Dinosaur-landscape interactions at a diverse Early Cretaceous tracksite (Lee Ness Sandstone, Ashdown Formation, southern England)

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Keywords: Wealden, Fluvial, Floodplain, Footprint, Ichnology, Zoogeomorphology

Abstract

An assemblage of dinosaur footprints is reported from the Lower Cretaceous (Berriasian-Valanginian) Ashdown Formation of East Sussex, southern England. The ichnofauna is concentrated around a 2 m thick stratigraphic marker, the Lee Ness Sandstone, where recent cliff retreat has revealed 85 recognisable footprints attributable to 13 morphotypes, many of which bear high-fidelity skin impressions. The newly identified morphotypes mean that this tracksite hosts one of the most diverse dinosaur ichnoassemblages in the well-documented Mesozoic record of Britain; recording the activity of theropod, ornithopod, thyreophoran and possibly sauropod tracemakers. Most of the footprints were emplaced on a single floodplain mudstone horizon beneath a fluvial crevasse splay sandstone, where preservation was favoured by cohesive sediment and a prolonged interval of sedimentary stasis, during which trackways could be imparted. The sedimentological context of the trackways reveals evidence of interactions between dinosaurs and the riverine landscape that they inhabited; including the development of microtopographies around footprints, which impacted invertebrate burrowing activity, and evidence for dinosaur wading below the bankfull level of small meandering

channels and oxbow lakes. Modern analogue suggests that the large dinosaurs may have played a significant role as zoogeomorphic engineers within the ancient floodplain setting, but the imperfect translation of sedimentary environment to sedimentary rock means that geological evidence for such is ambiguous.

1. Introduction

Ichnoassemblages of dinosaur footprints shed light on the diversity and community structure of their tracemakers (Lockley, 1989; Falkingham, 2014), but their form and abundance is often biased by the composition and sedimentary mechanics of the substrate onto which they were emplaced, as well as the outcrop of strata in which they are preserved (Milàn and Bromley, 2007; Falkingham et al., 2011; Gatesy and Falkingham, 2017).

In this paper we report a diverse ichnoassemblage of dinosaur footprints that have been revealed within an outcrop that is constantly evolving due to coastal erosion, and which is well-suited to recognise the sedimentological, palaeoenvironmental and outcrop controls on the morphology and distribution of the hosted footprints. The outcrop forms part of the Lower Cretaceous Wealden Group (East Sussex, southern England), a late-stage rift succession of non-marine and marginal-marine strata within the Wessex Basin, which has been the focus of geological investigation for almost two centuries (Martin, 1828; Topley, 1875; Rawson et al., 1978; Hopson et al., 2008; Radley and Allen, 2012).

The Wealden Group has both historic and ongoing significance for dinosaur research: it yielded the first known *Iguanodon* (Mantell, 1825) and ankylosaur fossils (Mantell, 1833), and much more recently has seen the discovery of an exceptionally-preserved fossil iguanodontian brain (Brasier et al., 2017). Whilst diverse body fossils from 39 dinosaur species are described from the Wealden (Batten, 2011; Austen and Batten, 2018), its vertebrate ichnology is less well described. Sporadic reports of footprints have been made since 1846 (Tagart, 1846; Beckles, 1851; Tylor, 1862; Ticehurst, 1928; Sarjeant, 1974; Delair, 1989; Woodhams and Hines, 1989; Parkes, 1993; Sarjeant et al., 1998), but no new major discoveries have been described for the last quarter of a century (Parkes, 1993). The previously described vertebrate ichnofauna is dominated by tracks reported as "*Iguanodon* footprints" (e.g. Tylor, 1862; Delair and Sergeant, 1985) and two morphotypes of theropod track (Woodhams and Hines, 1989), although three putative sauropod footprints have also recently been reported (Jarzembowski et al., 2015; Austen and Batten, 2018).

Here, we describe new trackway material exposed by ongoing cliff collapse between 2014-2018. Our findings greatly increase the number of footprint morphotypes from 4 to 13; these are attributable to theropod, ornithopod, thyreophoran and possibly sauropod dinosaur tracemakers, and some show exceptionally well-preserved skin impressions. The purpose of this paper is to (1) describe these newly-discovered trace fossils and discuss their implications for the dinosaur communities known from the Lower Cretaceous of the UK; (2) demonstrate that the sporadic discovery of footprints from the Wealden Group reflects the recent and ongoing geomorphic evolution of a cliff outcrop which contains a prominent dinosaur footprint-bearing horizon; (3) discuss why this particular tracksite yields so many high-fidelity traces; and (4) discuss the extent to which ancient dinosaur-landscape interactions can be understood using footprint and sedimentary records which are naturally incomplete.

2. Study Location – the Lee Ness Sandstone and Ashdown Formation

The footprints described here were discovered in the Ashdown Formation, in a near-continuous 6 km-long coastal cliff section extending between Fairlight Cove (50° 52' 35.66" N, 0° 40' 16.13" E) and Hastings (50° 51' 25.03" N, 0° 35' 58.20" E). In this eastern part of the Wessex Basin (the Weald Sub-Basin), the Wealden Group has a thickness of c. 400 m (Gallois and Worssam, 1993) (Fig. 1). Historically the internal stratigraphy of the group has been inconsistently applied, but here we follow the most recent stratigraphic nomenclature of the British Geological Survey (Hopson et al., 2008) whereby the group comprises, in ascending order; the Ashdown Formation, the Wadhurst Clay Formation, the Tunbridge Wells Sand Formation, and the Weald Clay Formation.

The Ashdown Formation is a 180-215 m thick coarsening-upwards succession of fine- to medium-grained sandstones and silty mudstones (Fig. 2A, B), of which only the upper 130 m is exposed, cropping out as a gentle anticline along the Hastings-Fairlight section (Lake and Shephard-Thorn, 1987). Footprint-bearing strata are most common within and beneath the Lee Ness Sandstone (hereafter, "LNS"), an informal stratigraphic marker consisting of a prominent 2 m thick tabular body of grey-yellow, very fine- to fine-grained, lithic arenite (Fig. 2C, D), 125 m beneath the top of the Ashdown Formation. The formation is Berriasian-Valanginian (c. 145-134 Ma) in age (Horne, 1995), based on ostracod biostratigraphy (index fossils from the *Cypridea propunctata* and *C. menevensis* subzones are known from the Fairlight borehole; Allen, 1985). However, the precise age of the LNS within this interval is poorly constrained, as the stratigraphic levels of ostracod index fossils are unreported (Anderson, 1985; Horne, 1995).

2.1 Depositional environment

The Ashdown Formation is dominated by overbank floodplain deposits of small meandering fluvial systems, which were active in southern Laurasia at a latitude of 30˚-35˚N, under subtropical-temperate climatic conditions (Allen, 1998). Mudstones are the dominant (c. 60%) lithology but are poorly exposed as they are commonly weathered deeply into the rock face. The deep weathering results in most of the strata at outcrop being obscured by sediment wash or slumped material arising from the mudstones. Where fresh mudstone surfaces can be observed they are seen to be pedogenic: variably purple, yellow, grey-brown or mottled, they contain abundant root traces, attesting to the development of gleysols and spodosols (Mack et al., 1993) on the alluvial floodplain. The dominant sandstone lithologies are either (1) tabular bodies 1-6 metres thick of fine- to medium-grained lithic arenites with planar-stratification and abundant bioturbation (such as comprise the LNS), or (2) unbioturbated medium-coarse-grained lithic arenites with cross-stratification, and sometimes organised as <4 metre-thick heterolithic lateral accretion sets (Fig. 2E). Respectively, these two architectural styles record overbank crevasse splay deposition of coarser sediment and in-channel point bar development in meandering river channels. Carbonaceous strata, in the form of coalified plant debris beds, are common (Fig. 3) and, together with an infrequent macroflora, show that the floodplains were colonized by a floral assemblage of gymnosperms, ferns and minor lycopods (Watson and Alvin, 1996). Both the stratigraphic distribution of plant fossils and chemical weathering proxies, from clay minerals, suggest that the climate of deposition was warm to subtropical, and seasonally wet (Watson and Alvin, 1996; Allen et al., 1998; Akinlotan, 2017).

2.2. Discovery of new footprints in the Ashdown Formation

The footprints described here significantly expand the known dinosaur ichnofauna of the Wealden Group of the Weald sub-basin, as described over 160 years of prior research (Tagart, 1846; Beckles, 1851; Tylor, 1862; Ticehurst, 1928; Sarjeant, 1974; Delair, 1989; Woodhams and Hines, 1989; Parkes, 1993; Sarjeant et al., 1998). The increased diversity does not arise from reclassification of older specimens, but the discovery of new material, made possible by the exhumation of new outcrop exposure through actively ongoing coastal erosion. Footprints were observed on five different occasions (November 2014, May 2015, February 2016, February 2017, and January 2018) at the study site, dominantly within fallen blocks that originated from the base of the LNS, where this unit this crops out near the modern beach level in the core of a local anticline between Lee Ness (50° 52' 06.1" N, 0° 39' 01.3" E) and Goldbury Point (50° 52′ 17.83″ N, 0° 39′ 58.82″ E). Multiple separate visits permitted the recognition of different material on each occasion: new material was revealed in freshly fallen blocks, while material seen on previous visits was often lost to coastal erosion. As a result, the majority of traces are individual footprints: trackway series are rarely observed extending for more than 2-3 footprints (and never more than 5, Fig. 4). Other than two specimens preserved in cross-section internally within the LNS, one oriented along the anteroposterior axis (Fig. 5A) and one along the mediolateral axis (Fig. 5B), tracks are preserved as positive hyporelief casts (Fig. 6). The silty mudstone that lies beneath the LNS onto which the majority of tracks were emplaced is a recessive and friable lithology, which degrades during cliff collapse episodes. Thus, the actual substrate onto which the footprints were emplaced is not visible, and only its internal lithology can be seen, exposed as vertical profiles within the receding cliff face. In total, of the 85 footprints discovered in this study, 79 (including all known footprints with skin impressions) are known from the base of the LNS. A further two occurred internally within the 2 m thick series of approximately 13 beds of bioturbated yellow-grey very fine-fine-grained sandstones that comprise the LNS, with only four scattered throughout the rest of the Ashdown Formation.

3. Dinosaur footprints

Where possible, traces have been placed within established, ichnotaxonomically valid ichnospecies. In cases where a suitable ichnospecies could not be found, footprints have been differentiated as morphotypes using equivalent ichnotaxobases, e.g. length, width, orientation and shape of digital impressions; and presence, shape and size of a heel pad impression. We have avoided establishing new ichnotaxa as it was not possible to collect holotypes from the large, transient fallen blocks. A total of 13 different footprint morphotypes are described, with likely tracemakers including theropod (4), ornithopod (4), thyreophoran (4), and sauropod (1) dinosaurs (Table 1).

3.1. Theropod footprints

Theropod footprints are identified as didactyl or tridactyl impressions with a larger digit III than digits II or IV, presence of claw marks with sharp edges, and occasional elongated posterior margin (due to tarsometatarsus) and/or hallux impressions (Moreno et al., 2012). 19 examples of tracks fitting this description were observed, which can then be subdivided into four distinct morphotypes (Fig. 7).

Morphotype A, observed in 8 specimens, is a tridactyl footprint with narrow (length: width ratio greater than 2) digits including a long digit III. These digits taper sharply towards the anterior and converge onto a possible tarsometatarsus impression at the posterior (Fig. 7A). The size of the footprint casts ranges from 18-32 cm wide by 17-33 cm long. Morphotype B, observed in 7 specimens, is a tridactyl footprint similar in shape to morphotype A, distinguished from it by the lack of a heel pad impression (Fig. 7B). The digits maintain a consistent width for their entire length, and the size of the footprints ranges from 11-25 cm wide by 13-26 cm long. Morphotype C is a single small tridactyl pes cast, 2.1 cm in length by 1.8 cm width (Fig. 7C). The size of this footprint cast is an informative character, as it is significantly smaller than any others observed in the section. All of the digits are narrow, and digit III appears markedly longer than digits II and IV.

Morphotype D, of which three examples were observed, differs from the other footprints observed in the section, as it appears to be didactyl (Fig. 7D). One specimen, from a fallen block containing many footprint casts, is comprised of weakly defined digits III and IV, and a pronounced hallux impression. The tip of this impression is perpendicular to the bed and penetrates to a lesser depth than that of digits III and IV. The footprint is 13 cm wide by 19 cm long excluding the hallux impression, which is 6 cm long, distally situated, and appears to be medially oriented. The remaining two examples, both larger (26 cm wide by 30 cm long and

15 cm wide by 25 cm long), occur in association on another fallen block, oriented in opposite directions. It is unclear if any of these specimens are truly didactyl, or whether this is an artefact of weathering or erosional processes.

3.2. Ornithopod footprints

The ichnotaxonomy of large ornithopod footprints is robust, following a recent review by Diaz-Martinez et al. (2015). Large ornithopod footprints are differentiated from theropod and thyreophoran footprints as they are tridactyl impressions with similar dimensions in anteroposterior and mediolateral directions, and similar lengths of digits II, III and IV, all of which are wide with rounded ends (Moreno et al., 2012). Three large ornithopod ichnotaxa are described herein (Fig. 8), all belonging to the ichnofamily Iguanodontipodidae Vialov (1988), along with one gracile ornithopod morphotype. Iguanodontipodidae includes all large iguanodontian tracks, generally characterized by tridactyl, subsymmetrical pes tracks with one pad impression in the heel and another in each digit. Tracks are typically as wide, or wider, than long (Diaz-Martinez et al., 2015).

In the original descriptions of footprints from the Hastings cliffs all traces were hypothesised to have been made by *Iguanodon* (Delair, 1989). However, the Berriasian-Valanginian footprints from the Fairlight-Hastings section pre-date any known specimens of *Iguanodon* from the Wealden (Barremian-lower Aptian age). Four species of large ornithopod dinosaur are potential tracemakers known from the Valanginian of the Wealden; *Barilium dawsoni*, Dryosauridae (genus and species unnamed), *Hypselospinus fittoni*, and *Kukufeldia tilgatensis*. One or more of these species could be responsible for the observed footprints, however intimate details of their pedal anatomy are presently unknown, so the footprints cannot be reliably assigned to particular taxa (Norman, 2011).

3.2.1. *Caririchnium magnificum* Leonardi 1984

Thirty-one pes casts can be confidently assigned to *Caririchnium magnificum*, occurring both with and without an associated manus print (Fig. 8A and 8B respectively). Pes casts are large and tridactyl, with rounded heel impressions and similar width and length (25-38 cm wide by 26-42 cm long). The digits are wide and of approximately equivalent lengths. The manus impressions are approximately elliptical in shape, and much smaller than the pes (9-11 cm wide by 9-11 cm long). No examples contain more than a single manus and pes. Four examples exhibit skin impressions on the heel or digits. This ichnospecies is known from throughout the Lower Cretaceous, and the type specimen is thought to have been produced by an iguanodontian (Diaz-Martinez et al., 2015).

3.2.2. *Caririchnium isp*.

Eighteen of the footprint cast specimens are tridactyl pes casts with approximately the same length as width, preserved in positive hyporelief (Fig. 8B). Digits are wide and of approximately equivalent lengths, occasionally preserved in high fidelity with skin and claw impressions. The heel pad cast is typically poorly preserved or obscured by striations, precluding identification at ichnospecific level. The traces range in width from 16-44.2 cm, and in length from 19-50.2 cm.

3.2.3. Unnamed Iguanodontipodidae Vialov 1988

These tridactyl pes casts have widely splayed digits with large, rounded ends and no claw marks (Fig. 9). The heel cast is rounded and approximately the same width as the distal end of digit III. However, the primary ichnotaxobase differentiating these footprint casts from other described examples is a sub-round prod mark located medially to the rear of the heel impression. This is considered to be due to a hallux impacting the sediment. Impressions of digits II-IV have approximately the same dimensions as one another, whilst the hallux prod mark is narrower than other digits (diameter 3 – 4 cm). Two examples are observed, with lengths (excluding hallux prod mark) 19 cm and 22 cm, and widths 24 cm and 25 cm (Fig. 9). The morphology of these footprints places them within the established ichnofamily Iguanodontipodidae, but outside any current taxonomically valid ichnogenera (Diaz-Martinez et al., 2015).

The pes of the tracemaker appears to have been functionally tridactyl, with an accessory digit I attached to the medial-posterior region of metatarsal II, based upon the positioning of the prod marks in relation to other digital impressions. These pronounced hallux impressions suggest that the tracks could not have been produced by hadrosaurid iguanodontians, as they are known not to possess a hallux (Norman, 2015). Amongst the more basal iguanodontians, camptosaurs and dryosaurids are known to have possessed a small, non-functional digit I adhered to the medial surface of metatarsal II (Escaso et al., 2014; Norman, 2015), rendering these possible tracemakers.

3.2.4. Gracile ornithopod

Five footprints ascribed to gracile ornithopods have been observed, occurring together in a series five impressions (Fig. 4). The footprints are all tridactyl pes casts preserved in positive hyporelief, differing from tracks made by gracile theropods as the digital impressions are wider and all of equivalent dimensions, with a pronounced heel pad and a width approximately equal to length. The footprint casts range in width from 28.8-36 cm and in length from 31.3-33.8 cm, but as they occur in a series they can confidently be considered to have been produced by the same animal.

3.3. Thyreophorans

Some footprint casts in the LNS have characters that suggest they were made by neither ornithopods or theropods. These occur in four morphotypes (Fig. 10), three of which are tetradactyl casts with rounded digits and claw impressions which differ in the positioning and length of the outer digits, the interdigital angles, and the shape of the heel impression. The final example is pentadactyl with a reduced heel impression, recording a manus impression. Both thyreophoran dinosaurs and crocodylomorphs are known from the Wealden (Barrett and Maidment, 2011; Salisbury and Naish, 2011), and both could create tetradactyl pes impressions and tetradactyl or pentadactyl manus impressions. All of the footprint casts discussed here are attributed to thyreophoran dinosaurs due to their morphology. Tracks which are assigned to *Tetrapodosaurus* are highly similar to those of ankylosaur footprint casts reported from the middle Cretaceous Dakota Group (Lockley and Gierlinski, 2014; Lockley et al., 2014), of the same ichnogenus. Crocodylomorph tracemakers are ruled out as Cretaceous forms are known to leave more elongate, sharp digital impressions (Lockley et al., 2010).

Thyreophoran fossil material is rare in the Wealden (Barrett & Maidment, 2011), with three known species of ankylosaur and one probable stegosaur. Of these species, pedal material is only known from partial specimens of *Polacanthus foxii* (Pereda-Suberbiola, 1993). As this precludes any comparative osteology amongst thyreophorans from the Wealden fauna, tracemakers are inferred from general ankylosaur and stegosaur manual and pedal anatomy (Thulborn, 1990; Whyte and Romano, 2001).

3.3.1. *Tetrapodosaurus* isp. morphotype A Sternberg 1932

Tetrapodosaurus is a tetradactyl footprint with elongate, elliptical digits and pronounced claw marks (Fig. 10A). Digits are forward facing, producing a near-symmetrical print preserved in positive hyporelief. The heel pad cast is short and rounded, but larger than all digital impressions, which are approximately equivalent in all dimensions. Two examples are observed, one of which is highly detailed with skin and claw impressions. This example has footprint width 26 cm, length 27 cm, digit width 5-7 cm, and digit length 6-10 cm. Figure 10A shows the detailed textures along with claw marks on proximal regions of the digit pads.

3.3.2. *Tetrapodosaurus* isp. morphotype B Sternberg 1932

Another tetradactyl cast in positive hyporelief, with elliptical digits and pronounced claw marks, (Fig. 10B) is also assigned to *Tetrapodosaurus*, but is sufficiently different to be considered a distinct morphotype. Digits II and III are forward facing, with digits I and IV more laterally positioned. A pronounced, angular heel pad cast larger than all digital impressions extends towards the posterior. Digits have approximately equal dimensions. One example is reported, with footprint width 33 cm, length 30 cm, digit width 4-6 cm, and digit length 5-8 cm.

3.3.3. *Stegopodus* manus Lockley and Hunt 1998

The third form considered to be a thyreophoran footprint is seen in a single example as a tetradactyl cast in positive hyporelief, with elongate rounded digits and a pronounced heel impression (Fig. 10C). Digits I, II and III are of equivalent length (11-13 cm) and positioned at the anterior of the foot, whereas digit IV is shorter (7 cm) and more medially situated. All digits are oriented approximately towards the anterior, with digit I slightly turned in. The distal end of the digit IV impression has a small centrally positioned mound, interpreted as a claw mark. The overall cast has maximum dimensions of length 34 cm and width 29 cm.

This specimen closely resembles the original holotype of *Stegopodus czerkazi*, a manus cast from the Upper Jurassic Morrison Formation (Lockley and Hunt, 1998) which is thought to have a stegosaur tracemaker. Whilst the ichnogenus has subsequently been revised to introduce a pedal holotype (Gierlinski and Sabath, 2008), it is still considered of stegosaur origin.

3.3.4. Unnamed thyreophoran footprint

A pentadactyl right manus cast in positive hyporelief is seen in one instance (Fig. 10D). Digits are short and rounded without claw impressions, and no clear heel impression is present. Digits I and V are laterally oriented, and digits II, III and IV are oriented towards the anterior. The footprint cast has width 28 cm and length 18 cm. This specimen is attributed to an ankylosaur, as it closely resembles the expected morphology of an ankylosaur manus cast (Whyte and Romano, 2001).

3.4. Putative Sauropod Footprints

Jarzembowski et al. (2015) noted two large impressions, apparently occurring in a series, and suggested that they may be sauropod tracks (see Fig. 4, Fig. 11A), due to a possible crescentic manus, and the approximately ovoid morphology of the interpreted pes casts. No digital impressions are observed with these amorphous imprints, and the pes casts range in size from 58-61 cm long and 49-51 cm wide. Jarzembowski et al. (2015) also figured a third suspected sauropod footprint, discovered in an isolated block, and at least one further example with a similar morphology and dimensions was discovered at the base of the LNS in this study (Fig. 11B). It is plausible that these imprints may record sauropod tracks (Jarzembowski et al., 2015; Austen and Batten, 2018), but until a more defined series of such impressions is discovered, this interpretation must remain tentative due to the amorphous nature of the imprints and the possibility that they may be poorly-preserved undertraces of other footprints.

3.5 Surface traces and undertraces revealed by skin impressions

Many of the footprints on the base of the LNS exhibit well-preserved skin impressions. These present as small (2 – 5 mm), raised, sub-rounded polygons ranging in shape from approximately circular, to rounded trigonal, to elongate (Fig. 12), and are commonly associated with narrow furrowed striations (c. 2.5 mm across individually and 2-7 cm in length) that extend for the entire width of the heel or tarsometatarsus impression (recording slip-marks which developed as the footprint was emplaced (Fig. 13; Davies et al., 2016)). Footprints with skin impressions are preferentially seen at the base of the LNS, where they have been cast directly into the underlying mudstone, and are clear evidence of the complete preservation of true surface traces (see Section 4.2.1).

Conversely, many of those instances of footprints that lack skin impressions are likely undertraces – emplaced later at a higher stratigraphic level within the lower crevasse splay sandstones of the LNS (Fig. 6D). This is implied by the size range of footprints with and without skin impressions: for example, in specimens of *C. magnificum*, 4 had skin impressions and 27 lacked skin impressions. Those *C. magnificum* specimens with skin impressions occupy the lower end of the size range of all specimens of the ichnospecies, with a mean length 13.3 cm smaller than the overall mean, and mean width 9.9 cm smaller (Fig. 14). As the size of footprints is greater in undertraces than surface traces (because deformation radiates out downwards from a surface footprint; Milàn et al., 2004) it is likely that larger casts lacking skin impressions arose from the translation of footprints down through the sediment, resulting in loss of fine detail (Milàn and Bromley, 2007).

3.6. Implications of the Dinosaur Ichnofauna

The reported dinosaur ichnofauna assemblage of theropod, ornithopod, thyreophoran, and possible sauropod footprints is one of the most diverse known from the Mesozoic of the UK (Fig. 15), rivalling those of the Jurassic Ravenscar Group of Yorkshire (Whyte et al., 2007) and the Cretaceous Wealden of the Isle of Wight (Lockwood et al., 2014). When considered alongside the body fossil record of dinosaurs from the Wealden Group, this assemblage provides insights into the constituent dinosaur community immediately before the deposition of the LNS. Ornithopod tracks from the LNS are assigned to three distinct tracemakers: styracosternans, basal iguanodontians and gracile ornithopods; theropods are dominated by gracile forms, with possible evidence for didactyl theropods; thyreophoran tracks are likely produced by ankylosaurians and stegosaurs; and there is putative evidence for sauropods.

A challenge of assessing population ecology with ichnology is the difficulty in assessing the proportion of traces that were produced by unique tracemakers, i.e. it is possible for a small number of individuals to produce a large number of footprints. In the LNS, ornithopod tracks were likely produced by a large number of unique tracemakers because footprint dimensions have a high scatter (Fig. 16A) and tracks are commonly solitary. Conversely, theropod tracks have clustered dimensions (Fig. 16B), and are often observed in series, suggesting fewer unique tracemakers. Estimates of the original dinosaur populations can be refined to some degree by looking only at surface traces with skin impressions. These show that the instantaneous population that traversed the pre-LNS substrate included at least styracosternans (eleven tracks), ankylosaurians (two tracks) and stegosaurs (one track).

Even with caveats of uncertainty (i.e., the number of unique trace-makers, the limited number of specimens seen with skin impressions, and syn-depositional and post-depositional limitations on footprint fidelity), the footprints of the LNS imply a community dominated by large herbivorous dinosaurs (dominantly styracosternans), with a smaller theropod component. This is in keeping with expected predator-prey population dynamics in modern ecosystems (Duffy, 2002).

4. Controls on the diversity, distribution and discovery of dinosaur footprints

4.1. Outcrop controls on footprint discovery

The LNS tracksite provides a case study in how the revisiting of non-conservated, dynamic outcrops may yield new insights into diversity: because, while local fossil diversity may be biased by rock availability and sampling (Smith and McGowan, 2007), an increase in rock availability at a previously sampled site can yield improved diversity estimates. In this instance, rock availability was enhanced by multiple cliff falls in the Hastings-Fairlight area (Fig. 17), uncovering the large amounts of fresh material discovered between 2014-2018. Each of the five visits saw the exposure of new material and the degradation or disappearance of previously observed tracks (Fig. 18).

As new discoveries of footprints are dependent on the collapse of new material, the historically sporadic nature of new reports (Tagart, 1846; Beckles, 1851; Tylor, 1862; Ticehurst, 1928; Sarjeant, 1974; Delair, 1989; Woodhams and Hines, 1989; Parkes, 1993) suggests that there are prolonged intervals where the actively-eroding tracts of the basal LNS lack dinosaur footprints. Intervals of discovery reflect periods when spatially-concentrated clusters of footprints (trackways) are coincident with the plane of the exposed cliff face, and thus more likely to erode out as fallen blocks (Fig. 19).

Cliff retreat in the Hastings-Fairlight section has been fairly consistent over long time scales (Thorburn, 1977; Cleeve and Williams, 1987), but is stochastic over short timescales because it primarily occurs as discrete cliff collapse events (between 1998-2004, 86.4 m of cliff retreat occurred, including 25.7 m in 2002-2003 alone; Rother District Council, 2012). This means that any estimates of trackway spacing have a large error bar, but they may be crudely calculated. The barren intervals between reported footprint finds in the period 1862-2018 are 56 years, 63 years, 10 years, and 22 years respectively, so with the maximum average rate of cliff retreat during this period (77 cm per year; Cleeve and Williams, 1987), the minimum distance between previously exposed trackway-bearing tracts of the basal LNS would be 48.5 m (Table 2).

Dinosaur behaviour is responsible for this uneven distribution of their footprints on the original substrate. The dominant large ornithopod tracemakers are thought to have exhibited herding behaviour (Lockley, 1989; Cotton et al., 1998; Lockley et al., 2012), the movement of which would lead to large numbers of tracks grouped together in the areas the herd traversed, and a much sparser distribution away from the main route.

4.2. Depositional controls on footprint distribution

The high concentration of trackways around the LNS reflects the distinct sedimentary character of the amalgamated sandy crevasse splay deposits that comprise the unit. Depositional controls on the footprints must be considered separately for those internally and at the base of the LNS because of the variable sediment type, palaeoenvironment and chronostratigraphic significance of the stratigraphic horizons involved.

4.2.1. Footprints at the base of the Lee Ness Sandstone

The lowermost crevasse splay sandstone of the LNS has cast dinosaur footprints that were emplaced onto a cohesive substrate and which now marks the top of the underlying grey silty mudstone, in conjunction with casts of ripple marks (Fig. 20A) and desiccation cracks (Fig. 20B-C). The base of the LNS also contains a dense invertebrate ichnofauna of passively-filled burrows of *Palaeophycus*, with rare *Ophiomorpha* and *Cochlichnus* (Table 3, Fig. 21). These record infaunal communities on the stable but damp overbank floodplain substrate and are sometimes overprinted with actively-filled *Taenidium* (deeper tier traces from overlying crevasse splay sands).

Footprints with intricate detail of skin impressions are notable from the base of the LNS. The preservation of skin textures within demonstrable surface traces shows that this stratigraphic surface can be considered to be a true substrate (Davies et al., 2017; Davies and Shillito, 2018): a sedimentary bedding plane which existed at the sediment-water or sediment-air interface at the time of deposition, and which was not degraded during the deposition of the overlying sands. The preservation of delicate footprint textures on a true substrate need not be unexpected, because the distal point source of the overlying crevasse splay sands means that their deposition at a specific footprint location was not necessarily coupled with erosion (Davies and Shillito, 2018). However, the initial imparting of skin impressions was favoured by antecedent sedimentary conditions: namely, a moist, cohesive substrate which would have behaved as a ductile media when impressed (Fig. 22; Laporte and Behrensmeyer, 1980; Milàn and Bromley, 2006).

The presence of multiple morphotypes of dinosaur footprint, and the pedogenesis of the Ashdown Formation mudstones, imply that the sub-LNS substrate remained in sedimentary stasis (i.e., experiencing neither deposition nor erosion: Tipper, 2015) for a prolonged interval at the time of deposition, and was able to be imparted with multiple generations of dinosaur trackway. Prolonged stasis is also revealed by evidence that the vertebrate and invertebrate ichnofauna were temporally offset in their emplacement onto the same horizon. Invertebrate burrows (particularly *Palaeophycus*) are near ubiquitous on the base of the lowest crevasse splay deposit, but never occur internally within dinosaur footprints. The implication of this is that invertebrate burrowing was an ongoing process on the substrate but that, once footprints had been emplaced, it was impeded: likely because the compaction of intra-footprint sediment rendered it inimical to excavation (Dorgan et al., 2006).

4.2.2. Footprints within the Lee Ness Sandstone

Internally within the LNS, dinosaur tracks that were emplaced onto crevasse splay top sandy substrates (i.e., between flooding events) are observed in cross-section, where bedding is truncated or downturned around footprints (Fig. 6). These are seen in association with a low-density invertebrate ichnoassemblage of *Arenicolites* and *Taenidium* that records the infaunal colonization of crevasse splay deposits, immediately after their deposition during flood events (i.e., while they were still wet with standing water) (Table 3, Fig. 21).

The relative rarity of footprints internally within the LNS appears to be a sedimentological rather than palaeoecological artefact. The deposition of crevasse splay sands is sporadic, occurring only when a river channel breaches its levees during flood events (e.g., Smith et al., 1989), so the horizons which separate the 13 constituent sandstone layers of the LNS can also be considered to be true substrates, which may be expected to have been imparted with footprints as frequently as the antecedent mudstone. However, the fact that footprints internal to the LNS are only evident in profile reflects the granular nature of the sandy crevasse splay substrates. These would have been unfavourable to preserving casts of footprints as wet sand would be too loose and prone to collapse to hold the form of a trace (Fig. 22; Laporte and Behrensmeyer, 1980). This is in contrast to the wet, plastic mud at the base of the LNS which, in addition to true surface traces, also hosts some undertraces transmitted down from the lower internal layers of the LNS.

4.3. Dinosaur controls on deposition?

Modern large vertebrates are effective zoogeomorphic agents (e.g. Haynes, 2012; Jones, 2012; Statzner, 2012), modifying the spatial distribution of landforms and sedimentary processes within riverine environments, and it has long been suspected that dinosaurs may have played an analogous role in ancient environments (Butler, 1995; Jones and Gustason, 2006). The combination of footprints and alluvial architecture within the Ashdown Formation permit the opportunity to here briefly assess whether such activity leaves a diagnostic sedimentary signature, or whether the limitations resulting from the imperfect translation of geomorphology into the sedimentary record (e.g., McMahon and Davies, 2018) only permits the recognition of such life-landscape interaction through abductive modern analogue.

Large animals act as zoogeomorphic agents at a variety of scales. At one end of the spectrum individual footfalls distort the microtopography and internally-stratified anatomy of substrates, resulting in sediment dewatering and uneven substrate surfaces (Schanz et al., 2013). On a meso-scale, large groups of animals can trample a substrate, obliterating sedimentary textures (Laporte and Behrensmeyer, 1980; Scott et al., 2012) and changing its susceptibility to erosion (Trimble and Mendel, 1995). At the largest scale, trails produced by large herbivores have been commonly linked to the formation of new river channels, as flowing water preferentially accumulates and diverts along herding trails, the substrates of which are more compacted and less porous, and thus inhibit water infiltration (McCarthy et al., 1992; McCarthy et al., 1998; Jones et al., 2009).

In the Ashdown Formation, the strongest evidence for dinosaurs as geomorphic agents occurs at the smallest scale, often as three-dimensional evidence of 'dinoturbation' – the impact of dinosaur trampling on sediments (Dodson et al., 1980) (Fig. 23). Downturned bedding around certain footprints sometimes records a synoptic microtopography created by the weight of a passing dinosaur, with the inner parts of the trace infilled with homogenous unlaminated fine sediment (Fig. 23). Further evidence for original microtopography may be seen in instances where desiccation cracks are seen to divert around footprints (Fig. 20C), indicating that the depressions left by footprints remained waterlogged, likely having accumulating water as small puddles. Although a minor zoogeomorphic element, such features would have had defined effects on microhabitats due to differential compaction of the substrate. For example, this is seen by the mutual avoidance of footprints and invertebrate burrows (Section 4.2.1.), and, at other dinosaur tracksites, such moisture-retaining footprints can be seen to have acted as favourable loci for the development of small plant thickets (Fig. 24).

Through comparison with analogous modern environments that host large vertebrates it is likely that dinosaurs acted as geomorphic agents at a larger scale during the fluvial deposition of the Ashdown Formation. Large herbivores such as cows and hippopotamuses are known today to promote the formation of small fluvial channels and encourage channel avulsion due to breaching levees and forming accessory channels by trampling (McCarthy et al., 1992; Trimble and Mendel, 1995). If such features were to be translated into the sedimentary record, the only physical signatures would be indirect evidence for a propensity to avulse, such as stacked crevasse splay sandstones (Smith et al., 1989) as within the LNS, or the resultant abandoned channel elements. However, it is impossible to diagnose an organismal trigger for such architectural elements because they may have multiple alternative causes (Jones et al., 2009) and because the direct evidence of the trigger (i.e., footprints organised within trackways on the channel floor) would have been obliterated by the physical processes of erosion which they induced. Thus, while modern analogue can tell us that dinosaurs (with similar behaviour and greater weight than extant fauna) must have promoted channel avulsion during the Mesozoic, the rock record is unlikely to ever provide a 'smoking gun' for specific instances of dinosaur-induced avulsion.

There is evidence for other interaction between the Ashdown Formation dinosaurs and the rivers that formed landscape components of their habitats. In one stratigraphic horizon below the LNS, lateral accretion sets are seen to occur in opposite directions, indicating the cross-sectional anatomy of a meander neck cut-off (Fig. 2E). Individual sets containing abundant fossil woody debris and recording iterations of point bar growth can be seen to be deformed in discrete packages (Fig. 2E, Fig. 3), suggestive of highly localized sources of soft-sediment deformation (e.g., by foot-falls). While no high-fidelity footprints are preserved, these deformation horizons occur on the slopes of inclined strata below the inclined heterolithic topsets, indicating that they were emplaced below the bankfull level of the river. With no other trigger that could induce such localized soft-sediment deformation, the only explanation is that these indicate the wading activity of dinosaurs in the shallow water inner bends of vegetated river channels. Such instances provide high-resolution snapshots of direct dinosaur interactions with the ancient Ashdown Formation landscapes, even when our understanding of how dinosaurs may have actively engineered those landscapes is accessible only through modern analogue.

5. Conclusions

- The Lee Ness Sandstone contains a dinosaur ichnofauna with a previously underestimated diversity.
- The ichnofauna reveals a community of ornithopod, theropod, thyreophoran, and sauropod dinosaurs (styracosternans, basal iguanodontians, gracile ornithopods, ankylosaurians, stegosaurs, gracile theropods, possible didactyl theropods and possible sauropods), some of which have limited body fossil evidence within the Cretaceous Wealden Group.
- The latest discoveries have occurred during an interval of cliff retreat in which the actively eroding cliff face has recessed beyond a trackway with a concentration of footprints.
- Some of the footprints contain high fidelity skin impressions, and the varying level of fine detail observed in the footprint casts attests to the variable consistency of the substrate, both spatially and temporally.
- The stratigraphic restriction of the most abundant and high-fidelity of footprints to the base of the Lee Ness Sandstone is controlled by favourable factors at the time of deposition, namely (1) a cohesive sediment substrate that could be imparted with fine detail; (2) a prolonged interval of sedimentary stasis during which multiple generations of surface trace footprint could be imparted; and (3) the palimpsesting of further generations of undertrace footprints after the substrate was interred by the first crevasse splay sands of the Less Ness Sandstone.

- Evidence for dinosaur controls on the sedimentary environment are dominantly small scale, but larger scale influences (e.g., the promotion of avulsion) are likely from abductive analogue and fit with the general facies and architectural evidence from the Ashdown Formation.

Acknowledgments

The authors thank Dr C.J. Rogers for assistance in the field and Dr David Norman for helpful discussion on dinosaur foot morphology. Constructive reviews from Prof. Martin Lockley and Dr Susannah Maidment, along with valuable comments from the editor Prof. Howard Falcon-Lang have helped this paper to reach its final form. APS was supported by the Natural Environment Research Council [grant number NE/L002507/1].

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Woodhams, K.E. & Hines, J.S. 1989. Dinosaur Footprints from the Lower Cretaceous of East Sussex, England. *In:* Gilette, D.D. and Lockley M.G. (eds.) *Dinosaur Tracks and Traces*, Cambridge University Press, 301-307.

Figure Captions

Figure 1 – A) A map of south-east England showing the Lower Cretaceous Wealden geology. The inset map shows the area between Hastings and Fairlight, where the dinosaur ichnofauna was discovered, in greater detail. The section of coastline in red marks the extent of sea defences. The section in blue illustrates where the dinosaur footprint casts described in this study were found. B) A schematic stratigraphic column, illustrating the position of the Ashdown Formation and Lee Ness Sandstone (red line) within the Lower Cretaceous Wealden of the Weald sub-basin (after Radley and Allen, 2012).

Figure 2 – A representative overview of the geology of the cliffs near Lee Ness. A) An annotated photograph highlighting different lithologies and key horizons observed in the cliffs (2017). B) A sketch stratigraphic log of a 14 m cliff section including the Lee Ness Sandstone. Grain size scale ranges from mud (m) to coarse sand (c), although the coarsest material in the logged section is fine sandstone. C) A close up view of the Lee Ness Sandstone (LNS) with distinguishable yellow and grey layers (2014). A significant overhang has formed beneath it due to preferential weathering of the underlying mudstone (scale bar 1 m). D) Inset showing a close up of the base of the Lee Ness Sandstone, where part of a dinosaur footprint cast is observed in cross section (scale bar 20 cm). E) Cross bedded sandstones recording a neck cut-off event (2017). Major surfaces are picked out by thicker lines. At the base of the section is a green gleysol (GS), topped by cross-bedded sandstone foresets dipping to the NW (yellow). This is truncated by overlying cross bedded sandstones dipping to the SE (blue). Above this, fine, planar laminated sandstones (red) transition upwards into grey mudstone followed by a

red, rooted, spodosol horizon (SS). Several dinosaur footprints are observed in cross section at different horizons (FP). Flow directions are recorded after Davies et al. (2018). Person for scale is 1.8 m tall.

Figure 3 - Plant fossil material in the Ashdown Formation. A) Coalified bands marking plant debris beds (2018). B) Large fossilised gymnosperm trunk, indicating the presence of trees on the alluvial plain (2018). C) Dense root traces in a palaeosol horizon, with major traces labelled (r.) (2017). The overlying crevasse splay deposit contains *Taenidium barretti* burrows (*Ta.*). D) A carbonaceous plant fossil (arrowed) in association with dinosaur footprints on the base of the Lee Ness Sandstone (2014). Scale bars 10 cm.

Figure 4 – A) A reconstructed series of 5 successive footprints, assigned to a gracile ornithopod (2017). Note the wide digital impressions and the equivalent length and width of the footprint casts. This series is associated with putative sauropod footprints (1 manus, 2 pes) in a trackway. B) a line drawing showing the relative locations of the footprints, with the heel of the prints highlighted (red). Putative sauropod footprints are labelled Sa. C) A reconstruction of the stride length of the dinosaur, and separation between the path of the left and right legs. Mean stride length is 1.86 m. Scale bar 1 m.

Figure 5 – A) A dinosaur track viewed in anteroposterior cross section (2017). The impression cuts through bedding to either side, causing some down-turning (arrows). Bedding underneath is distorted, curving beneath the footprint. A claw mark at the front of the impression (c.) shows where the angle of the foot in the sediment has changed during the course of the step. B) A putative didactyl theropod track viewed in mediolateral cross section (2017). As in A, bedding is truncated at the sides of the impression and distorted and down-turned beneath (arrows). The footprint is identified as produced by a didactyl theropod as two clear digit impressions (III-IV) cut deeply into the sediment, with a third, raised impression (II) indicating the elevated

digit II. An example of *Taenidium barretti* is observed in the sediment next to the footprint (*Ta.*). Scale bars 20 cm.

Figure 6 – Schematic cartoon showing the variety of substrates that dinosaur footprints could be emplaced upon, and the different sedimentary expressions of those footprints, as recorded in the Lee Ness Sandstone. A-C show simplified hypothetical maps of the Ashdown Formation depositional environment at three successive time intervals of deposition (above), and a vertical profile through footprint-hosting sediments at the location starred (below). A) Interval immediately preceding the deposition of the Lee Ness Sandstone: footprint (F1) imparted onto moist overbank floodplain mud (the pre-Lee Ness substrate). B) Interval subsequent to the deposition of the first layer of Lee Ness Sandstone, deposited as a crevasse splay of sand breaches marginal channel levees. During the flood event, footprints on the underlying substrate are cast (C1) and, following the event, new footprints (F2) compress and extend downwards as undertraces into the underlying muds (U2). C) An interval after a second flood event has exploited the same breach point as the first: again, casting (C2) underlying footprints and establishing as a quiescent substrate after the flood event such that new footprints (F3) and undertraces (U3) are generated. Note that, although only 2 beds are illustrated, the Lee Ness Sandstone comprises 13 internal beds in total, suggesting that this process repeated multiple times until the breach point in the main river channel was healed/abandoned. D) Present day expression of the record of events in A-C. Amalgamated crevasse splay deposits have lithified as sandstone and present as a fallen block. The block does not split along internal planes so F2, F3 and U3 are observable only in vertical profile. Casts and undertraces (C1 and U2) are observable as distinct footprints on the base on the bed, but indented footprints on the top of the underlying mudrock have been destroyed due to the fissility and erodibility of that lithology.

Figure 7 – A) Theropod footprint morphotype A – tridactyl footprint cast attributed to a coelurosaur, with elongate digit III and a faint heel impression (2017). Digits narrow distally and have sharp ends, but no clear claw marks. B) Theropod footprint morphotype B – tridactyl footprint cast attributed to a coelurosaur (2014). Digits are narrow and elongate, maintaining a consistent width for the whole length of the digit. Cast has no heel pad impression, and a long digit III. C) Theropod footprint morphotype C – small tridactyl footprint cast attributed to a maniraptoran (2014). Digit III is significantly longer than digits II and IV. D) Theropod footprint morphotype D – footprint cast showing two clear narrow, elongate digit impressions, and a medially situated hallux prod mark (2014). The outline of the footprint cast is highlighted in white, and digits I, III and IV are identified. This cast has been attributed to a didactyl theropod. Scale bars 5 cm.

Figure 8 – A) *Caririchnium magnificum* – right pes cast preserved in positive hyporelief, with associated manus cast (man.) (2014). B) *C. isp* - wide pes cast with large heel pad, associated with desiccation cracks (2015). Scale bars 10 cm.

Figure 9 – The 2 examples of the unnamed *Iguanodontipodidae* trace observed in the Lee Ness Sandstone (2018). A and B show photographs of the footprint casts, with large heel pad and splayed, rounded digit impressions, and clear hallux prod marks. C and D show the corresponding line drawings. Scale bars 10 cm.

Figure 10 – A) *Tetrapodosaurus* isp. morphotype A – tetradactyl pes cast, with claw marks and interdigital skin impressions (2018). Footprint has elongate, rounded digits and a rounded heel impression. B) *T.* isp. morphotype B – tetradactyl pes cast with claw marks and an elongated, angular heel impression (2014). C) *Stegopodus* manus – right manus cast with elongate, rounded digits I-III and a medially positioned short digit IV with claw impression (2014). Digit

I is turned slightly turned in. D) Thyreophoran Footprint – pentadactyl right manus cast with short, rounded digits and no heel impression (2015). Digits numbered I-V. Scale bars 10 cm.

Figure 11 – A) Possible sauropod manus (man.) and pes footprint casts associated with a gracile ornithopod footprint cast, as reported in Jarzembowski et al. (2015). Casts are highly indistinct with few distinguishing features (2017). B) A similar large amorphous cast preserved in positive hyporelief. Whilst it is possible that this records a sauropod footprint, it is also possible it is an indistinct undertrace of another footprint morphotype (2016). Scale bars 10 cm.

Figure 12 – Dinosaur skin textures on footprint casts from the base of the Lee Ness Sandstone (2016). A, B) Polygonal skin texture on a theropod footprint cast. A) The full extent of the texture on the toe of the footprint cast. Black box shows the extent of B. B) A close up of the skin texture in A. It is comprised of small, raised sub-rounded polygons. Polygons are fairly uniform with small differences in eccentricity. C, D) Skin texture on an ornithopod footprint cast. C) Extent of the skin texture on the side of the footprint cast. Black box shows the extent of D. D) A close up of the skin texture in C. Polygons are more pronounced than those in B, with a greater microtopography but similar size and shapes. Scale bars 1 cm.

Figure 13 – Striations on the heels of footprint casts from the base of the Lee Ness Sandstone. A) *Caririchnium isp.* with striations extending for 7 cm at the back of the heel (2014). B) A close up of the striations in A. Striations are continuous along their full length, and approximately evenly spaced. C) A theropod footprint cast with striations at the back of the heel, associated with skin textures (2016). D) A close up of the striations and associated skin textures. Striations have approximately the same width as scale impressions towards the back of the heel. Scale bars 10 cm.

Figure 14 – A graphic representation of the size of footprint casts with and without skin impressions, from all examples of *C. magnificum*. The four examples in which skin impressions

were observed occur at the bottom end of the observed size range, and the average footprint dimensions are significantly smaller than the overall average.

Figure 15 – An illustrated record of known dinosaur footprint diversity in the UK. The Lee Ness Sandstone (Wealden Gp - Sussex) records the greatest diversity in the Cretaceous, and the greatest diversity of thyreophoran footprints. (Delair and Sarjeant, 1985; Ensom, 2002; Clark et al., 2004; Day et al., 2004; Clark et al., 2005; Marshall, 2005; Whyte et al., 2007; Lockwood et al., 2014)

Figure 16 – A graphic representation of footprint dimensions of A) ornithopod and B) theropod footprint casts reported herein. Note the wide scatter of dimensions observed in ornithopod footprint dimensions, suggesting a large number of unique tracemakers. The smaller scatter and clumping of data points observed in theropod footprint casts suggests a smaller proportion of unique tracemakers.

Figure 17 – A section of cliff exposure viewed in 2014 and again in 2018. Over the course of 4 years a large amount of material has collapsed from the rock face. Dinosaur footprints are observed in cross section on several horizons (FP). Underlying gleysol (GS) and overlying spodosol (SS) are highlighted. Two horizons are highlighted to aid in comparison of the photographs, red at the base of the spodosol, and yellow within the heterolithic lateral accretion sets. This panel is illustrated in greater detail in figure 4. Person for scale is 1.8 m tall.

Figure 18 – A record of the alterations to dinosaur footprint casts exposed to one year of weathering. Feb 2016) *Caririchnium isp.* first seen in February 2016 when they had freshly fallen from the cliff. Feb 2017) The same footprint casts observed a year later. Note the absence of detailed textures and the minor change in shape.

Figure 19 – A diagrammatic summary of the exhumation of trackways from the base of the Lee Ness Sandstone showing how, over decadal timescales, episodic cliff retreat alternately yields footprint-bearing and footprint-barren fallen blocks because of the concentration of high-fidelity footprints into particular tracts of the underlying substrate.

Figure 20 – A) A dinosaur footprint cast occurring on a rippled surface (2017). B) Discontinuous desiccation cracks in positive hyporelief (DC), in association with a theropod footprint cast (2015). C) Desiccation cracks (DC) between digits II and III, and digit II and heel pad impressions of an ornithopod track (2017). This suggests the desiccation occurred after the formation of the tracks, and the morphology of the cracks was influenced by the footprint impressions. D) A muddy injectite between digit impressions II and III of a theropod footprint cast (2015). This illustrates dewatering of the soft underlying substrate associated with the dinosaur tracks. Scale bars 10 cm.

Figure 21 – A) *Taenidium barretti* – unlined meniscate burrows occurring on the base of a bedding surface (2017). B) *Palaeophycus striatus* – simple horizontal burrows showing occasional striations along the length (arrow) (2017). C) *P. striatus* – A densely burrowed surface illustrating abundant false branching due to overprinting of successive burrows (2017). D) *Arenicolites* isp. – paired burrows on the base of a bedding surface (*Ar.*), in association with *T. barretti* (2017). (*Ta.*) E) *Ophiomorpha nodosa* – sub-horizontal pellet lined burrow (*Op.*) on the base of the Lee Ness Sandstone (2018). F) *Cochlichnus anguineus* – A short length of smooth, non-branching sinusoidal burrow, on the base of the Lee Ness Sandstone (2017). Scale bars 2 cm.

Figure 22 – The record of dinosaur footprints in different mediums. A) Footprints on a mixed sand-mud substrate (2014). Sandstone (S) bedding is downturned and truncated, whereas mudstone (M) deforms into lenses. B) Footprints on a sand substrate (2014). Where the sand

contains enough moisture to retain the shape of a footprint bedding is sharply downturned (DTB) and truncated at the edges of the trace, and the centre is infilled with homogenous sediment. C-E) Footprints on a mud substrate, with increasing softness from C-E. C) On a relatively firm substrate, fine detail of the foot is recorded such as skin impressions (Sk.) and claw marks (Cl.) (2016) D) On a softer mud substrate the sediment behaves in a more fluid manner (2015). In the photographed example mud is squeezed between two of the digits (Mud esc.), although the sediment has enough integrity to accurately record the footprint. E) On a very soft mud substrate the act of walking on the substrate churns the sediment, homogenizing bedding but leaving no clearly defined individual footprints (2014).

Figure 23 – A) A dinosaur footprint cast observed in cross section. The bedding around the edges of the footprint is sharply downturned (arrows) (2017). An example of *T. barretti* is seen in association (*Ta.*). B) A line drawing highlighting the footprint. Towards the centre the infill is totally structureless (SI), with downturned bedding surrounding the print (DTB). The footprint widens with depth, suggesting that close to the surface the sediment contracted when the foot was removed. Scale bar 20 cm.

Figure 24 – A) A dinosaur footprint from the Scalby Formation observed in cross section, creating a topographic low in which a thicket of small plants has grown (2016). Black box shows the area in B. B) A close up of the footprint with small plant stems preserved in the overlying bedding. Beds above dip towards the centre of the footprint, creating a low point in the original topography. C) A line drawing highlighting the features of the footprint and plant thicket. Red line shows the outline of the footprint, infilled with homogenous fine sediment. Black lines show the downturned and truncated bedding to either side of the footprint (DTB), where the substrate was penetrated. Blue lines show the overlying bedding, dipping towards the centre of the footprint creating a topographic low. Green lines show small plant stems which grew in the hollow that formed above the footprint. Scale bars 20 cm.

Table 1 – Dinosaur footprint diversity

Table 2 – Rates of cliff retreat

Table 3 – Invertebrate ichnology

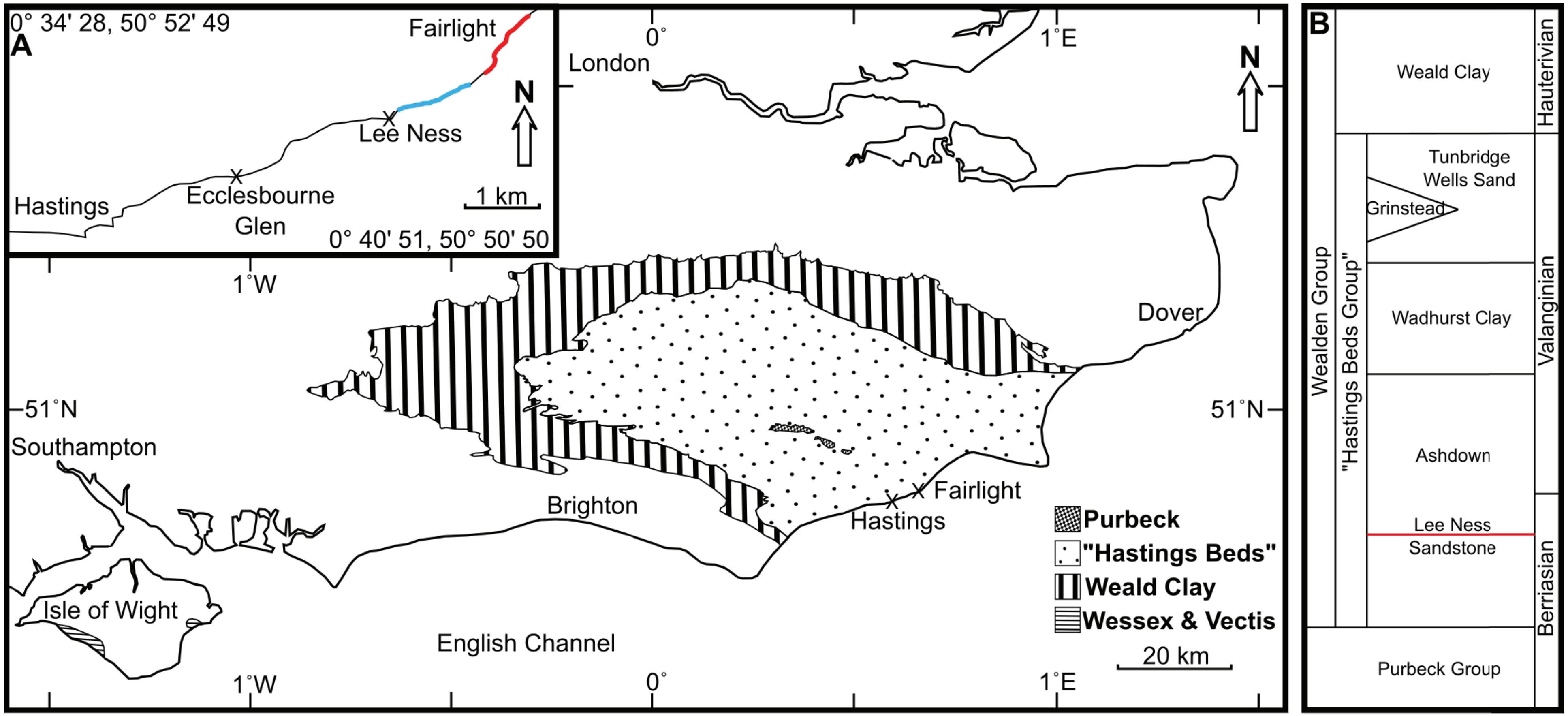

A
0° 34' 28, 50° 52' 49
Fairlight
Lee Ness
Ecclesbourne
Glen
Hastings
N
1 km
0° 40' 51, 50° 50' 50
0°
1°E
London
N
1°W
51°N
Southampton
Dover
51°N
Brighton
Fairlight
Hastings
Isle of Wight
English Channel
Purbeck
"Hastings Beds"
Weald Clay
Wessex & Vectis
20 km
1°W
0°
1°E
B
Wealden Group
"Hastings Beds Group"
Weald Clay
Tunbridge
Wells Sand
Grinstead
Wadhurst Clay
Ashdown
Lee Ness
Sandstone
Purbeck Group
Hauterivian
Valanginian
Berriasian

Figure 1

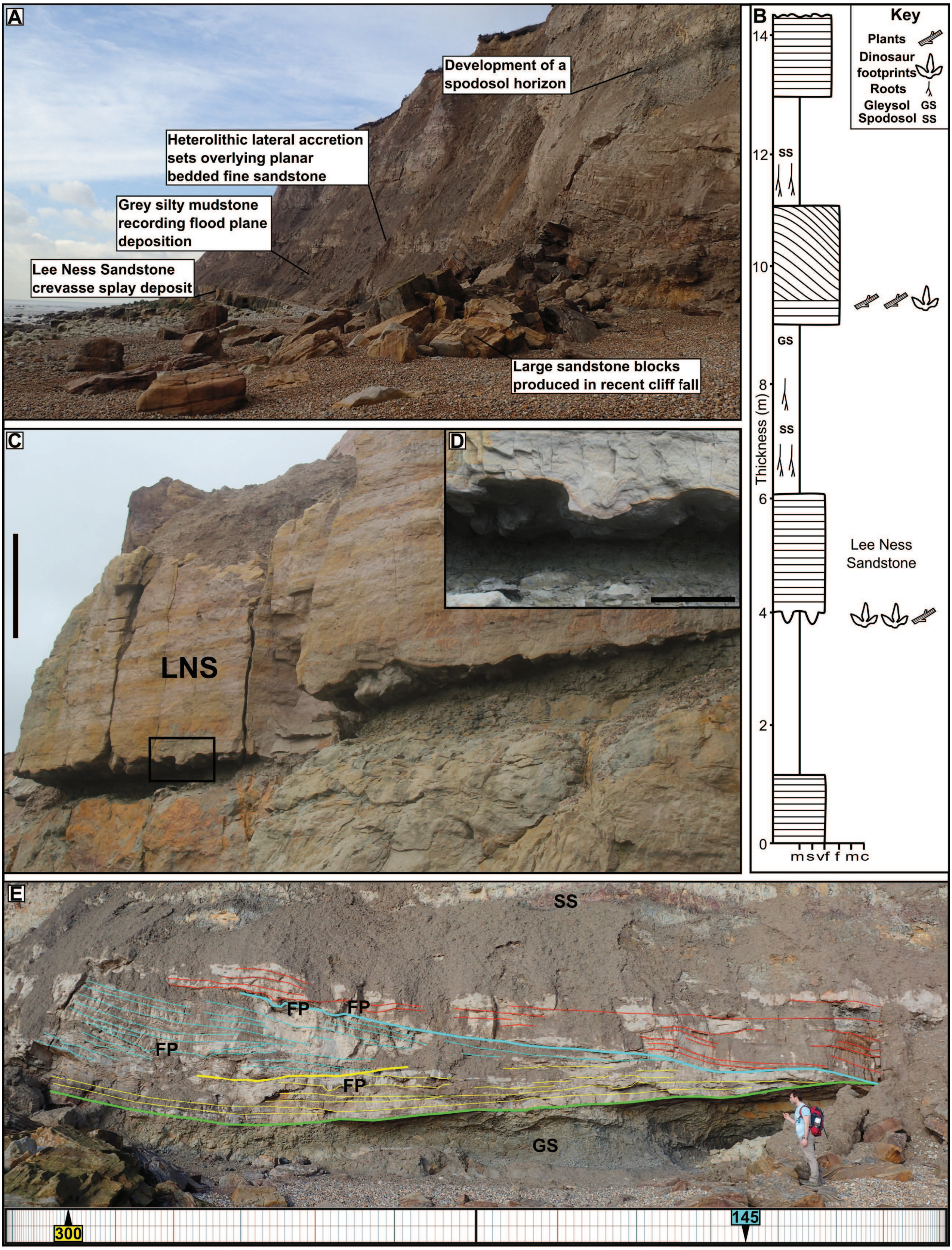

A
Development of a spodosol horizon
Heterolithic lateral accretion sets overlying planar bedded fine sandstone
Grey silty mudstone recording flood plane deposition
Lee Ness Sandstone crevasse splay deposit
Large sandstone blocks produced in recent cliff fall
B
Key
Plants
Dinosaur footprints
Roots
Gleysol GS
Spodosol SS
Thickness (m)
14
12
10
8
6
4
2
0
SS
GS
Lee Ness Sandstone
m s vf f m c
C
LNS
D
E
SS
FP
GS
300
145

Figure 2

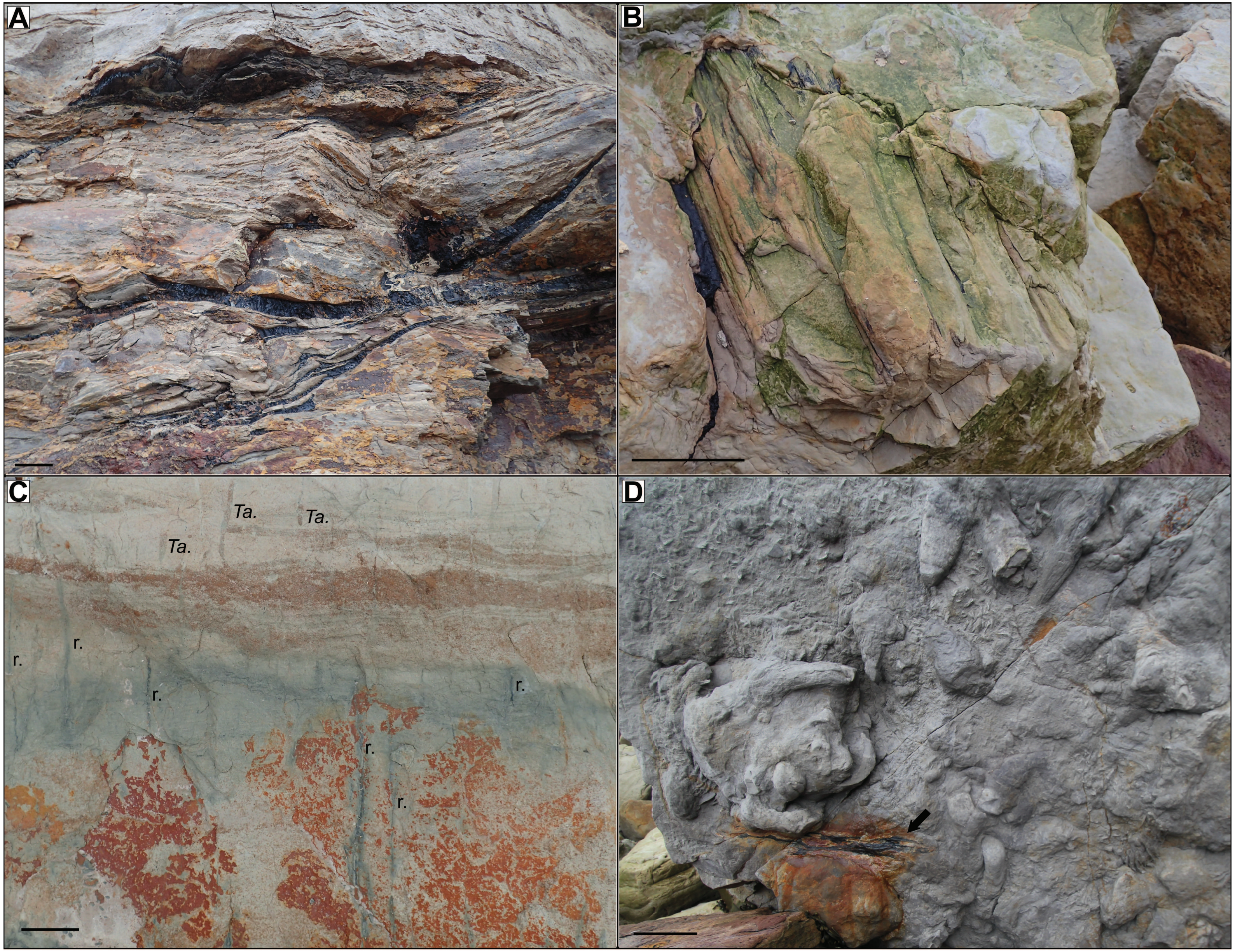


Figure 3

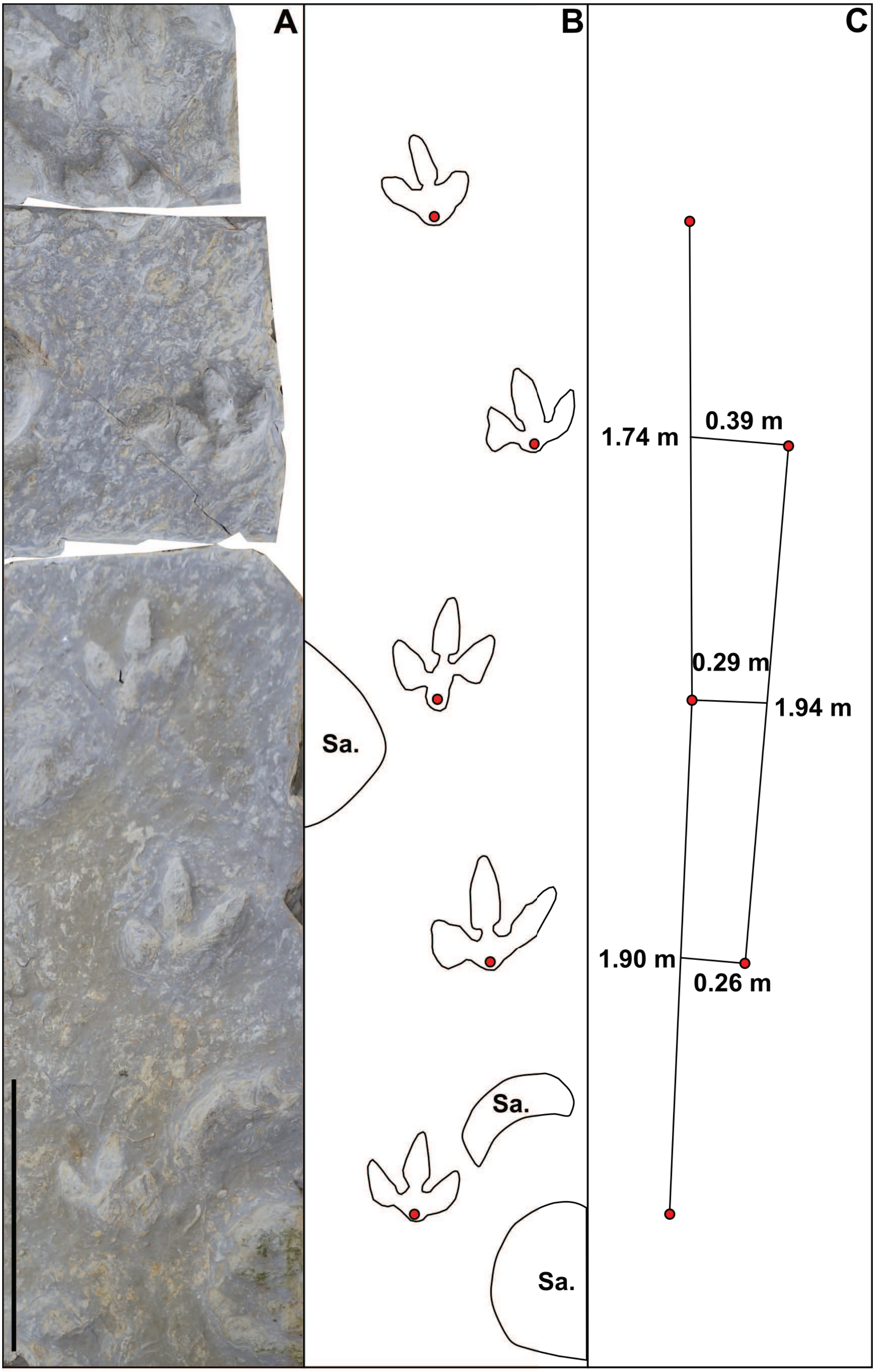


Figure 4

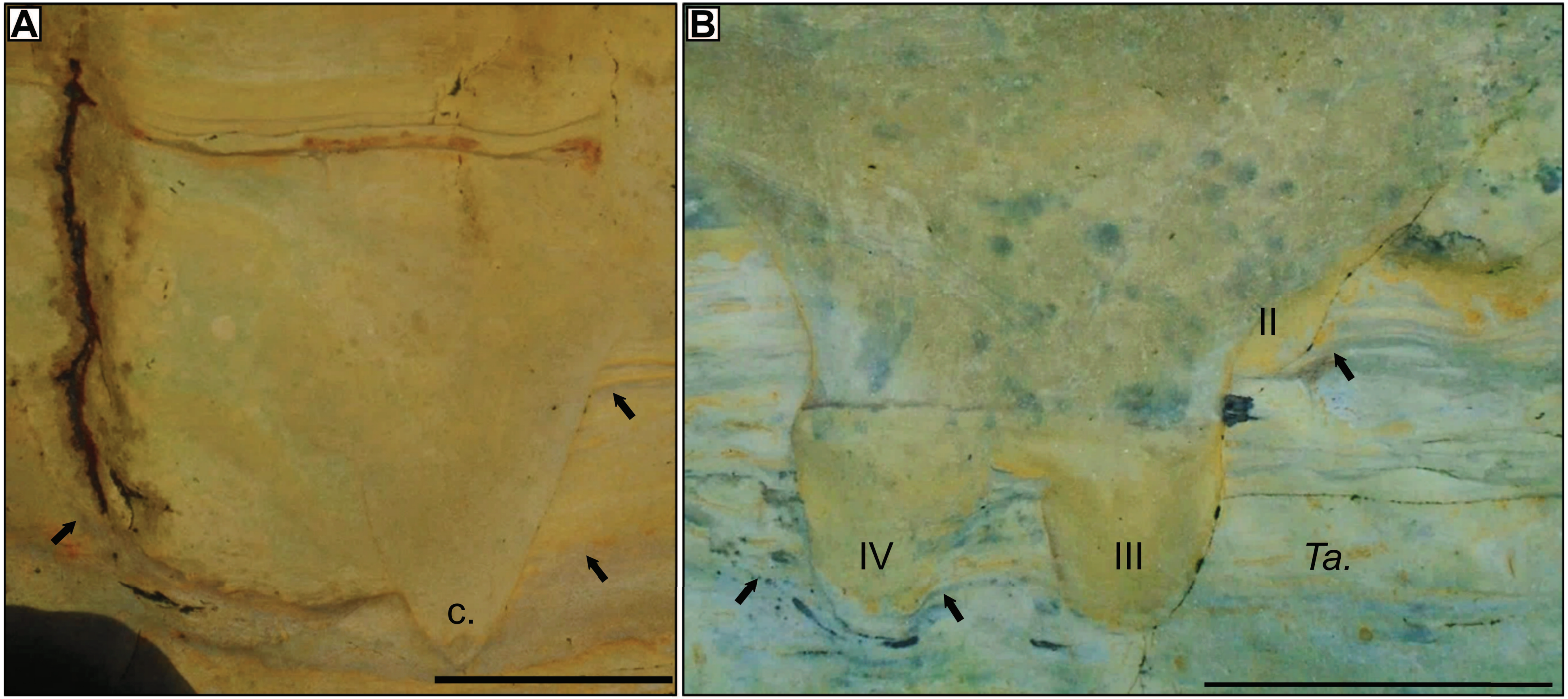
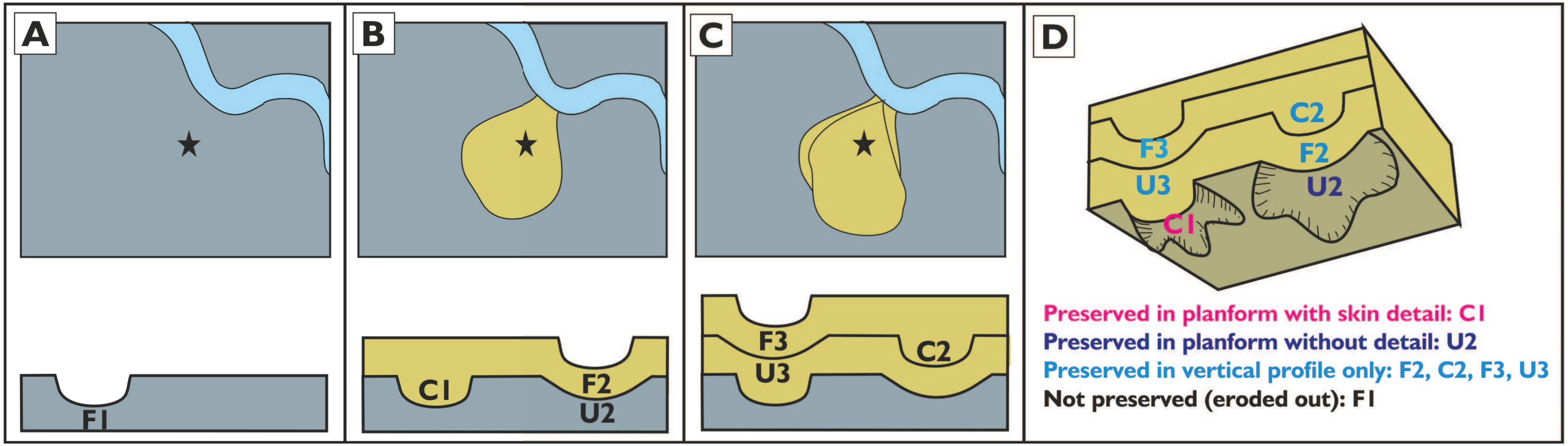


Figure 5


A
F1
B
C1
F2
U2
C
F3
U3
C2
D
C2
F3
F2
U3
U2
C1
Preserved in planform with skin detail: C1
Preserved in planform without detail: U2
Preserved in vertical profile only: F2, C2, F3, U3
Not preserved (eroded out): F1

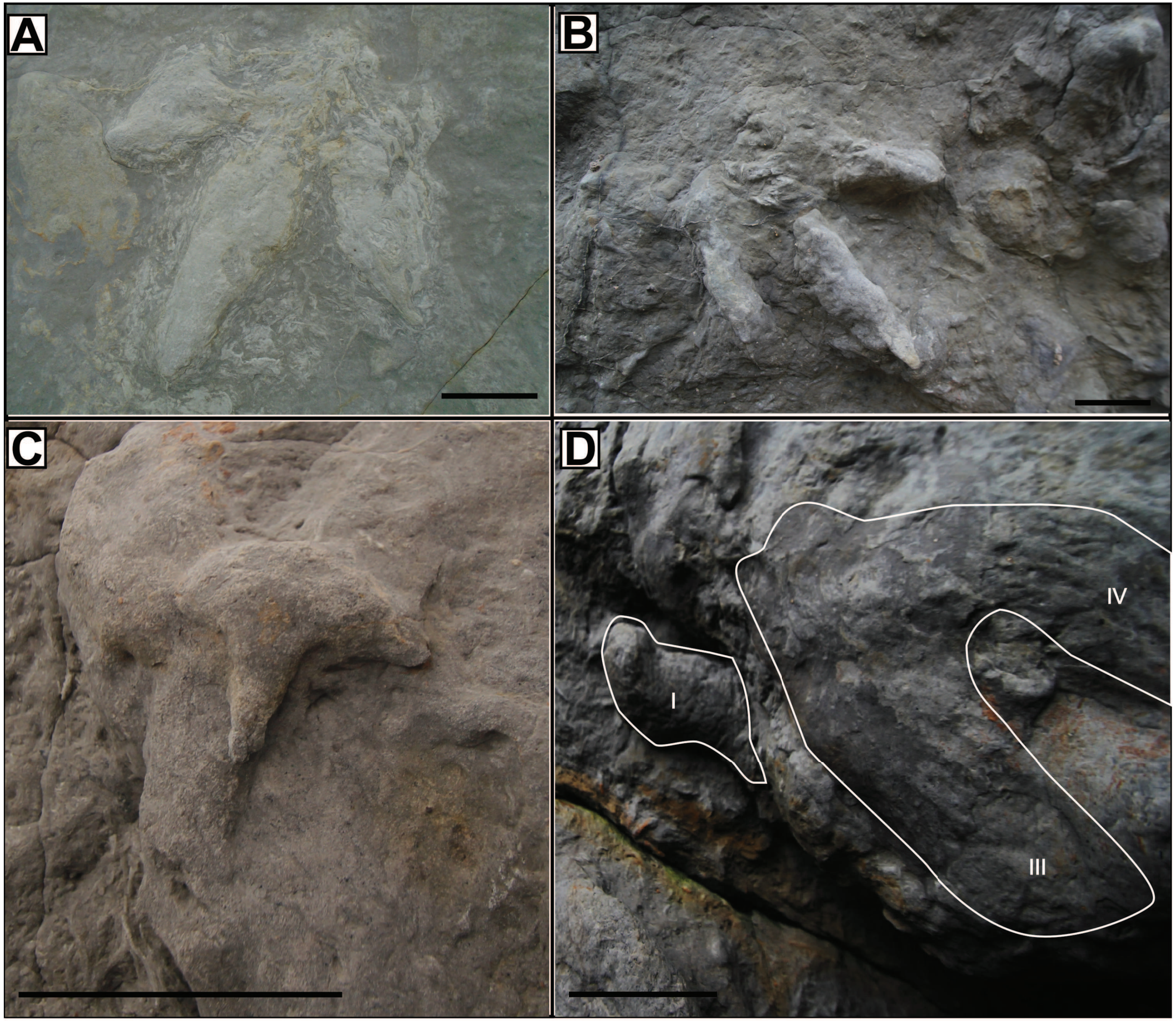


Figure 7

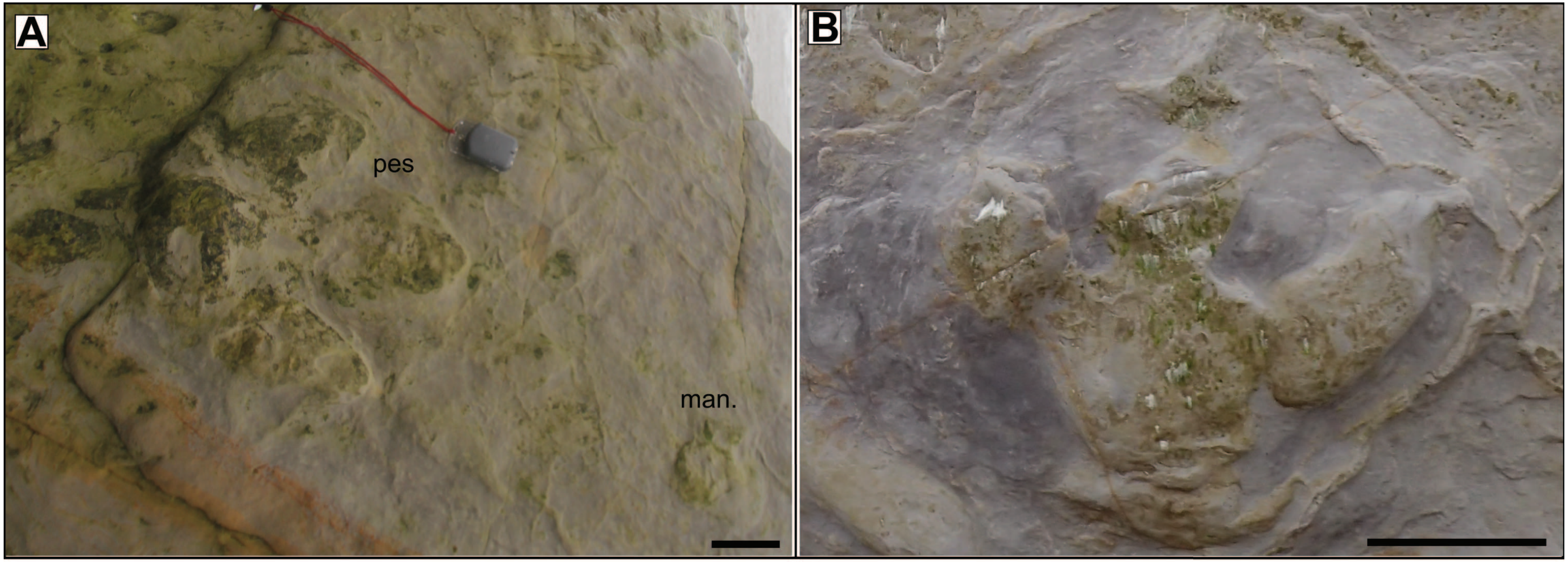


Figure 8

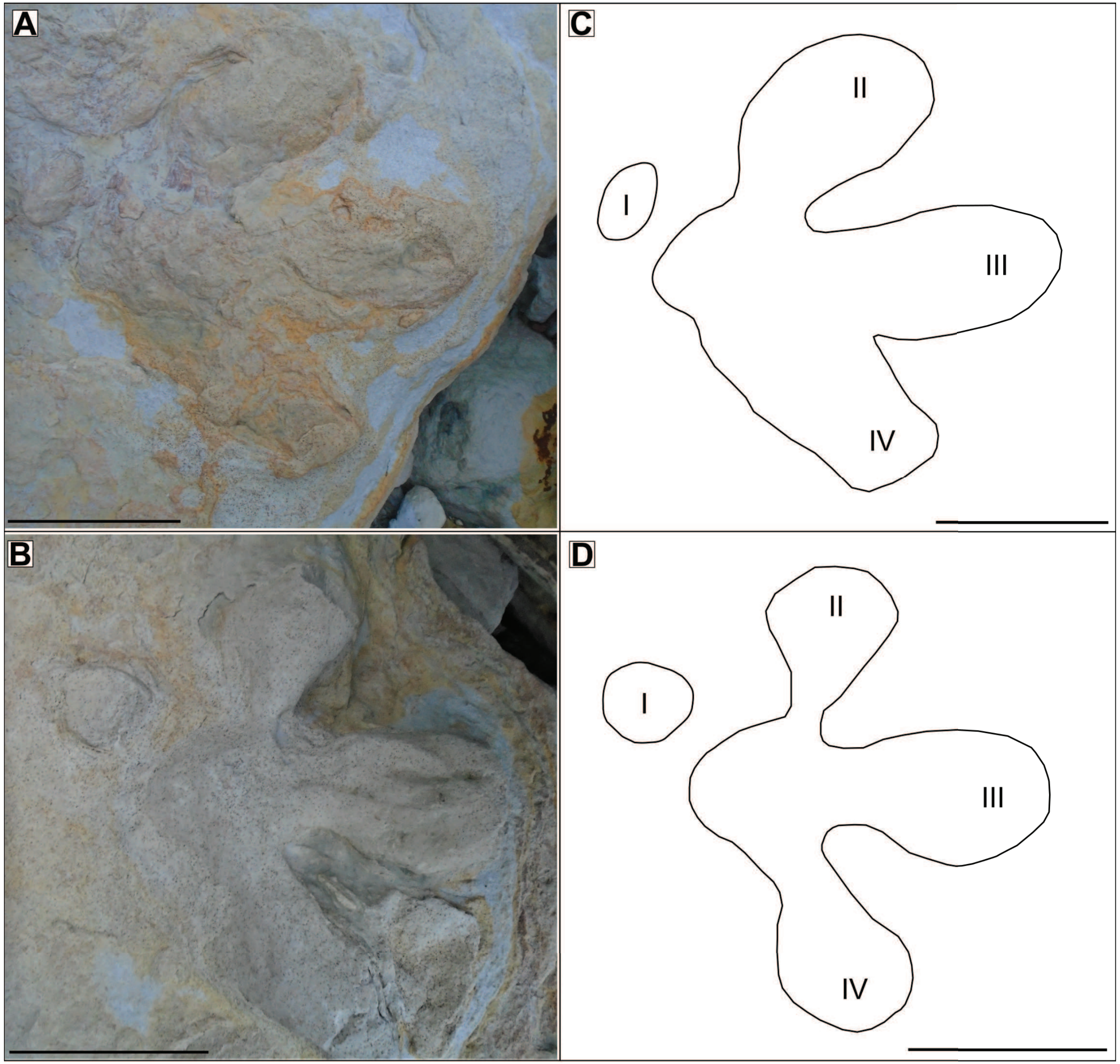


Figure 9

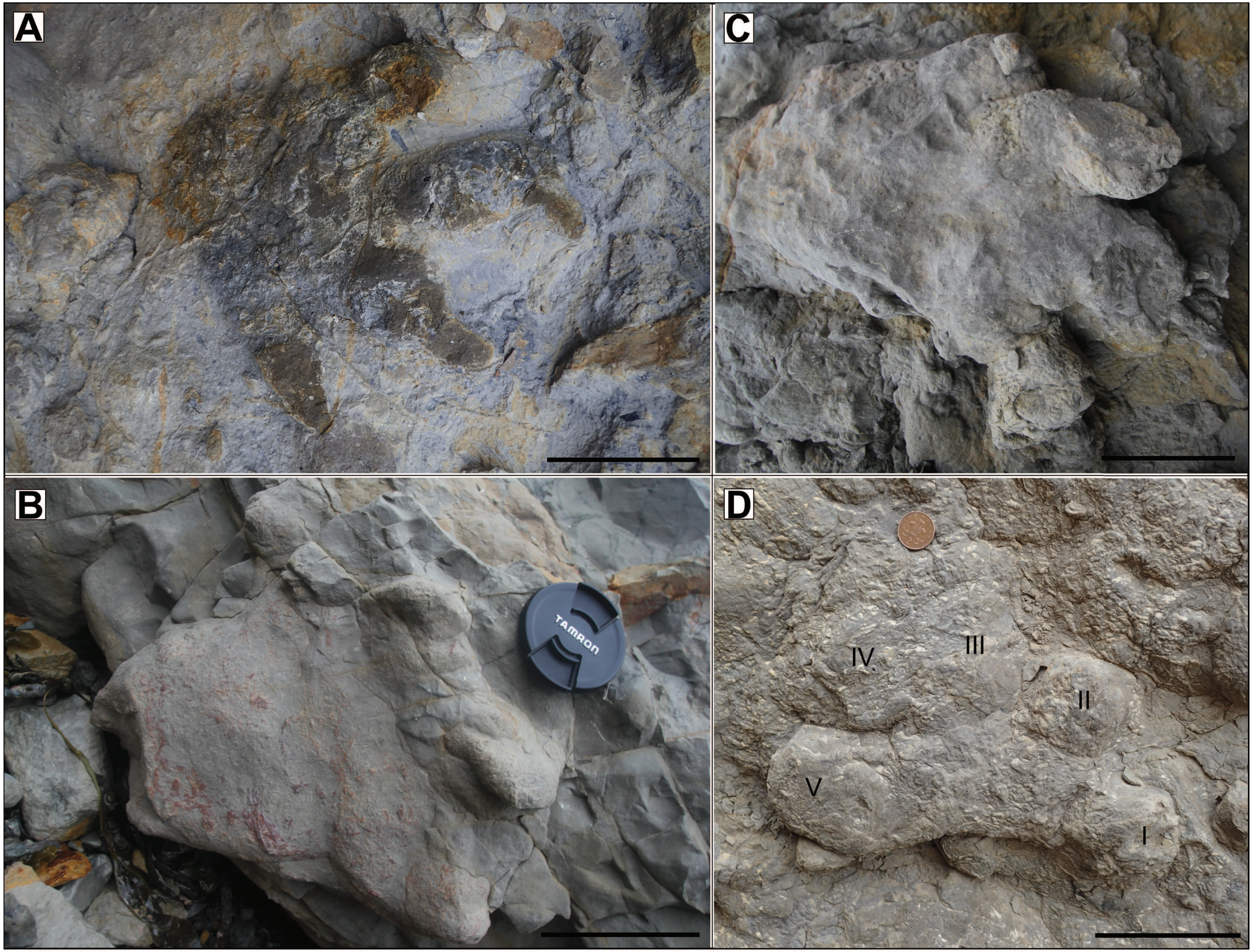


Figure 10

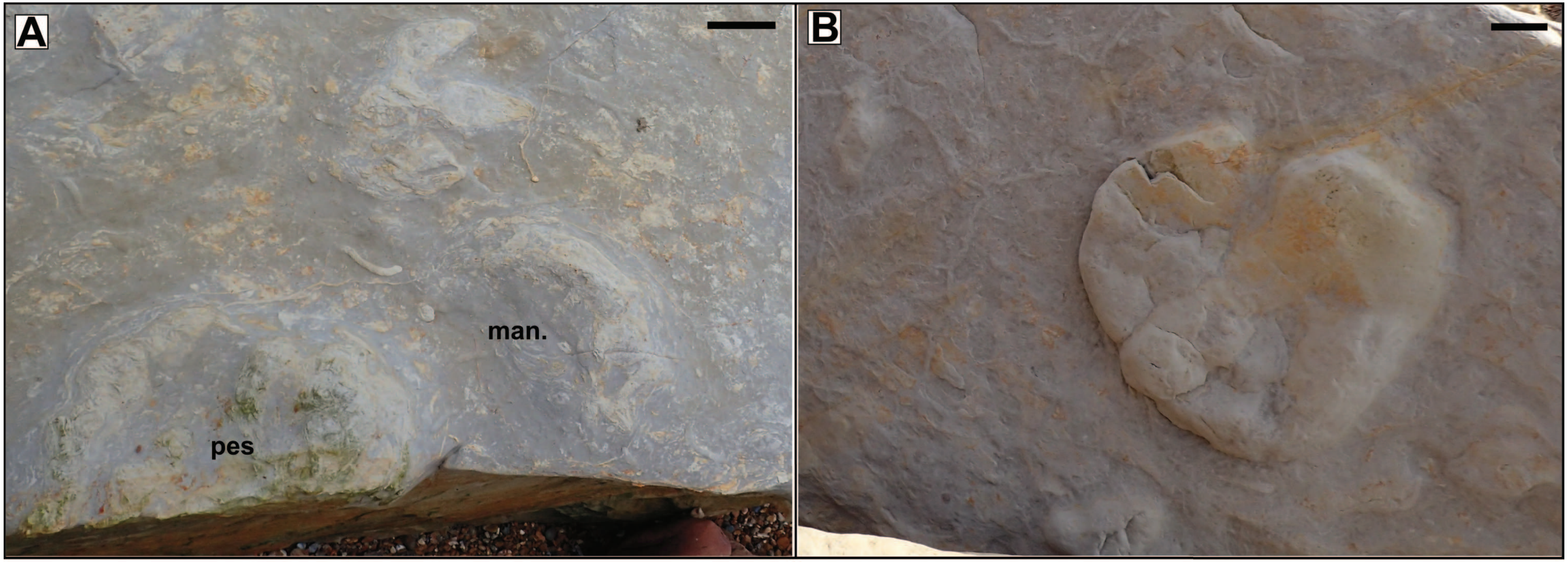


Figure 11

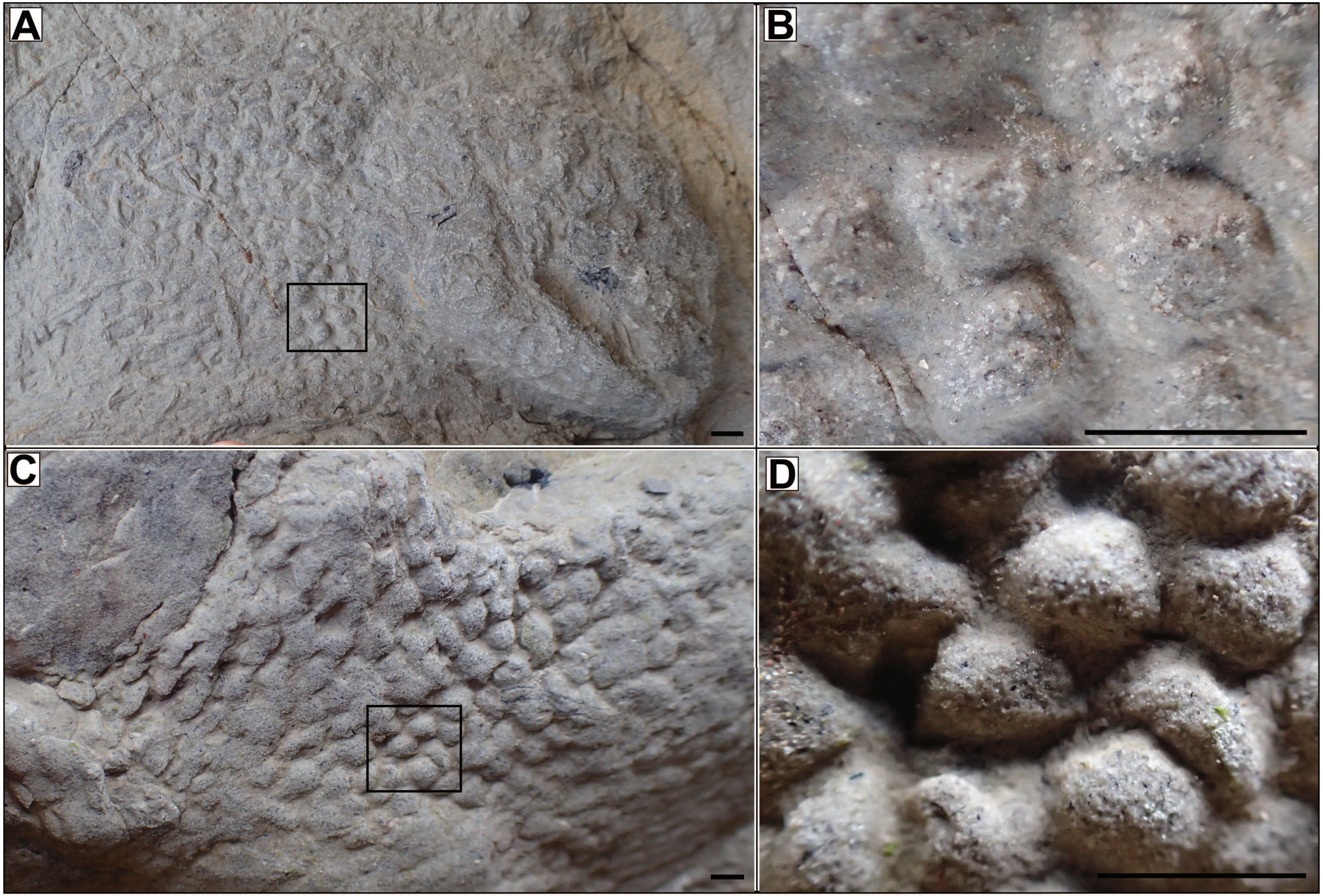


Figure 12

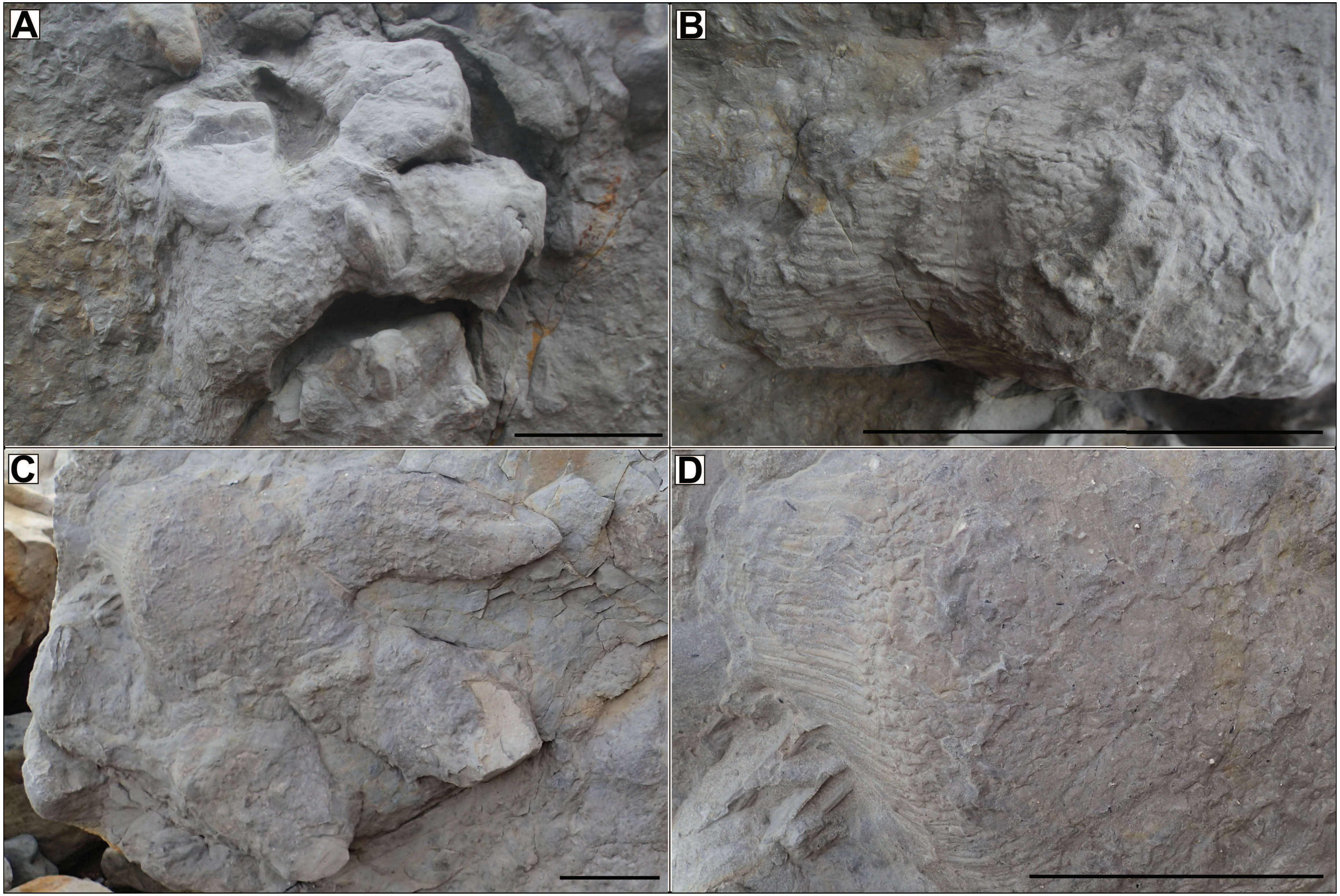


Figure 13

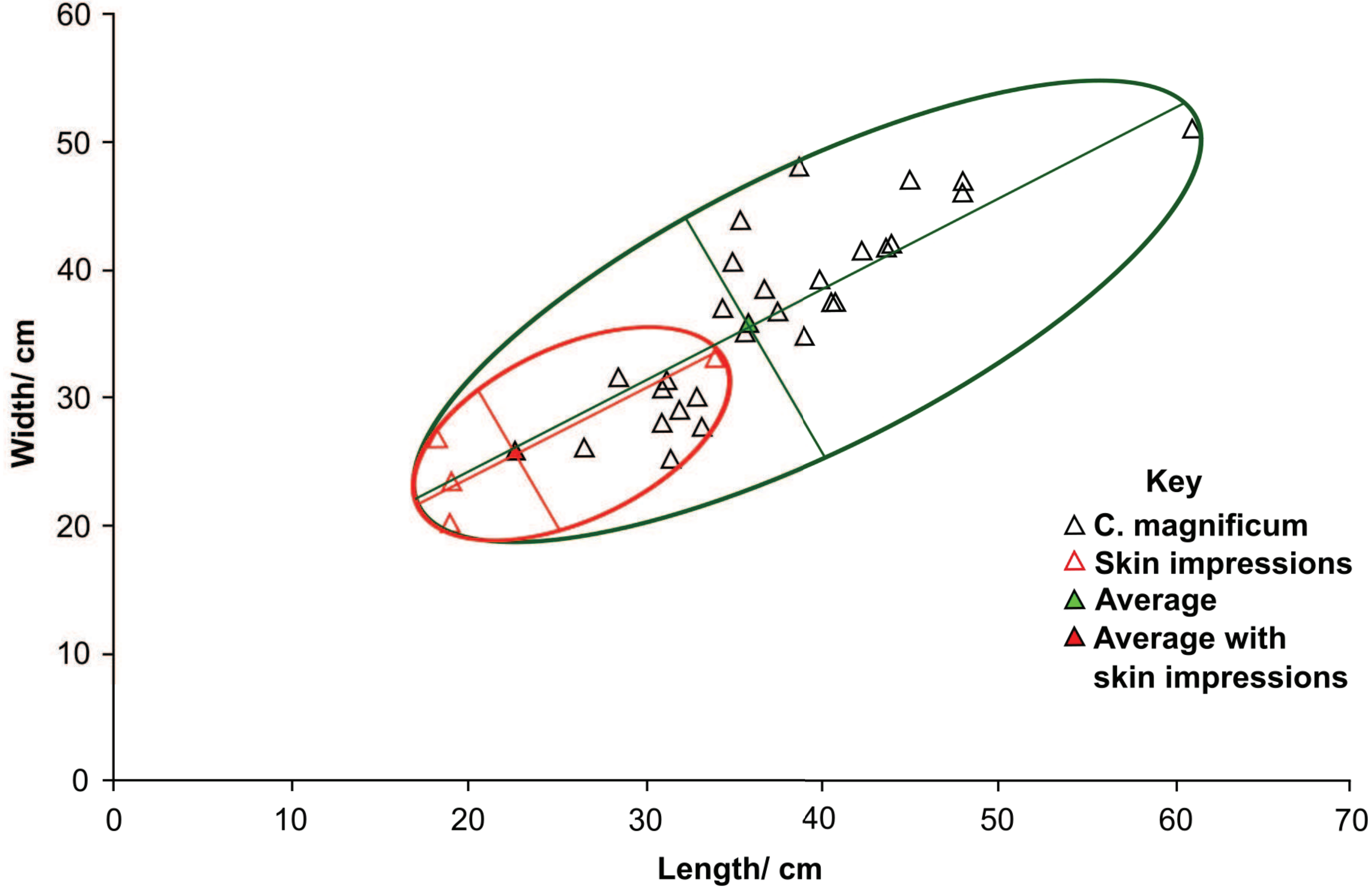

Width/ cm
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Length/ cm
Key
C. magnificum
Skin impressions
Average
Average with skin impressions

Figure 14

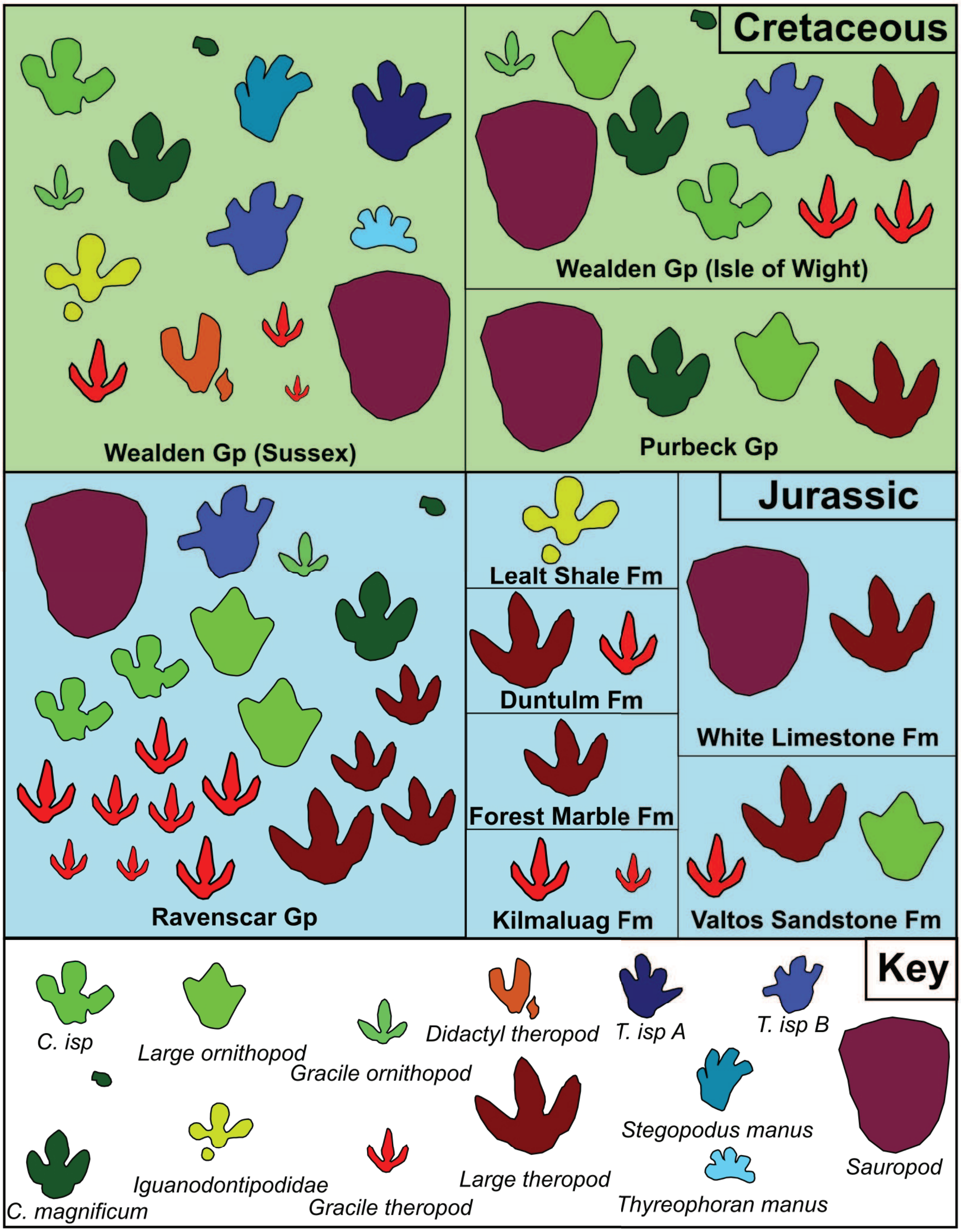
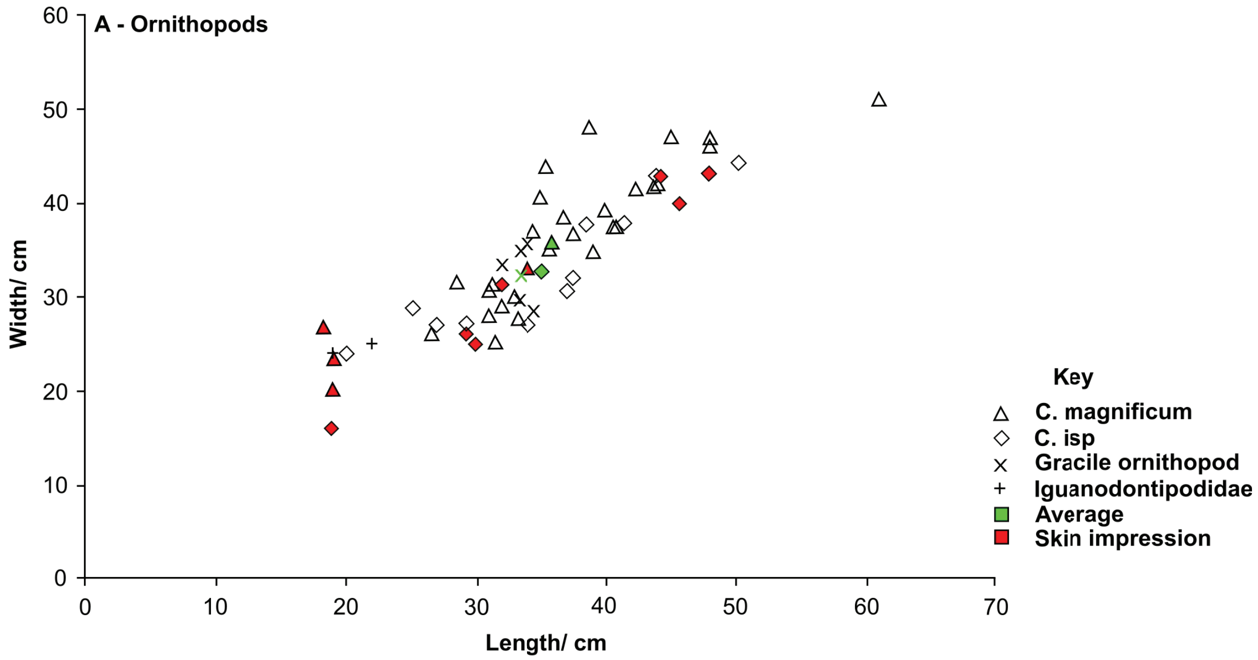

Cretaceous
Wealden Gp (Sussex)
Wealden Gp (Isle of Wight)
Purbeck Gp
Jurassic
Ravenscar Gp
Lealt Shale Fm
Duntulm Fm
Forest Marble Fm
Kilmaluag Fm
White Limestone Fm
Valtos Sandstone Fm
Key
C. isp
Large ornithopod
Gracile ornithopod
Didactyl theropod
T. isp A
T. isp B
Stegopodus manus
Sauropod
C. magnificum
Iguanodontipodidae
Gracile theropod
Large theropod
Thyreophoran manus

Figure 15


A - Ornithopods
Width/ cm
Length/ cm
Key
C. magnificum
C. isp
Gracile ornithopod
Iguanodontipodidae
Average
Skin impression

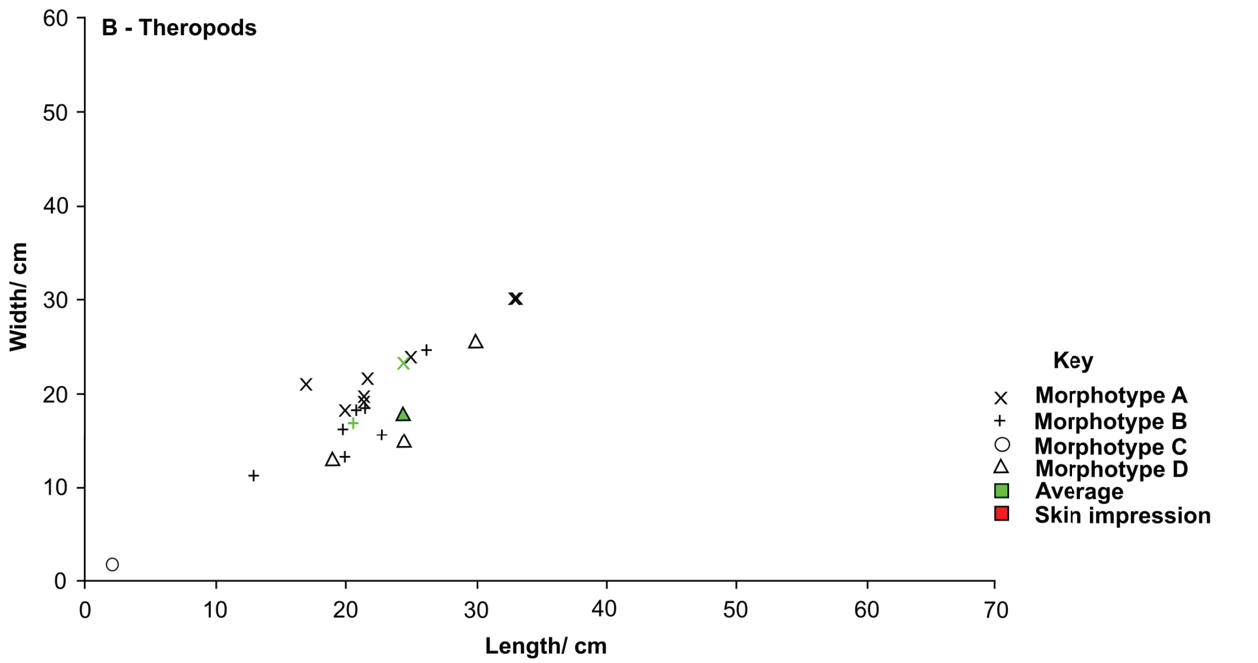

B - Theropods
Width/ cm
Length/ cm
Key
Morphotype A
Morphotype B
Morphotype C
Morphotype D
Average
Skin impression

Figure 16

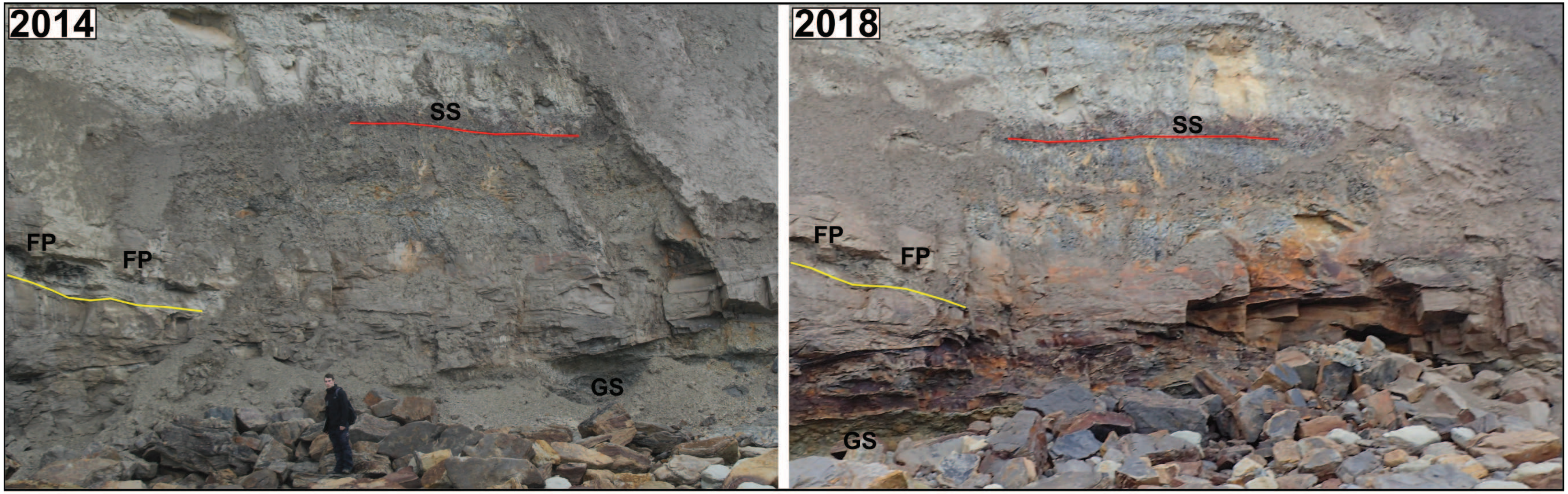
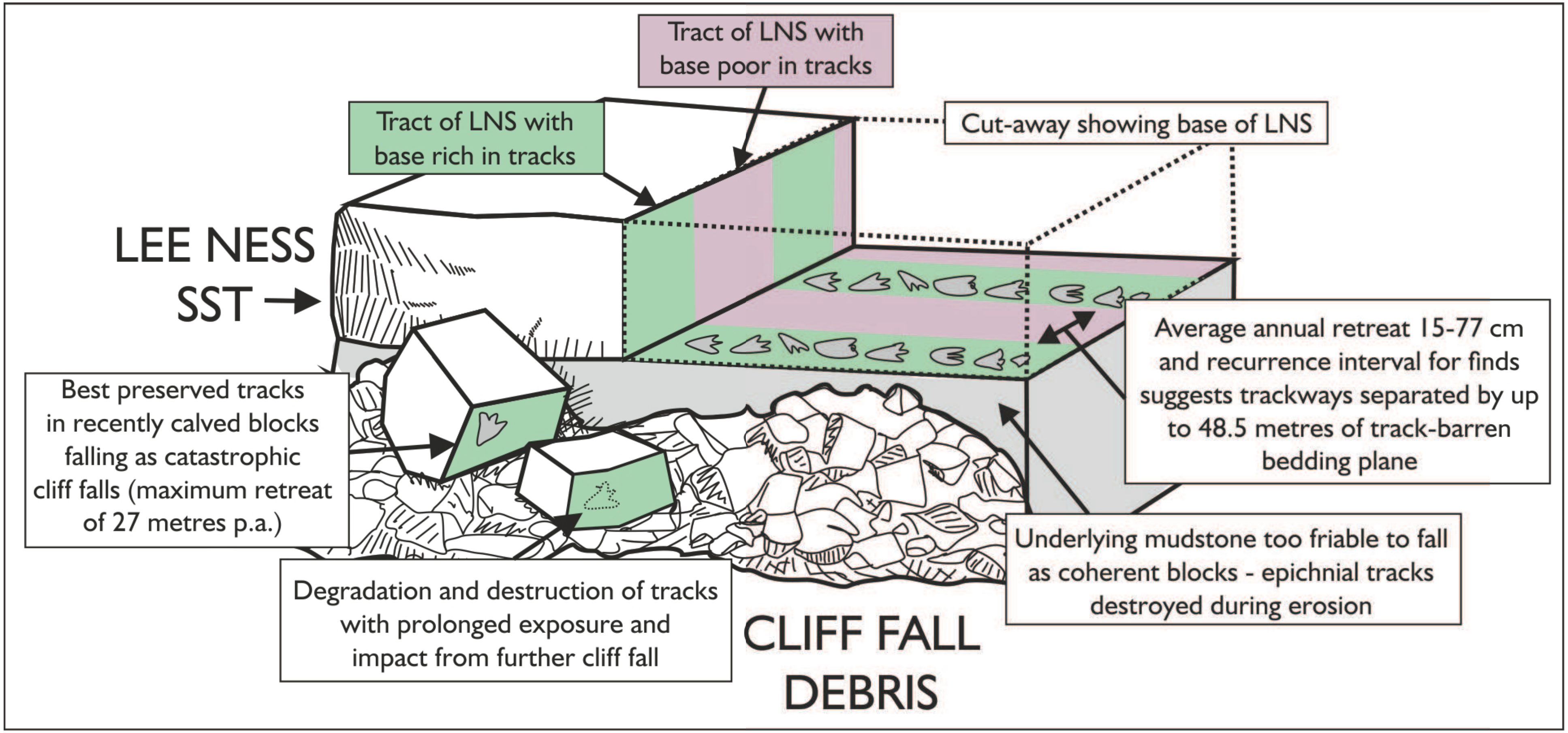


Figure 17

Figure 18


Tract of LNS with base poor in tracks
Tract of LNS with base rich in tracks
Cut-away showing base of LNS
LEE NESS SST
Average annual retreat 15-77 cm and recurrence interval for finds suggests trackways separated by up to 48.5 metres of track-barren bedding plane
Best preserved tracks in recently calved blocks falling as catastrophic cliff falls (maximum retreat of 27 metres p.a.)
Underlying mudstone too friable to fall as coherent blocks - epichnial tracks destroyed during erosion
Degradation and destruction of tracks with prolonged exposure and impact from further cliff fall
CLIFF FALL DEBRIS

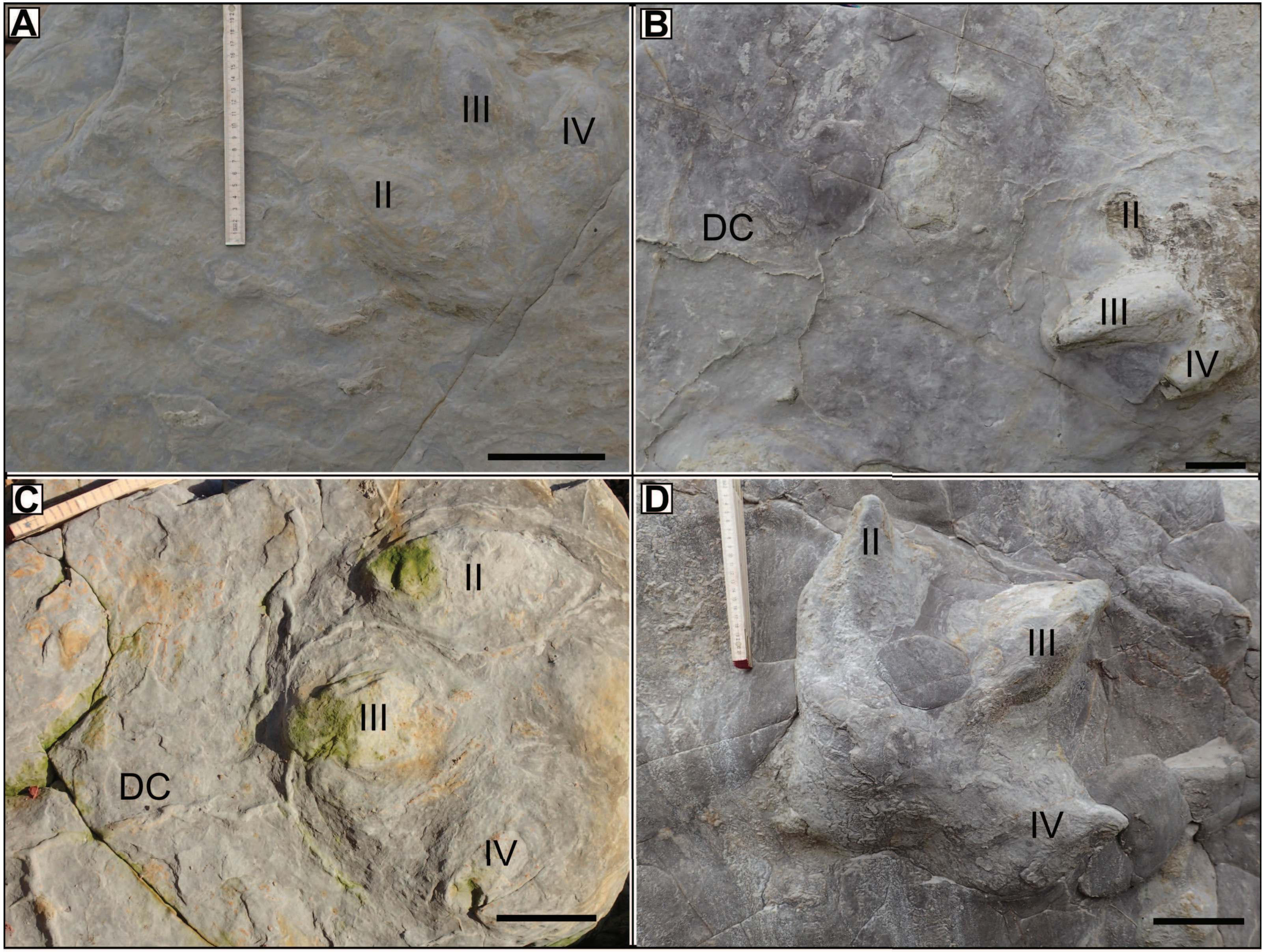


Figure 20

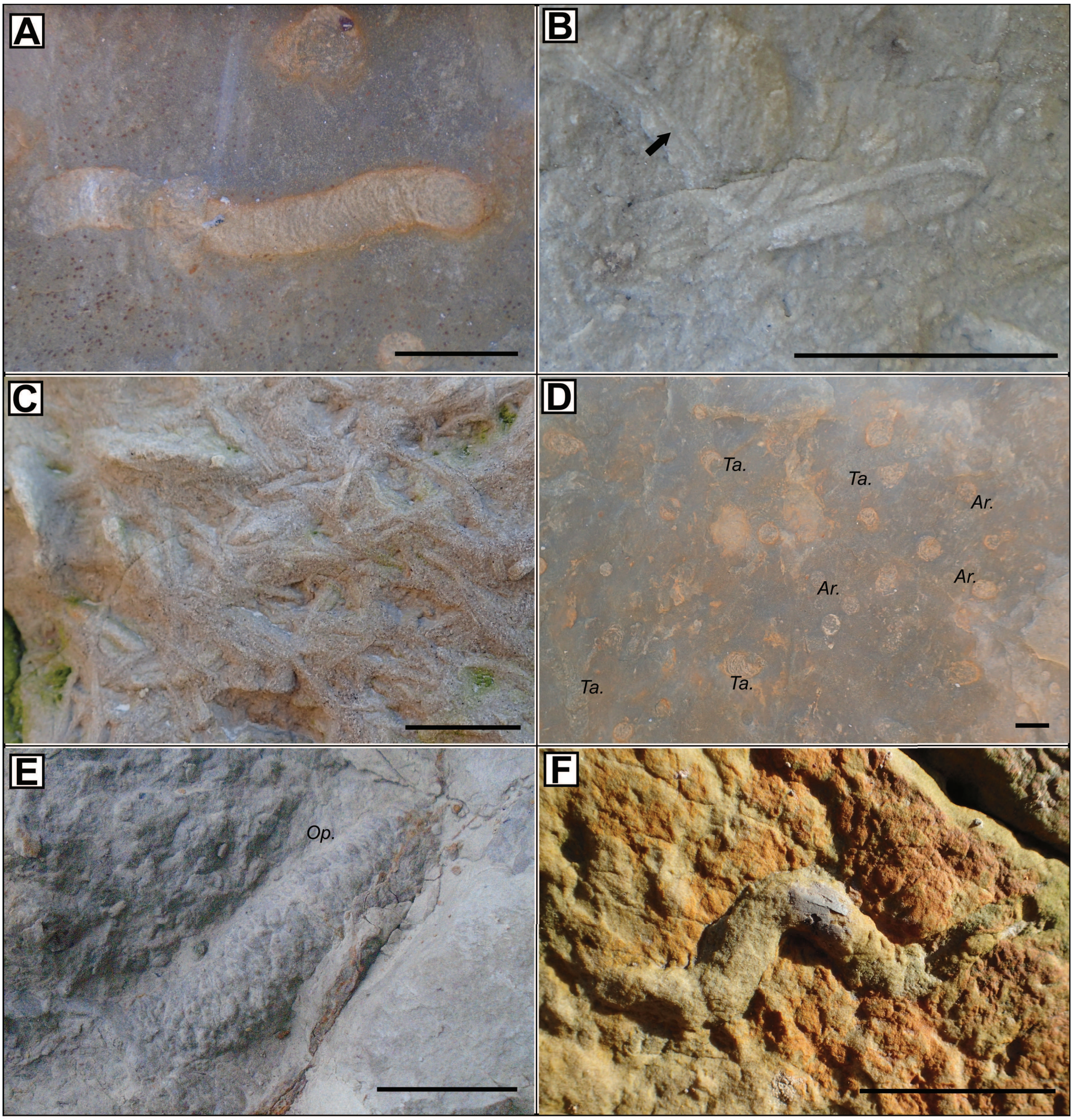
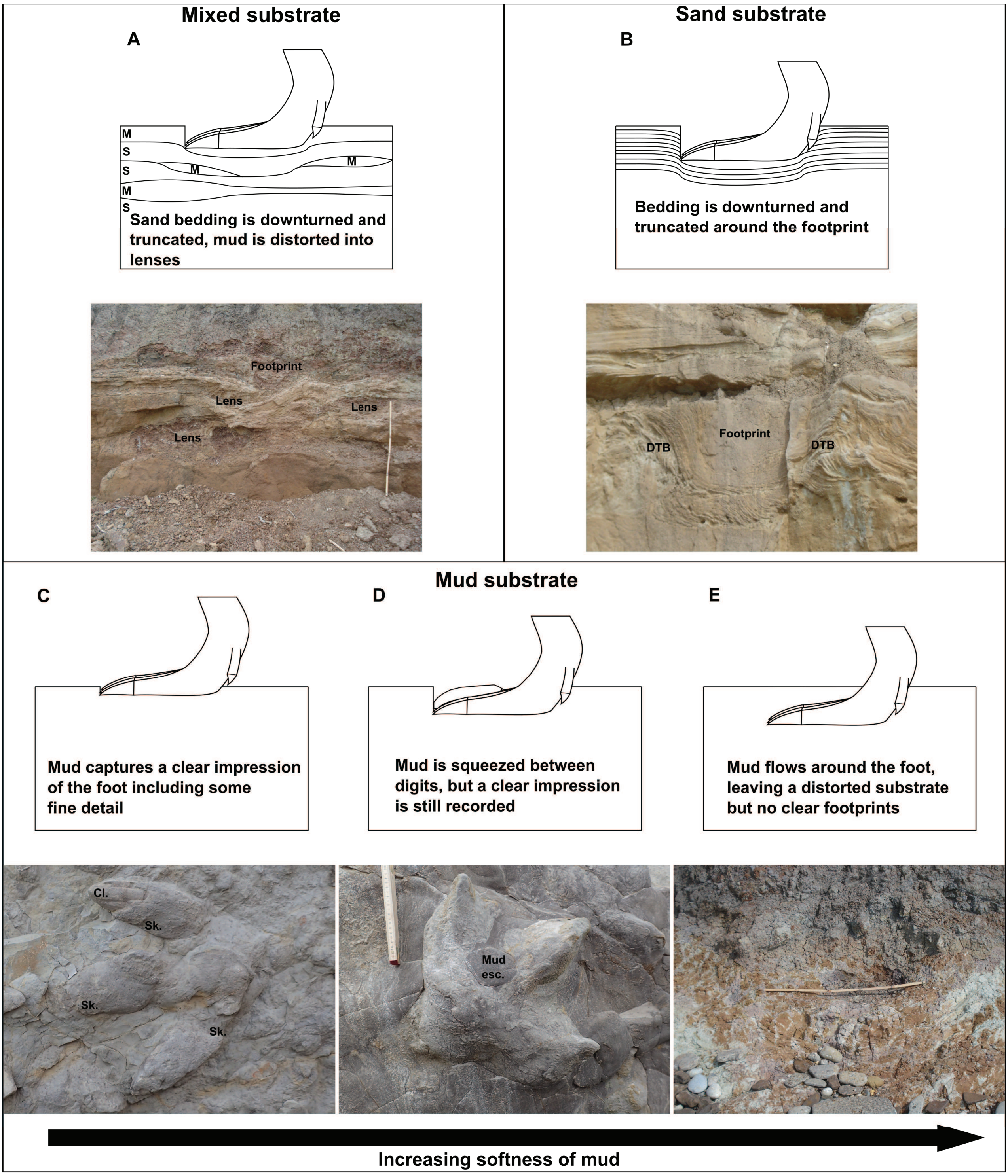


Figure 21



Mixed substrate
A
M
S
S
M
M
M
S
Sand bedding is downturned and truncated, mud is distorted into lenses
Footprint
Lens
Lens
Lens
Sand substrate
B
Bedding is downturned and truncated around the footprint
Footprint
DTB
DTB
Mud substrate
C
Mud captures a clear impression of the foot including some fine detail
D
Mud is squeezed between digits, but a clear impression is still recorded
E
Mud flows around the foot, leaving a distorted substrate but no clear footprints
Cl.
Sk.
Sk.
Sk.
Mud esc.
Increasing softness of mud

Figure 22

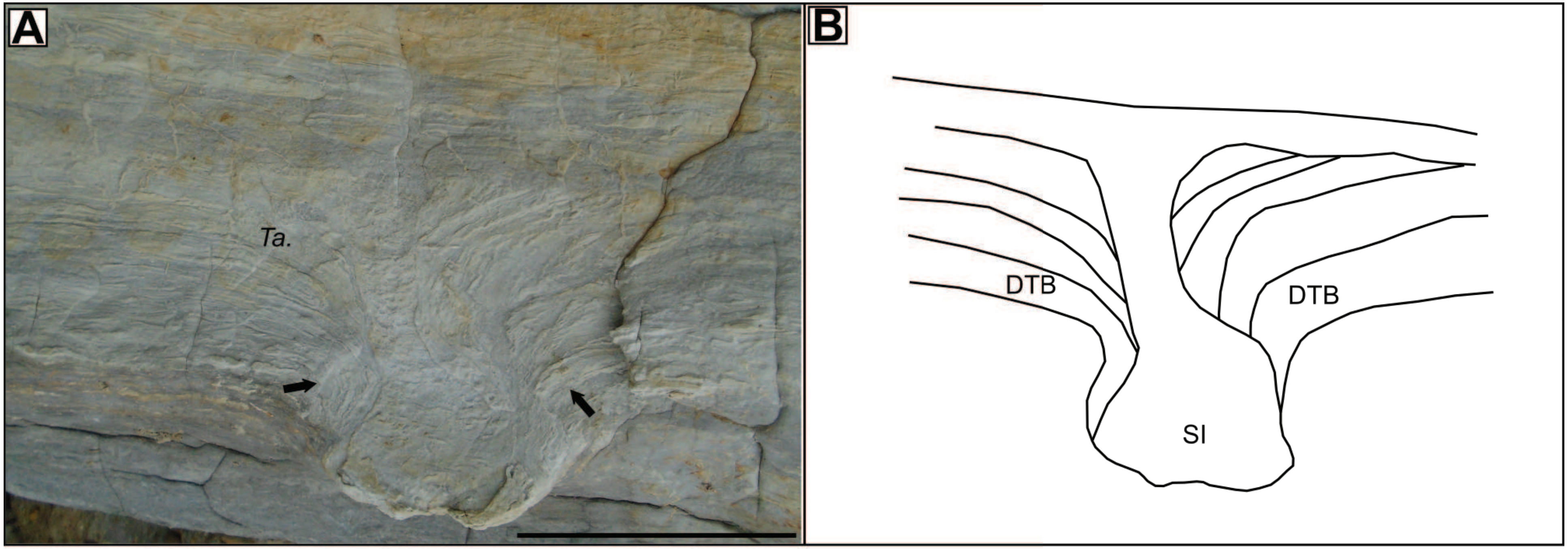


Figure 23

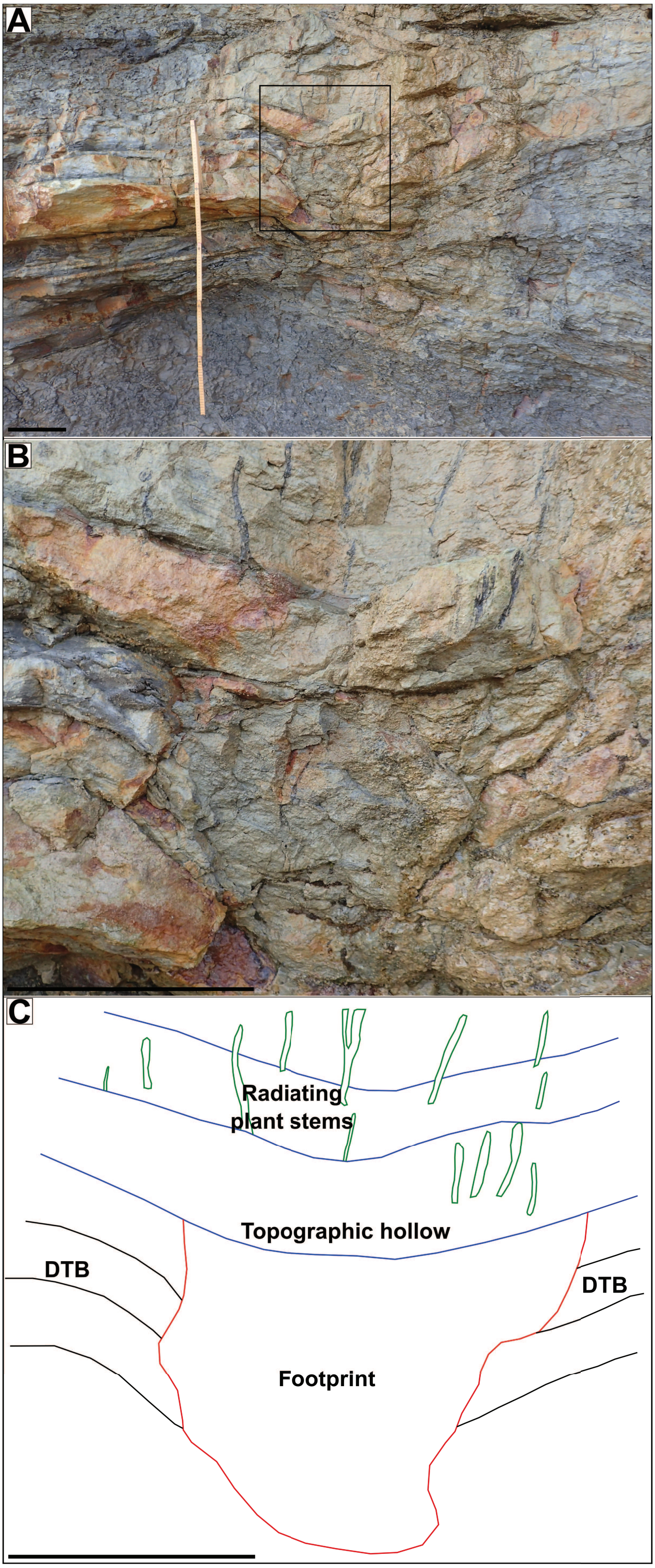

A
B
C
Radiating
plant stems
Topographic hollow
DTB
DTB
Footprint

Figure 24

Morphotype	Abundance	Abundance of skin impressions	Length/ cm	Width/ cm
Ornithopod	**56**	**11**	**18.3 – 61 average 34.7**	**16 – 51 average 33.8**
Caririchnium magnificum	31	4	18.3 – 61 average 36	20.1 – 51 average 35.7
Caririchnium isp.	18	7	19 – 50.2 average 35.1	16 – 44.2 average 32.4
Iguanodontipodidae	2	0	19 – 22 average 20.5	24 – 25 average 24.5
Gracile ornithopod	5	0	31.3 – 33.8 average 32.8	28.8 – 36 average 32.7
Theropod	**19**	**0**	**2.1 – 33.1 average 21.7**	**1.8 – 30.2 average 18.8**
Theropod morphotype A	8	0	17 – 33.1 average 24.1	18.2 – 30.2 average 23
Theropod morphotype B	7	0	13 – 26.2 average 20.6	11.2 – 24.6 average 16.8
Theropod morphotype C	1	0	2.1	1.8
Theropod morphotype D	3	0	19 – 30 average 24.5	13 – 25.6 average 17.9
Thyreophoran	**5**	**3**	**25 – 34 average 29**	**26 – 33 average 29.2**
Tetrapodosaurus isp. (A)	2	2	25 – 27 average 26	26 – 28.8 average 27.4
Tetrapodosaurus isp. (B)	1	0	30	33
Stegopodus manus	1	1	34	29
Unnamed thyreophoran	1	0	18	28
Sauropod	**3**	**0**	**58-61 average 59.5**	**49-51 average 50**

A record of the dimensions of all new dinosaur footprint casts observed in the Ashdown Formation. Footprints are divided by ichnospecies and ordered by abundance within their tracemaker clade.

Period of cliff retreat between footprint finds	Minimum retreat (m)	Maximum retreat (m)	Average retreat (m)	Maximum short-term retreat (m)
1862-1918 (**56 yrs**)	8.40	43.12	25.76	-
1918-1981 (**63 yrs**)	9.45	48.51	28.98	-
1981-1991 (**10 yrs**)	1.50	7.70	4.60	123.40
1992-2014 (**22 yrs**)	3.30	16.94	10.12	271.48

Potential distance between dinosaur trackway sites in the Lee Ness Sandstone, based on different rates of cliff retreat. Maximum rate of retreat is 77 cm/year, minimum rate of retreat is 15 cm/year, average rate of retreat is 46 cm/year, from Cleeve and Williams (1987). The maximum short-term retreat is taken from the 1996-2002 cliff retreat (1,234 cm/year) from Rother District Council (2012), considering only periods of retreat under 25 years.

Ichnoassemblage	Ichnotaxa	Known Examples	Description	Likely tracemaker	Figure
A	*Arenicolites isp.*	Rare within fallen blocks of the LNS	Paired burrow shafts (8-12 mm in diameter) separated by 21-44 mm and viewed on bed surfaces. No discernible internal structure or spreite. Infill similar to the host sediment.	Vermiform organism (Häntzschel, 1975)	18D
	Taenidium barretti	Common throughout Ashdown Fm	Sub-vertical to sub-horizontal, unlined, sub-cylindrical, backfilled burrow. Burrow lengths range from 30-75 mm and burrow widths from 9-11 mm.	Small arthropods or vermiform organisms (Shillito & Davies, 2017).	18A, D
B	*Cochlichnus cochi*	Single example on base of LNS	40 mm-long smooth, non-branching, sinusoidal burrow of uniform 5 mm width.	Annelids (cf. Hasiotis, 2002) or insect larvae (cf. Metz, 1987).	18F
	Ophiomorpha nodosa	Three examples on base of LNS	Sub-cylindrical, sub-horizontal, unbranched pellet lined burrows (diameter 12-15 mm and length 50-80 mm).	Crustaceans (Frey et al., 1978)	18E
	Palaeophycus striatus	Common throughout Ashdown Fm and abundant on base of LNS	Unbranching horizontal burrows with striated ornamentation, preserved in positive hyporelief. Burrows are approximately cylindrical, with width 1-3 mm wide and length 6-28 mm long and consist of a structureless infill of the same lithology as the host rock. False branching is common, due to the overprinting of multiple burrows in dense assemblages.	Vermiform organism (Pemberton and Frey, 1982).	18B, C
	T. barretti	Common throughout Ashdown Fm	Sub-vertical to sub-horizontal, unlined, sub-cylindrical, backfilled burrow. Burrow lengths range from 30-75 mm and burrow widths from 9-11 mm.	Small arthropods or vermiform organisms (Shillito & Davies, 2017).	18A, D

A description of all invertebrate trace fossils observed in the Ashdown Formation. A total of five different ichnospecies were observed split across two commonly observed ichnoassemblages.