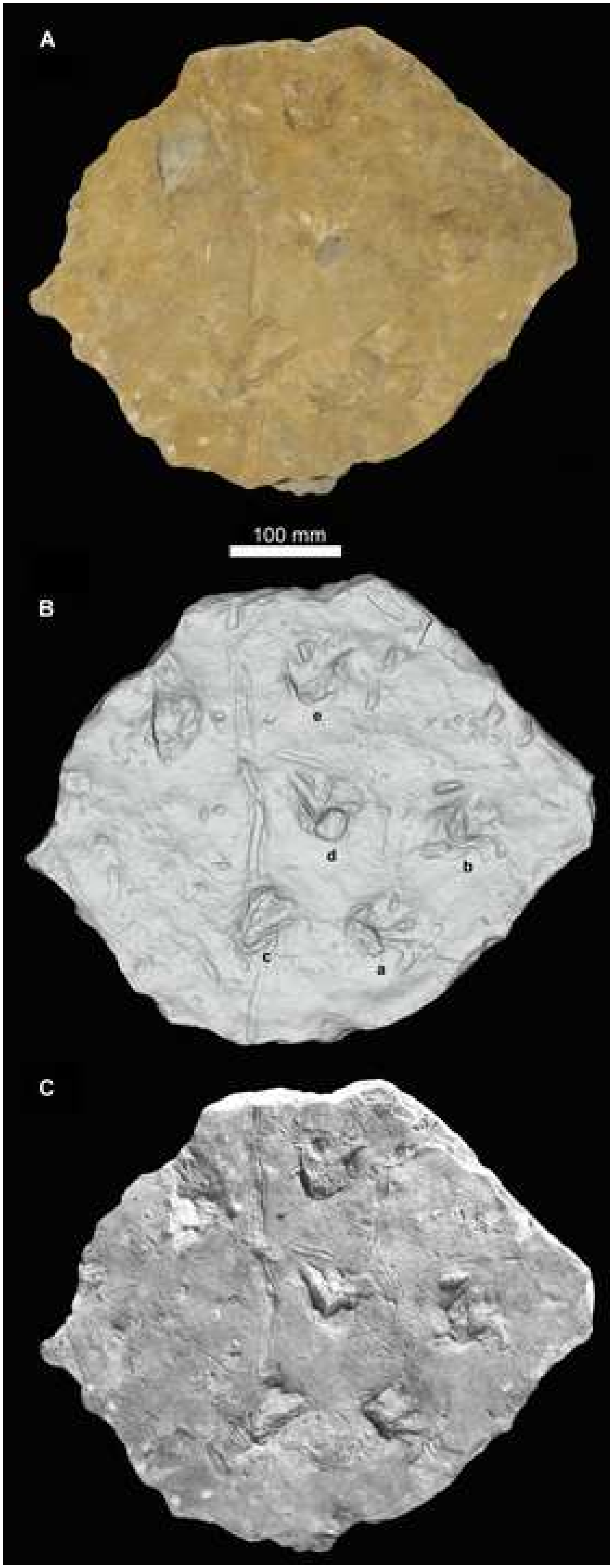

STAGE
SUBSTAGE
LITHOSTRATIGRAPHICAL UNITS
NAMURIAN
PENDLEIAN
VISEAN
BRIGANTIAN
c. 329 Ma
YOREDALE GROUP
STAINMORE FORMATION
ALSTON FORMATION
Grassington Grit
Crow Limestone
Richmond and Main Cherts
Main Limestone
Underset Limestone
Three Yard Limestone
Five Yard Limestone
Middle Limestone
Simonstone Limestone
Hardraw Scar Limestone
Gayle Limestone
Hawes Limestone
8
7
6
5
4
3
2
1
iii
ii
i
Limestone
Micaceous sandstone
Shales and siltstones
Massive sandstone
Seatearth (fire clay)
Seatearth (ganister)
Potential footprint-bearing horizon

figure 3



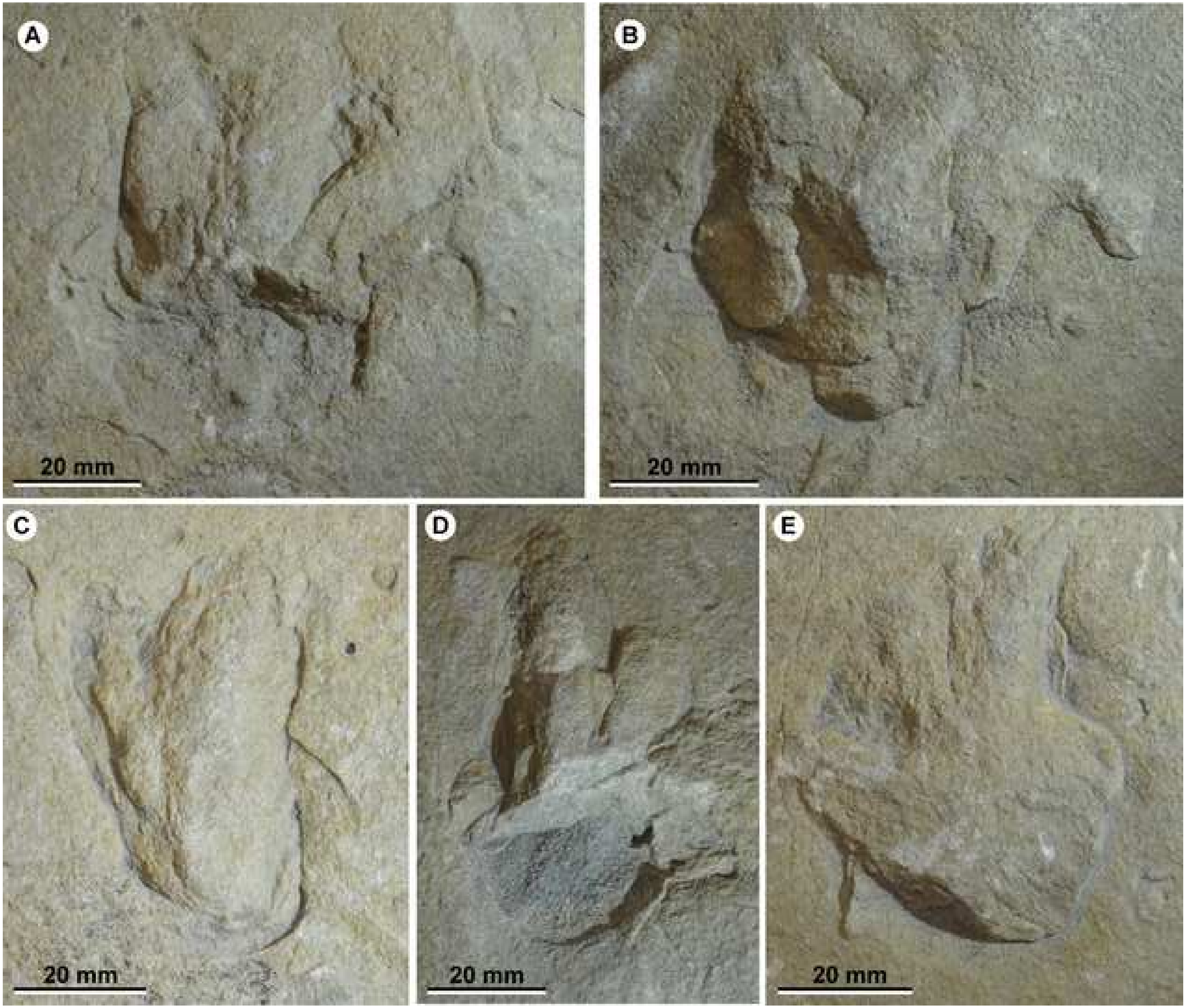

A
B
C
D
E
20 mm
20 mm
20 mm
20 mm
20 mm

figure 5

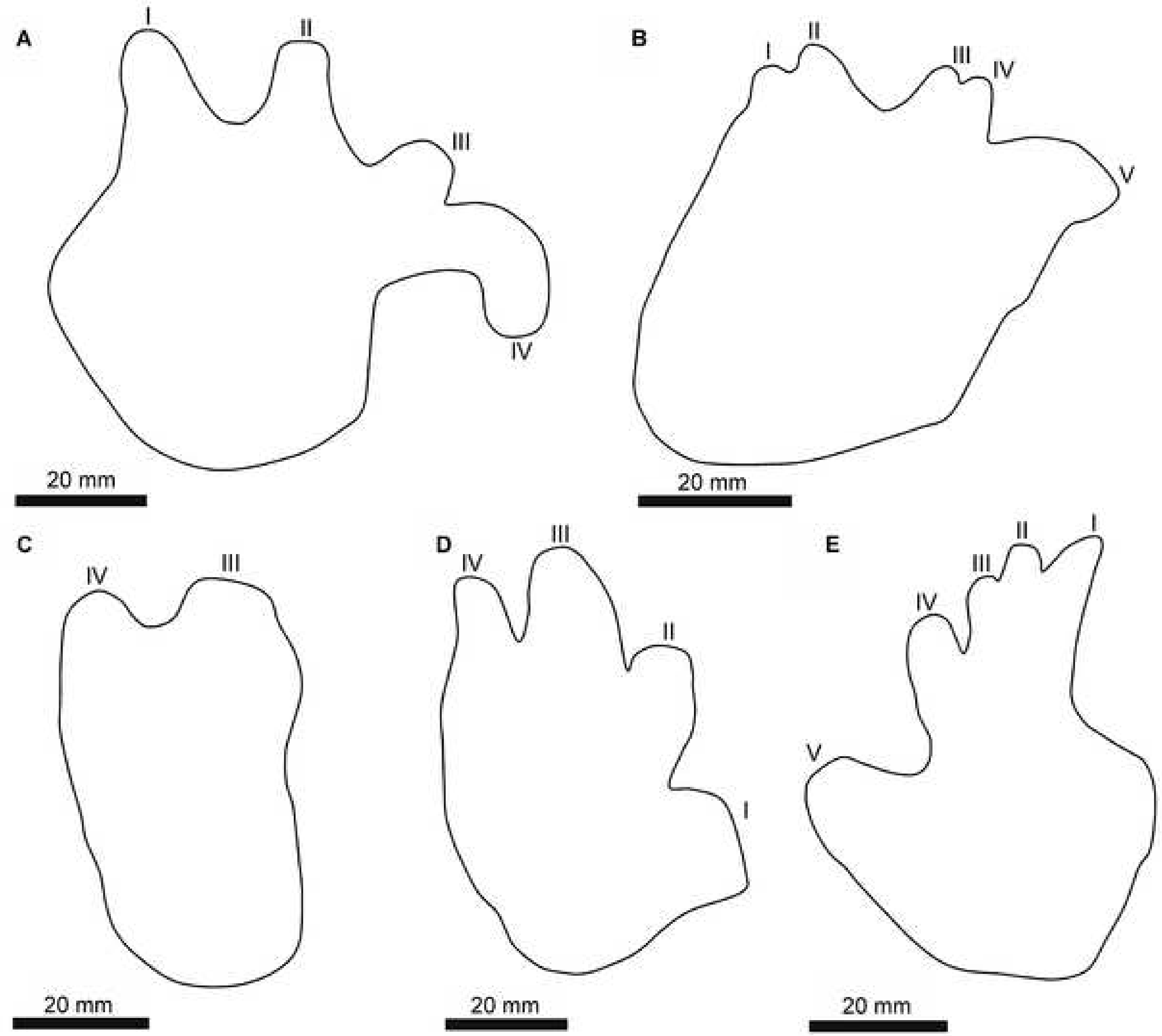

A
I
II
III
IV
20 mm
B
I
II
III
IV
V
20 mm
C
IV
III
20 mm
D
IV
III
II
I
20 mm
E
II
I
III
IV
V
20 mm

figure 6