

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

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8

9 **Abstract**

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

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

28 **1. Introduction**

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

34 In this paper we report a diverse ichnoassemblage of dinosaur footprints that have been
35 revealed within an outcrop that is constantly evolving due to coastal erosion, and which is well-
36 suited to recognise the sedimentological, palaeoenvironmental and outcrop controls on the
37 morphology and distribution of the hosted footprints. The outcrop forms part of the Lower
38 Cretaceous Wealden Group (East Sussex, southern England), a late-stage rift succession of
39 non-marine and marginal-marine strata within the Wessex Basin, which has been the focus of
40 geological investigation for almost two centuries (Martin, 1828; Topley, 1875; Rawson et al.,
41 1978; Hopson et al., 2008; Radley and Allen, 2012).

42 The Wealden Group has both historic and ongoing significance for dinosaur research: it
43 yielded the first known *Iguanodon* (Mantell, 1825) and ankylosaur fossils (Mantell, 1833), and
44 much more recently has seen the discovery of an exceptionally-preserved fossil iguanodontian
45 brain (Brasier et al., 2017). Whilst diverse body fossils from 39 dinosaur species are described
46 from the Wealden (Batten, 2011; Austen and Batten, 2018), its vertebrate ichnology is less well
47 described. Sporadic reports of footprints have been made since 1846 (Tagart, 1846; Beckles,

48 1851; Tylor, 1862; Ticehurst, 1928; Sarjeant, 1974; Delair, 1989; Woodhams and Hines, 1989;
49 Parkes, 1993; Sarjeant et al., 1998), but no new major discoveries have been described for the
50 last quarter of a century (Parkes, 1993). The previously described vertebrate ichnofauna is
51 dominated by tracks reported as “*Iguanodon* footprints” (e.g. Tylor, 1862; Delair and Sergeant,
52 1985) and two morphotypes of theropod track (Woodhams and Hines, 1989), although three
53 putative sauropod footprints have also recently been reported (Jarzembowski et al., 2015;
54 Austen and Batten, 2018).

55 Here, we describe new trackway material exposed by ongoing cliff collapse between 2014-
56 2018. Our findings greatly increase the number of footprint morphotypes from 4 to 13; these
57 are attributable to theropod, ornithopod, thyreophoran and possibly sauropod dinosaur
58 tracemakers, and some show exceptionally well-preserved skin impressions. The purpose of
59 this paper is to (1) describe these newly-discovered trace fossils and discuss their implications
60 for the dinosaur communities known from the Lower Cretaceous of the UK; (2) demonstrate
61 that the sporadic discovery of footprints from the Wealden Group reflects the recent and
62 ongoing geomorphic evolution of a cliff outcrop which contains a prominent dinosaur
63 footprint-bearing horizon; (3) discuss why this particular tracksite yields so many high-fidelity
64 traces; and (4) discuss the extent to which ancient dinosaur-landscape interactions can be
65 understood using footprint and sedimentary records which are naturally incomplete.

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

67 The footprints described here were discovered in the Ashdown Formation, in a near-
68 continuous 6 km-long coastal cliff section extending between Fairlight Cove (50° 52' 35.66"
69 N, 0° 40' 16.13" E) and Hastings (50° 51' 25.03" N, 0° 35' 58.20" E). In this eastern part of
70 the Wessex Basin (the Weald Sub-Basin), the Wealden Group has a thickness of c. 400 m
71 (Gallois and Worssam, 1993) (Fig. 1). Historically the internal stratigraphy of the group has

72 been inconsistently applied, but here we follow the most recent stratigraphic nomenclature of
73 the British Geological Survey (Hopson et al., 2008) whereby the group comprises, in ascending
74 order; the Ashdown Formation, the Wadhurst Clay Formation, the Tunbridge Wells Sand
75 Formation, and the Weald Clay Formation.

76 The Ashdown Formation is a 180-215 m thick coarsening-upwards succession of fine- to
77 medium-grained sandstones and silty mudstones (Fig. 2A, B), of which only the upper 130 m
78 is exposed, cropping out as a gentle anticline along the Hastings-Fairlight section (Lake and
79 Shephard-Thorn, 1987). Footprint-bearing strata are most common within and beneath the Lee
80 Ness Sandstone (hereafter, “LNS”), an informal stratigraphic marker consisting of a prominent
81 2 m thick tabular body of grey-yellow, very fine- to fine-grained, lithic arenite (Fig. 2C, D),
82 125 m beneath the top of the Ashdown Formation. The formation is Berriasian-Valanginian (c.
83 145-134 Ma) in age (Horne, 1995), based on ostracod biostratigraphy (index fossils from the
84 *Cypridea propunctata* and *C. menevensis* subzones are known from the Fairlight borehole;
85 Allen, 1985). However, the precise age of the LNS within this interval is poorly constrained,
86 as the stratigraphic levels of ostracod index fossils are unreported (Anderson, 1985; Horne,
87 1995).

88 2.1 Depositional environment

89 The Ashdown Formation is dominated by overbank floodplain deposits of small meandering
90 fluvial systems, which were active in southern Laurasia at a latitude of 30°-35°N, under
91 subtropical-temperate climatic conditions (Allen, 1998). Mudstones are the dominant (c. 60%)
92 lithology but are poorly exposed as they are commonly weathered deeply into the rock face.
93 The deep weathering results in most of the strata at outcrop being obscured by sediment wash
94 or slumped material arising from the mudstones. Where fresh mudstone surfaces can be
95 observed they are seen to be pedogenic: variably purple, yellow, grey-brown or mottled, they

96 contain abundant root traces, attesting to the development of gleysols and spodosols (Mack et
97 al., 1993) on the alluvial floodplain. The dominant sandstone lithologies are either (1) tabular
98 bodies 1-6 metres thick of fine- to medium-grained lithic arenites with planar-stratification and
99 abundant bioturbation (such as comprise the LNS), or (2) unbioturbated medium-coarse-
100 grained lithic arenites with cross-stratification, and sometimes organised as <4 metre-thick
101 heterolithic lateral accretion sets (Fig. 2E). Respectively, these two architectural styles record
102 overbank crevasse splay deposition of coarser sediment and in-channel point bar development
103 in meandering river channels. Carbonaceous strata, in the form of coalified plant debris beds,
104 are common (Fig. 3) and, together with an infrequent macroflora, show that the floodplains
105 were colonized by a floral assemblage of gymnosperms, ferns and minor lycopods (Watson
106 and Alvin, 1996). Both the stratigraphic distribution of plant fossils and chemical weathering
107 proxies, from clay minerals, suggest that the climate of deposition was warm to subtropical,
108 and seasonally wet (Watson and Alvin, 1996; Allen et al., 1998; Akinlotan, 2017).

109 2.2. Discovery of new footprints in the Ashdown Formation

110 The footprints described here significantly expand the known dinosaur ichnofauna of the
111 Wealden Group of the Weald sub-basin, as described over 160 years of prior research (Tagart,
112 1846; Beckles, 1851; Tylor, 1862; Ticehurst, 1928; Sarjeant, 1974; Delair, 1989; Woodhams
113 and Hines, 1989; Parkes, 1993; Sarjeant et al., 1998). The increased diversity does not arise
114 from reclassification of older specimens, but the discovery of new material, made possible by
115 the exhumation of new outcrop exposure through actively ongoing coastal erosion. Footprints
116 were observed on five different occasions (November 2014, May 2015, February 2016,
117 February 2017, and January 2018) at the study site, dominantly within fallen blocks that
118 originated from the base of the LNS, where this unit this crops out near the modern beach level
119 in the core of a local anticline between Lee Ness (50° 52' 06.1" N, 0° 39' 01.3" E) and Goldbury
120 Point (50° 52' 17.83" N, 0° 39' 58.82" E). Multiple separate visits permitted the recognition of

121 different material on each occasion: new material was revealed in freshly fallen blocks, while
122 material seen on previous visits was often lost to coastal erosion. As a result, the majority of
123 traces are individual footprints: trackway series are rarely observed extending for more than
124 2-3 footprints (and never more than 5, Fig. 4). Other than two specimens preserved in cross-
125 section internally within the LNS, one oriented along the anteroposterior axis (Fig. 5A) and
126 one along the mediolateral axis (Fig. 5B), tracks are preserved as positive hyporelief casts (Fig.
127 6). The silty mudstone that lies beneath the LNS onto which the majority of tracks were
128 emplaced is a recessive and friable lithology, which degrades during cliff collapse episodes.
129 Thus, the actual substrate onto which the footprints were emplaced is not visible, and only its
130 internal lithology can be seen, exposed as vertical profiles within the receding cliff face. In
131 total, of the 85 footprints discovered in this study, 79 (including all known footprints with skin
132 impressions) are known from the base of the LNS. A further two occurred internally within the
133 2 m thick series of approximately 13 beds of bioturbated yellow-grey very fine-fine-grained
134 sandstones that comprise the LNS, with only four scattered throughout the rest of the Ashdown
135 Formation.

136 **3. Dinosaur footprints**

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

145 3.1. Theropod footprints

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

151 Morphotype A, observed in 8 specimens, is a tridactyl footprint with narrow (length: width
152 ratio greater than 2) digits including a long digit III. These digits taper sharply towards the
153 anterior and converge onto a possible tarsometatarsus impression at the posterior (Fig. 7A).
154 The size of the footprint casts ranges from 18-32 cm wide by 17-33 cm long. Morphotype B,
155 observed in 7 specimens, is a tridactyl footprint similar in shape to morphotype A,
156 distinguished from it by the lack of a heel pad impression (Fig. 7B). The digits maintain a
157 consistent width for their entire length, and the size of the footprints ranges from 11-25 cm
158 wide by 13-26 cm long. Morphotype C is a single small tridactyl pes cast, 2.1 cm in length by
159 1.8 cm width (Fig. 7C). The size of this footprint cast is an informative character, as it is
160 significantly smaller than any others observed in the section. All of the digits are narrow, and
161 digit III appears markedly longer than digits II and IV.

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

169 15 cm wide by 25 cm long), occur in association on another fallen block, oriented in opposite
170 directions. It is unclear if any of these specimens are truly didactyl, or whether this is an artefact
171 of weathering or erosional processes.

172 3.2. Ornithopod footprints

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

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

192 3.2.1. *Caririchnium magnificum* Leonardi 1984

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

202 3.2.2. *Caririchnium isp.*

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

209 3.2.3. Unnamed Iguanodontipodidae Vialov 1988

210 These tridactyl pes casts have widely splayed digits with large, rounded ends and no claw
211 marks (Fig. 9). The heel cast is rounded and approximately the same width as the distal end of
212 digit III. However, the primary ichnotaxobase differentiating these footprint casts from other
213 described examples is a sub-round prod mark located medially to the rear of the heel
214 impression. This is considered to be due to a hallux impacting the sediment. Impressions of
215 digits II-IV have approximately the same dimensions as one another, whilst the hallux prod
216 mark is narrower than other digits (diameter 3 – 4 cm). Two examples are observed, with

217 lengths (excluding hallux prod mark) 19 cm and 22 cm, and widths 24 cm and 25 cm (Fig. 9).
218 The morphology of these footprints places them within the established ichnofamily
219 Iguanodontipodidae, but outside any current taxonomically valid ichnogenera (Diaz-Martinez
220 et al., 2015).

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

229 3.2.4. Gracile ornithopod

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

237 3.3. Thyreophorans

238 Some footprint casts in the LNS have characters that suggest they were made by neither
239 ornithopods or theropods. These occur in four morphotypes (Fig. 10), three of which are

240 tetradactyl casts with rounded digits and claw impressions which differ in the positioning and
241 length of the outer digits, the interdigital angles, and the shape of the heel impression. The final
242 example is pentadactyl with a reduced heel impression, recording a manus impression. Both
243 thyreophoran dinosaurs and crocodylomorphs are known from the Wealden (Barrett and
244 Maidment, 2011; Salisbury and Naish, 2011), and both could create tetradactyl pes impressions
245 and tetradactyl or pentadactyl manus impressions. All of the footprint casts discussed here are
246 attributed to thyreophoran dinosaurs due to their morphology. Tracks which are assigned to
247 *Tetrapodosaurus* are highly similar to those of ankylosaur footprint casts reported from the
248 middle Cretaceous Dakota Group (Lockley and Gierlinski, 2014; Lockley et al., 2014), of the
249 same ichnogenus. Crocodylomorph tracemakers are ruled out as Cretaceous forms are known
250 to leave more elongate, sharp digital impressions (Lockley et al., 2010).

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

257 3.3.1. *Tetrapodosaurus* isp. morphotype A Sternberg 1932

258 *Tetrapodosaurus* is a tetradactyl footprint with elongate, elliptical digits and pronounced
259 claw marks (Fig. 10A). Digits are forward facing, producing a near-symmetrical print
260 preserved in positive hyporelief. The heel pad cast is short and rounded, but larger than all
261 digital impressions, which are approximately equivalent in all dimensions. Two examples are
262 observed, one of which is highly detailed with skin and claw impressions. This example has

263 footprint width 26 cm, length 27 cm, digit width 5-7 cm, and digit length 6-10 cm. Figure 10A
264 shows the detailed textures along with claw marks on proximal regions of the digit pads.

265 3.3.2. *Tetrapodosaurus* isp. morphotype B Sternberg 1932

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

273 3.3.3. *Stegopodus* manus Lockley and Hunt 1998

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

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

285 3.3.4. Unnamed thyreophoran footprint

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

292 3.4. Putative Sauropod Footprints

293 Jarzembowski et al. (2015) noted two large impressions, apparently occurring in a series,
294 and suggested that they may be sauropod tracks (see Fig. 4, Fig. 11A), due to a possible
295 crescentic manus, and the approximately ovoid morphology of the interpreted pes casts. No
296 digital impressions are observed with these amorphous imprints, and the pes casts range in size
297 from 58-61 cm long and 49-51 cm wide. Jarzembowski et al. (2015) also figured a third
298 suspected sauropod footprint, discovered in an isolated block, and at least one further example
299 with a similar morphology and dimensions was discovered at the base of the LNS in this study
300 (Fig. 11B). It is plausible that these imprints may record sauropod tracks (Jarzembowski et al.,
301 2015; Austen and Batten, 2018), but until a more defined series of such impressions is
302 discovered, this interpretation must remain tentative due to the amorphous nature of the
303 imprints and the possibility that they may be poorly-preserved undertraces of other footprints.

304 3.5 Surface traces and undertraces revealed by skin impressions

305 Many of the footprints on the base of the LNS exhibit well-preserved skin impressions.
306 These present as small (2 – 5 mm), raised, sub-rounded polygons ranging in shape from
307 approximately circular, to rounded trigonal, to elongate (Fig. 12), and are commonly associated
308 with narrow furrowed striations (c. 2.5 mm across individually and 2-7 cm in length) that
309 extend for the entire width of the heel or tarsometatarsus impression (recording slip-marks

310 which developed as the footprint was emplaced (Fig. 13; Davies et al., 2016)). Footprints with
311 skin impressions are preferentially seen at the base of the LNS, where they have been cast
312 directly into the underlying mudstone, and are clear evidence of the complete preservation of
313 true surface traces (see Section 4.2.1).

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

325 3.6. Implications of the Dinosaur Ichnofauna

326 The reported dinosaur ichnofauna assemblage of theropod, ornithopod, thyreophoran, and
327 possible sauropod footprints is one of the most diverse known from the Mesozoic of the UK
328 (Fig. 15), rivalling those of the Jurassic Ravenscar Group of Yorkshire (Whyte et al., 2007)
329 and the Cretaceous Wealden of the Isle of Wight (Lockwood et al., 2014). When considered
330 alongside the body fossil record of dinosaurs from the Wealden Group, this assemblage
331 provides insights into the constituent dinosaur community immediately before the deposition
332 of the LNS. Ornithopod tracks from the LNS are assigned to three distinct tracemakers:
333 styracosternans, basal iguanodontians and gracile ornithopods; theropods are dominated by

334 gracile forms, with possible evidence for didactyl theropods; thyreophoran tracks are likely
335 produced by ankylosaurians and stegosaurs; and there is putative evidence for sauropods.

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

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

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

353 4.1. Outcrop controls on footprint discovery

354 The LNS tracksite provides a case study in how the revisiting of non-conservated, dynamic
355 outcrops may yield new insights into diversity: because, while local fossil diversity may be
356 biased by rock availability and sampling (Smith and McGowan, 2007), an increase in rock

357 availability at a previously sampled site can yield improved diversity estimates. In this instance,
358 rock availability was enhanced by multiple cliff falls in the Hastings-Fairlight area (Fig. 17),
359 uncovering the large amounts of fresh material discovered between 2014-2018. Each of the
360 five visits saw the exposure of new material and the degradation or disappearance of previously
361 observed tracks (Fig. 18).

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

369 Cliff retreat in the Hastings-Fairlight section has been fairly consistent over long time scales
370 (Thorburn, 1977; Cleeve and Williams, 1987), but is stochastic over short timescales because
371 it primarily occurs as discrete cliff collapse events (between 1998-2004, 86.4 m of cliff retreat
372 occurred, including 25.7 m in 2002-2003 alone; Rother District Council, 2012). This means
373 that any estimates of trackway spacing have a large error bar, but they may be crudely
374 calculated. The barren intervals between reported footprint finds in the period 1862-2018 are
375 56 years, 63 years, 10 years, and 22 years respectively, so with the maximum average rate of
376 cliff retreat during this period (77 cm per year; Cleeve and Williams, 1987), the minimum
377 distance between previously exposed trackway-bearing tracts of the basal LNS would be 48.5
378 m (Table 2).

379 Dinosaur behaviour is responsible for this uneven distribution of their footprints on the
380 original substrate. The dominant large ornithopod tracemakers are thought to have exhibited

381 herding behaviour (Lockley, 1989; Cotton et al., 1998; Lockley et al., 2012), the movement of
382 which would lead to large numbers of tracks grouped together in the areas the herd traversed,
383 and a much sparser distribution away from the main route.

384 4.2. Depositional controls on footprint distribution

385

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

391 4.2.1. Footprints at the base of the Lee Ness Sandstone

392 The lowermost crevasse splay sandstone of the LNS has cast dinosaur footprints that were
393 emplaced onto a cohesive substrate and which now marks the top of the underlying grey silty
394 mudstone, in conjunction with casts of ripple marks (Fig. 20A) and desiccation cracks (Fig.
395 20B-C). The base of the LNS also contains a dense invertebrate ichnofauna of passively-filled
396 burrows of *Palaeophycus*, with rare *Ophiomorpha* and *Cochlichnus* (Table 3, Fig. 21). These
397 record infaunal communities on the stable but damp overbank floodplain substrate and are
398 sometimes overprinted with actively-filled *Taenidium* (deeper tier traces from overlying
399 crevasse splay sands).

400 Footprints with intricate detail of skin impressions are notable from the base of the LNS.
401 The preservation of skin textures within demonstrable surface traces shows that this
402 stratigraphic surface can be considered to be a true substrate (Davies et al., 2017; Davies and
403 Shillito, 2018): a sedimentary bedding plane which existed at the sediment-water or sediment-
404 air interface at the time of deposition, and which was not degraded during the deposition of the

405 overlying sands. The preservation of delicate footprint textures on a true substrate need not be
406 unexpected, because the distal point source of the overlying crevasse splay sands means that
407 their deposition at a specific footprint location was not necessarily coupled with erosion
408 (Davies and Shillito, 2018). However, the initial imparting of skin impressions was favoured
409 by antecedent sedimentary conditions: namely, a moist, cohesive substrate which would have
410 behaved as a ductile media when impressed (Fig. 22; Laporte and Behrensmeyer, 1980; Milàn
411 and Bromley, 2006).

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

423 4.2.2. Footprints within the Lee Ness Sandstone

424 Internally within the LNS, dinosaur tracks that were emplaced onto crevasse splay top sandy
425 substrates (i.e., between flooding events) are observed in cross-section, where bedding is
426 truncated or downturned around footprints (Fig. 6). These are seen in association with a low-
427 density invertebrate ichnoassemblage of *Arenicolites* and *Taenidium* that records the infaunal

428 colonization of crevasse splay deposits, immediately after their deposition during flood events
429 (i.e., while they were still wet with standing water) (Table 3, Fig. 21).

430 The relative rarity of footprints internally within the LNS appears to be a sedimentological
431 rather than palaeoecological artefact. The deposition of crevasse splay sands is sporadic,
432 occurring only when a river channel breaches its levees during flood events (e.g., Smith et al.,
433 1989), so the horizons which separate the 13 constituent sandstone layers of the LNS can also
434 be considered to be true substrates, which may be expected to have been imparted with
435 footprints as frequently as the antecedent mudstone. However, the fact that footprints internal
436 to the LNS are only evident in profile reflects the granular nature of the sandy crevasse splay
437 substrates. These would have been unfavourable to preserving casts of footprints as wet sand
438 would be too loose and prone to collapse to hold the form of a trace (Fig. 22; Laporte and
439 Behrensmeyer, 1980). This is in contrast to the wet, plastic mud at the base of the LNS which,
440 in addition to true surface traces, also hosts some undertraces transmitted down from the lower
441 internal layers of the LNS.

442 4.3. Dinosaur controls on deposition?

443 Modern large vertebrates are effective zoogeomorphic agents (e.g. Haynes, 2012; Jones,
444 2012; Statzner, 2012), modifying the spatial distribution of landforms and sedimentary
445 processes within riverine environments, and it has long been suspected that dinosaurs may have
446 played an analogous role in ancient environments (Butler, 1995; Jones and Gustason, 2006).
447 The combination of footprints and alluvial architecture within the Ashdown Formation permit
448 the opportunity to here briefly assess whether such activity leaves a diagnostic sedimentary
449 signature, or whether the limitations resulting from the imperfect translation of geomorphology
450 into the sedimentary record (e.g., McMahon and Davies, 2018) only permits the recognition of
451 such life-landscape interaction through abductive modern analogue.

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

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

475 Through comparison with analogous modern environments that host large vertebrates it is
476 likely that dinosaurs acted as geomorphic agents at a larger scale during the fluvial deposition

477 of the Ashdown Formation. Large herbivores such as cows and hippopotamuses are known
478 today to promote the formation of small fluvial channels and encourage channel avulsion due
479 to breaching levees and forming accessory channels by trampling (McCarthy et al., 1992;
480 Trimble and Mendel, 1995). If such features were to be translated into the sedimentary record,
481 the only physical signatures would be indirect evidence for a propensity to avulse, such as
482 stacked crevasse splay sandstones (Smith et al., 1989) as within the LNS, or the resultant
483 abandoned channel elements. However, it is impossible to diagnose an organismal trigger for
484 such architectural elements because they may have multiple alternative causes (Jones et al.,
485 2009) and because the direct evidence of the trigger (i.e., footprints organised within trackways
486 on the channel floor) would have been obliterated by the physical processes of erosion which
487 they induced. Thus, while modern analogue can tell us that dinosaurs (with similar behaviour
488 and greater weight than extant fauna) must have promoted channel avulsion during the
489 Mesozoic, the rock record is unlikely to ever provide a ‘smoking gun’ for specific instances of
490 dinosaur-induced avulsion.

491 There is evidence for other interaction between the Ashdown Formation dinosaurs and the
492 rivers that formed landscape components of their habitats. In one stratigraphic horizon below
493 the LNS, lateral accretion sets are seen to occur in opposite directions, indicating the cross-
494 sectional anatomy of a meander neck cut-off (Fig. 2E). Individual sets containing abundant
495 fossil woody debris and recording iterations of point bar growth can be seen to be deformed in
496 discrete packages (Fig. 2E, Fig. 3), suggestive of highly localized sources of soft-sediment
497 deformation (e.g., by foot-falls). While no high-fidelity footprints are preserved, these
498 deformation horizons occur on the slopes of inclined strata below the inclined heterolithic
499 topsets, indicating that they were emplaced below the bankfull level of the river. With no other
500 trigger that could induce such localized soft-sediment deformation, the only explanation is that
501 these indicate the wading activity of dinosaurs in the shallow water inner bends of vegetated

502 river channels. Such instances provide high-resolution snapshots of direct dinosaur interactions
503 with the ancient Ashdown Formation landscapes, even when our understanding of how
504 dinosaurs may have actively engineered those landscapes is accessible only through modern
505 analogue.

506 **5. Conclusions**

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

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

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765 Sussex, England. *In: Gilette, D.D. and Lockley M.G. (eds.) Dinosaur Tracks and Traces,*
766 Cambridge University Press, 301-307.

767 **Figure Captions**

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

775 Figure 2 – A representative overview of the geology of the cliffs near Lee Ness. A) An
776 annotated photograph highlighting different lithologies and key horizons observed in the cliffs
777 (2017). B) A sketch stratigraphic log of a 14 m cliff section including the Lee Ness Sandstone.
778 Grain size scale ranges from mud (m) to coarse sand (c), although the coarsest material in the
779 logged section is fine sandstone. C) A close up view of the Lee Ness Sandstone (LNS) with
780 distinguishable yellow and grey layers (2014). A significant overhang has formed beneath it
781 due to preferential weathering of the underlying mudstone (scale bar 1 m). D) Inset showing a
782 close up of the base of the Lee Ness Sandstone, where part of a dinosaur footprint cast is
783 observed in cross section (scale bar 20 cm). E) Cross bedded sandstones recording a neck cut-
784 off event (2017). Major surfaces are picked out by thicker lines. At the base of the section is a
785 green gleysol (GS), topped by cross-bedded sandstone foresets dipping to the NW (yellow).
786 This is truncated by overlying cross bedded sandstones dipping to the SE (blue). Above this,
787 fine, planar laminated sandstones (red) transition upwards into grey mudstone followed by a

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

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

797 Figure 4 – A) A reconstructed series of 5 successive footprints, assigned to a gracile ornithopod
798 (2017). Note the wide digital impressions and the equivalent length and width of the footprint
799 casts. This series is associated with putative sauropod footprints (1 manus, 2 pes) in a trackway.
800 B) a line drawing showing the relative locations of the footprints, with the heel of the prints
801 highlighted (red). Putative sauropod footprints are labelled Sa. C) A reconstruction of the stride
802 length of the dinosaur, and separation between the path of the left and right legs. Mean stride
803 length is 1.86 m. Scale bar 1 m.

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

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

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

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

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

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

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

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

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

866 Figure 12 – Dinosaur skin textures on footprint casts from the base of the Lee Ness Sandstone
867 (2016). A, B) Polygonal skin texture on a theropod footprint cast. A) The full extent of the
868 texture on the toe of the footprint cast. Black box shows the extent of B. B) A close up of the
869 skin texture in A. It is comprised of small, raised sub-rounded polygons. Polygons are fairly
870 uniform with small differences in eccentricity. C, D) Skin texture on an ornithopod footprint
871 cast. C) Extent of the skin texture on the side of the footprint cast. Black box shows the extent
872 of D. D) A close up of the skin texture in C. Polygons are more pronounced than those in B,
873 with a greater microtopography but similar size and shapes. Scale bars 1 cm.

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

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

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

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

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

895 Figure 17 – A section of cliff exposure viewed in 2014 and again in 2018. Over the course of
896 4 years a large amount of material has collapsed from the rock face. Dinosaur footprints are
897 observed in cross section on several horizons (FP). Underlying gleysol (GS) and overlying
898 spodosol (SS) are highlighted. Two horizons are highlighted to aid in comparison of the
899 photographs, red at the base of the spodosol, and yellow within the heterolithic lateral accretion
900 sets. This panel is illustrated in greater detail in figure 4. Person for scale is 1.8 m tall.

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

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

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

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

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

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

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

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

954 Table 1 – Dinosaur footprint diversity

955 Table 2 – Rates of cliff retreat

956 Table 3 – Invertebrate ichnology

Wealden Group	Berrastian	
	Lee Ness Sandstone	Purbeck Group
"Hastings Beds Group"	Ashdown	Wadhurst Clay
	Tunbridge Wells Sand	
	Weald Clay	Grimstead
Valanginian		Hauterivian

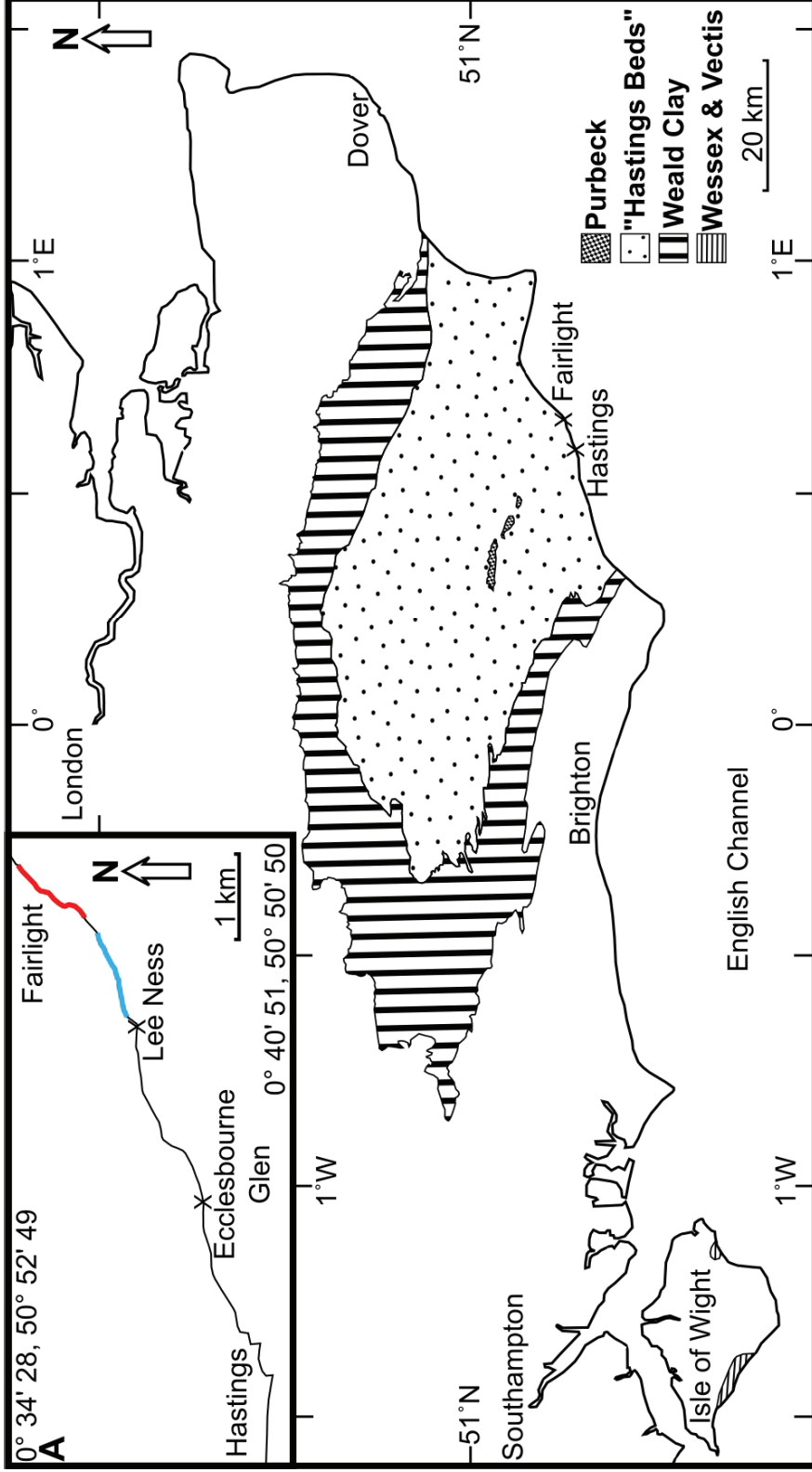


Figure 1

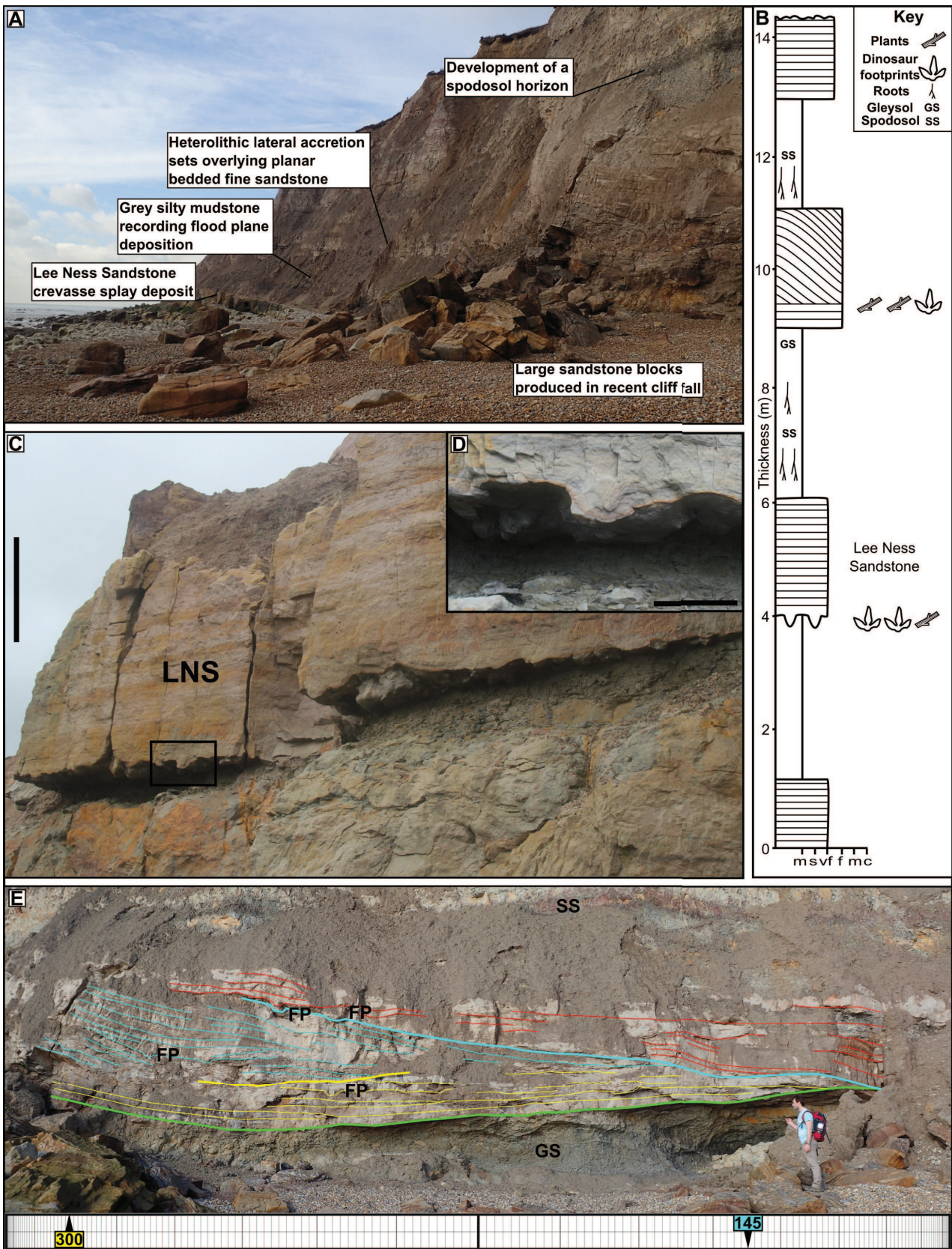


Figure 2

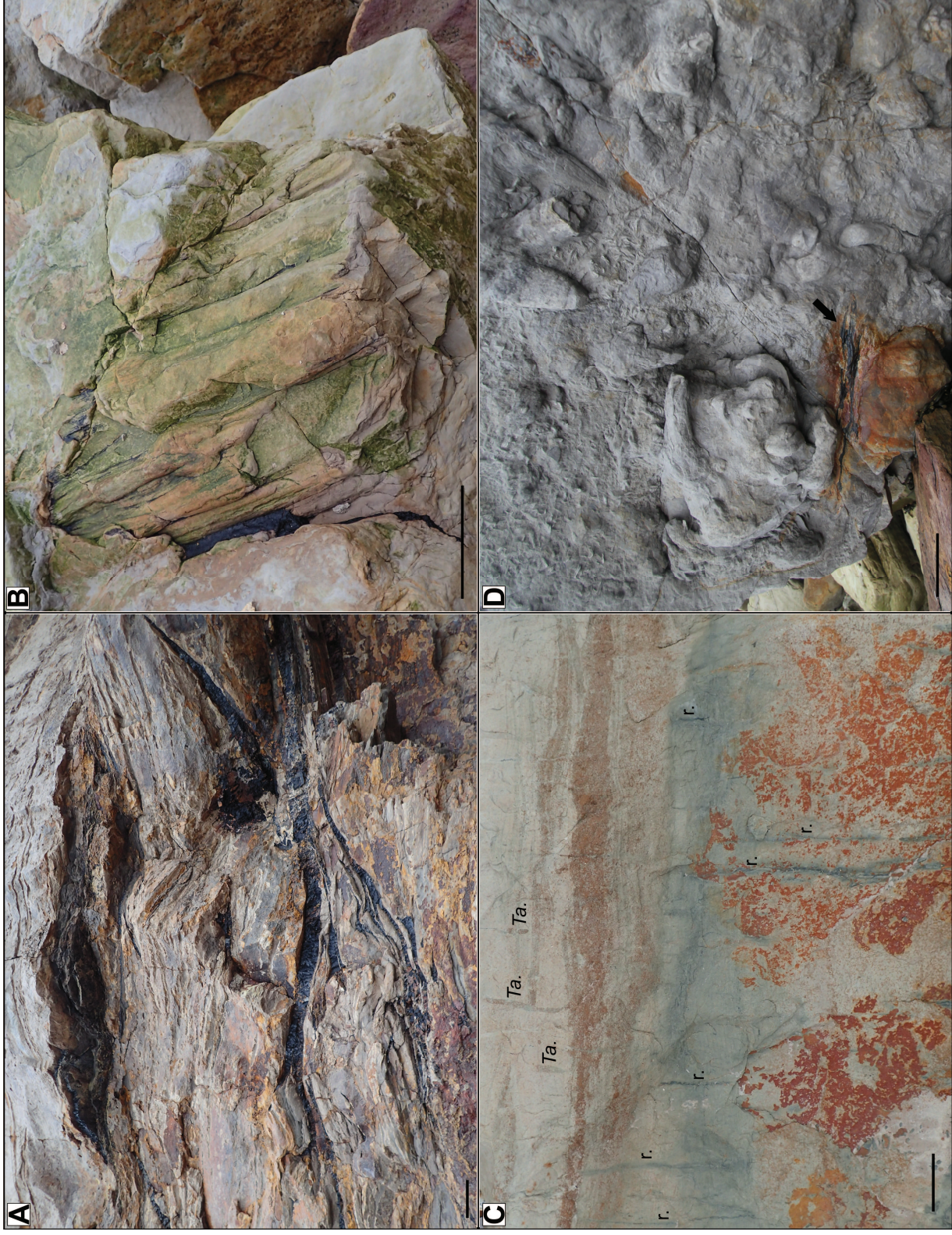


Figure 3

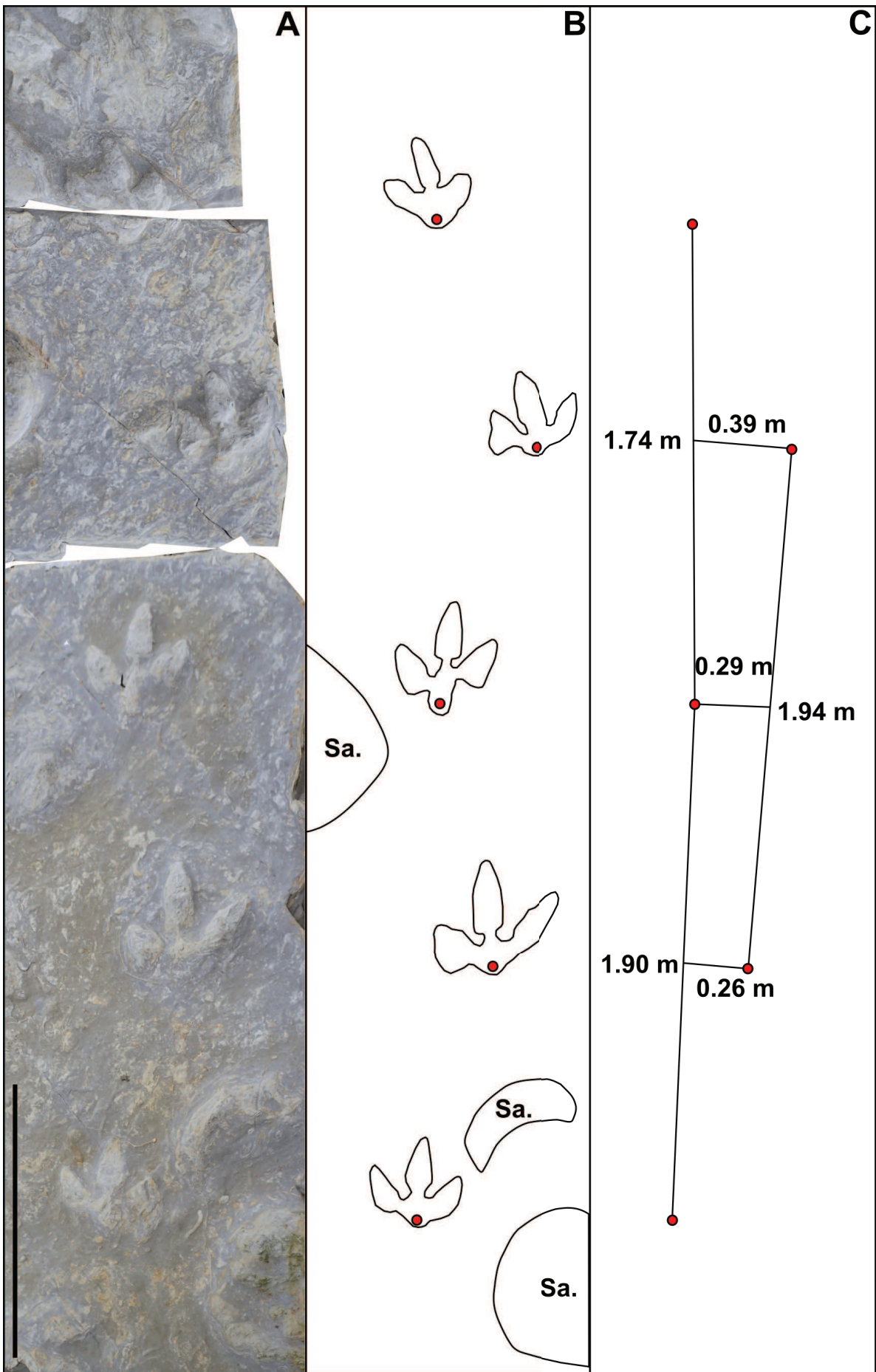


Figure 4



Figure 5

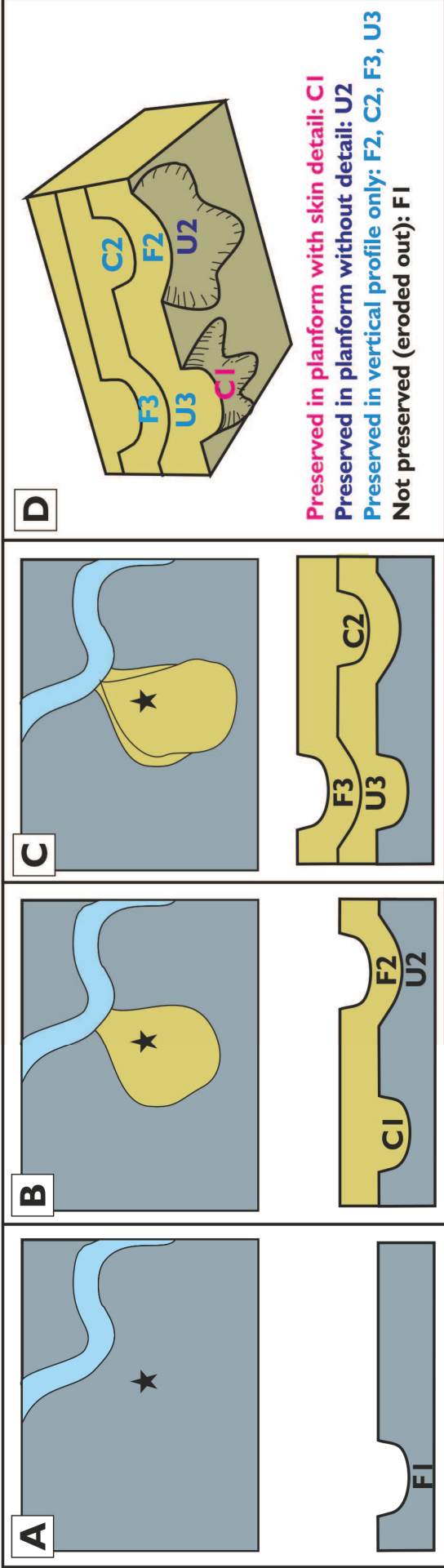




Figure 7

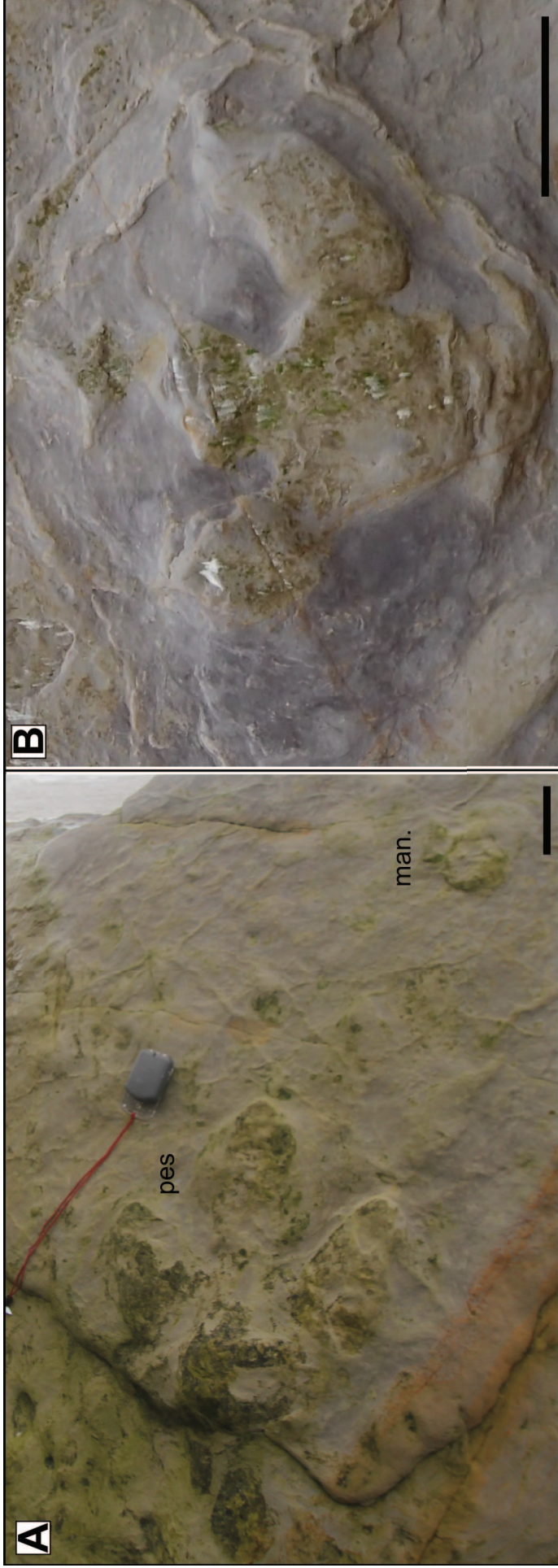


Figure 8

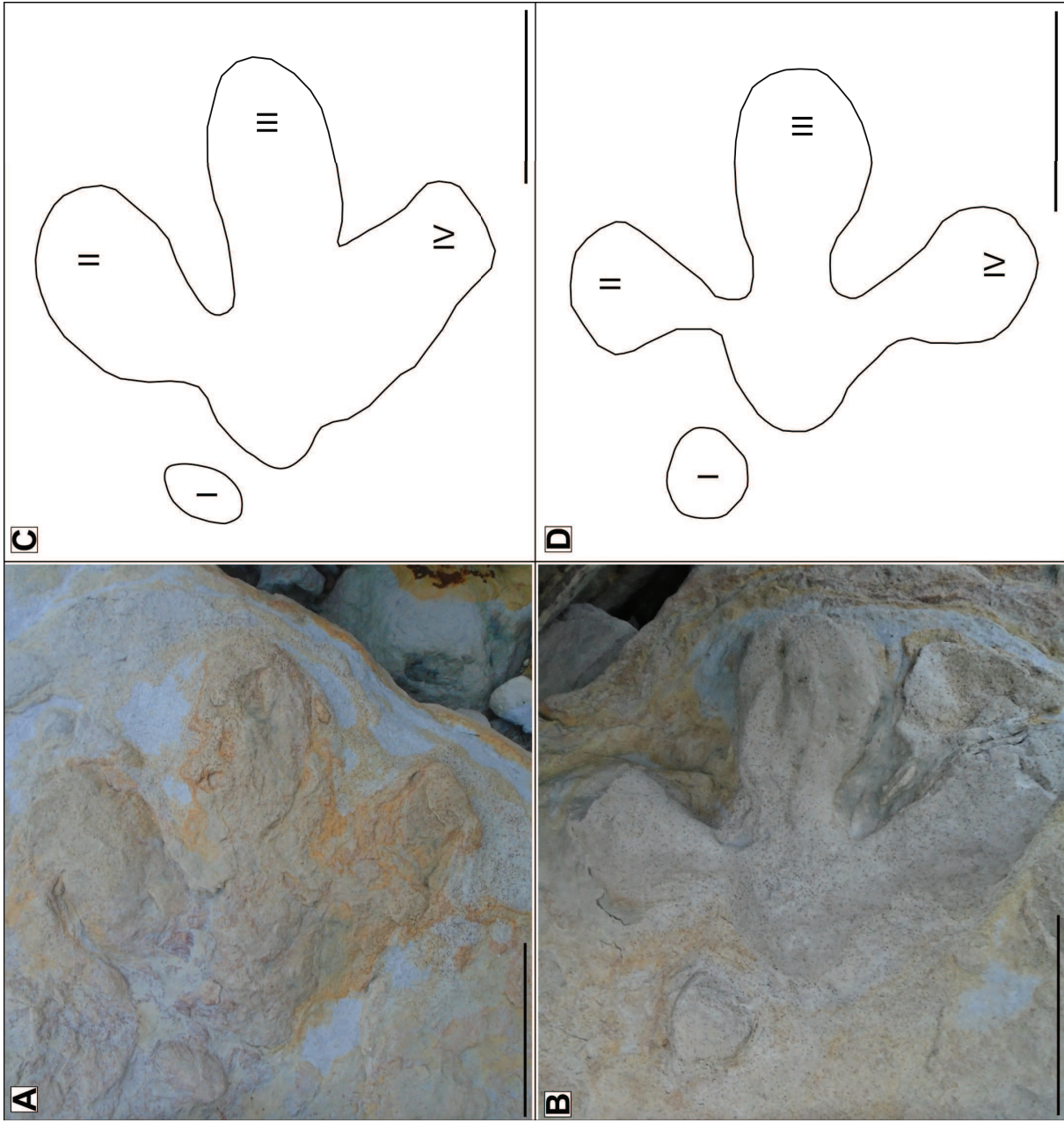


Figure 9

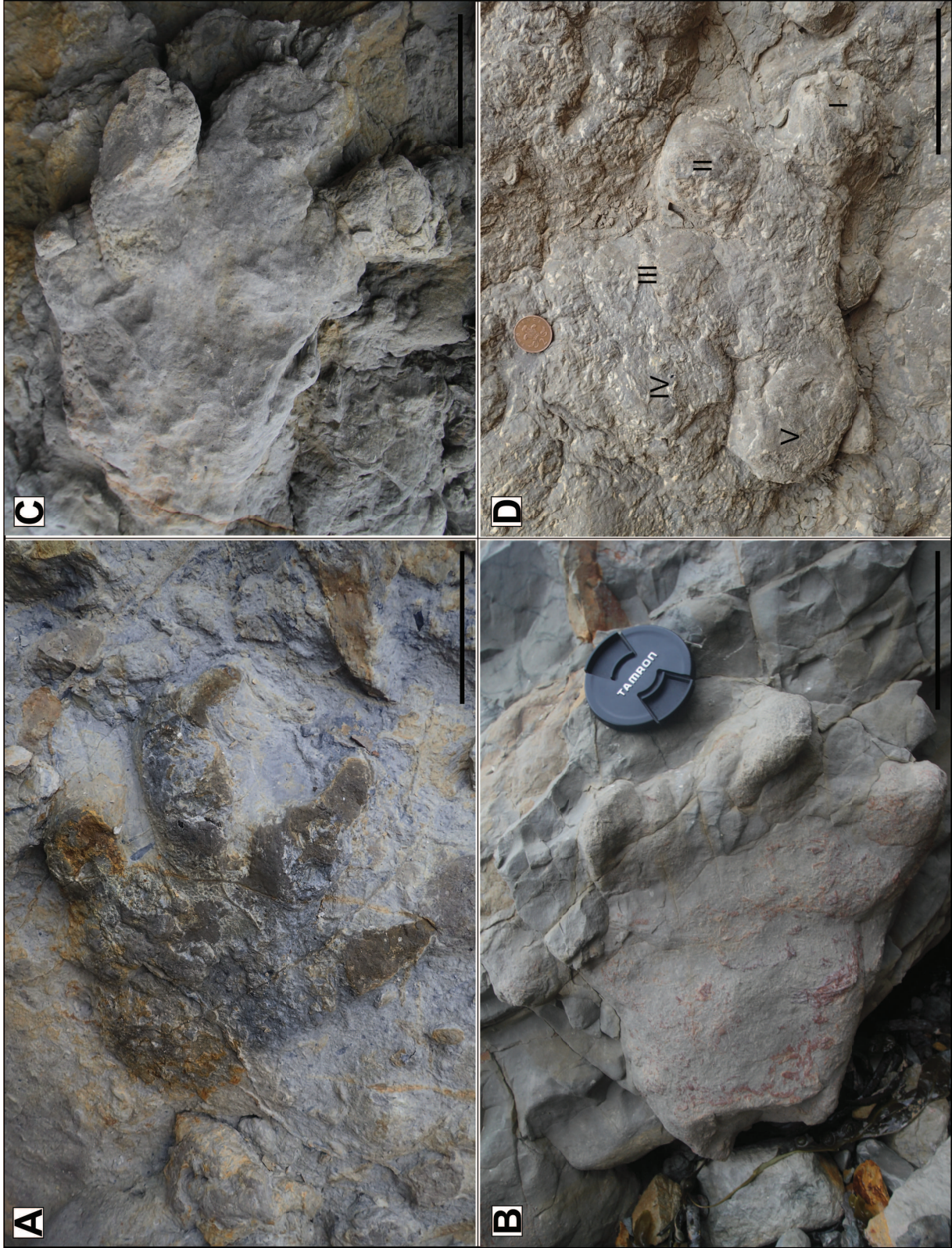


Figure 10

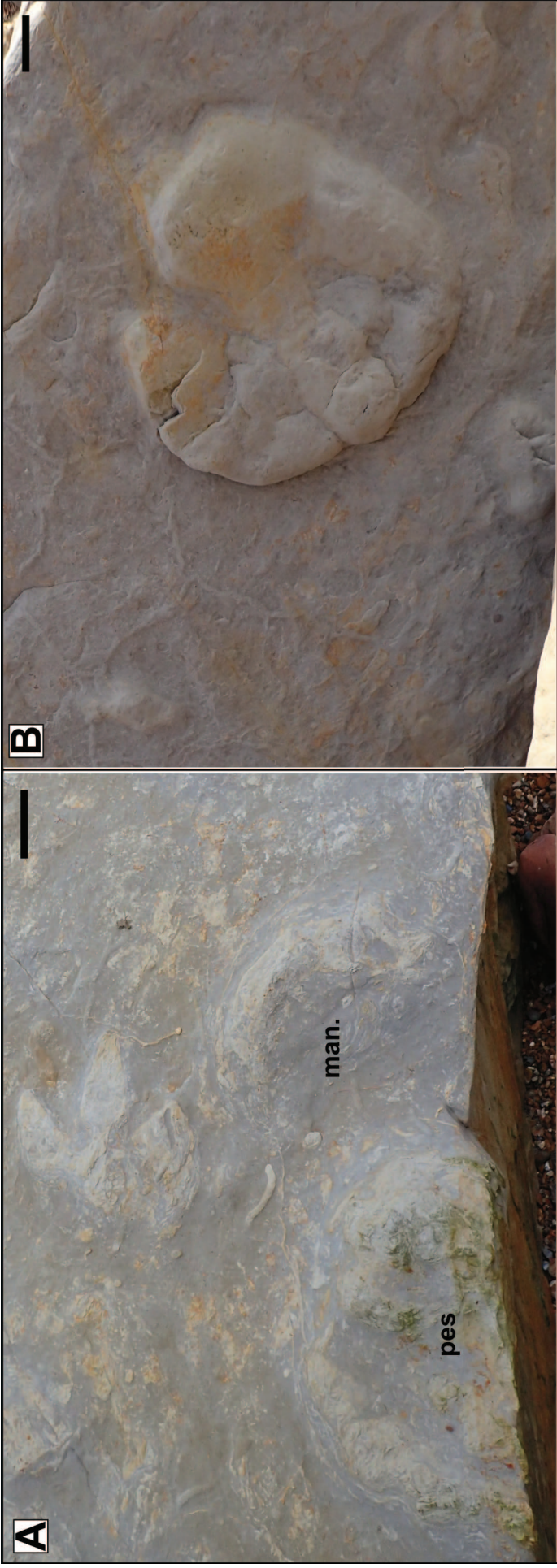


Figure 11

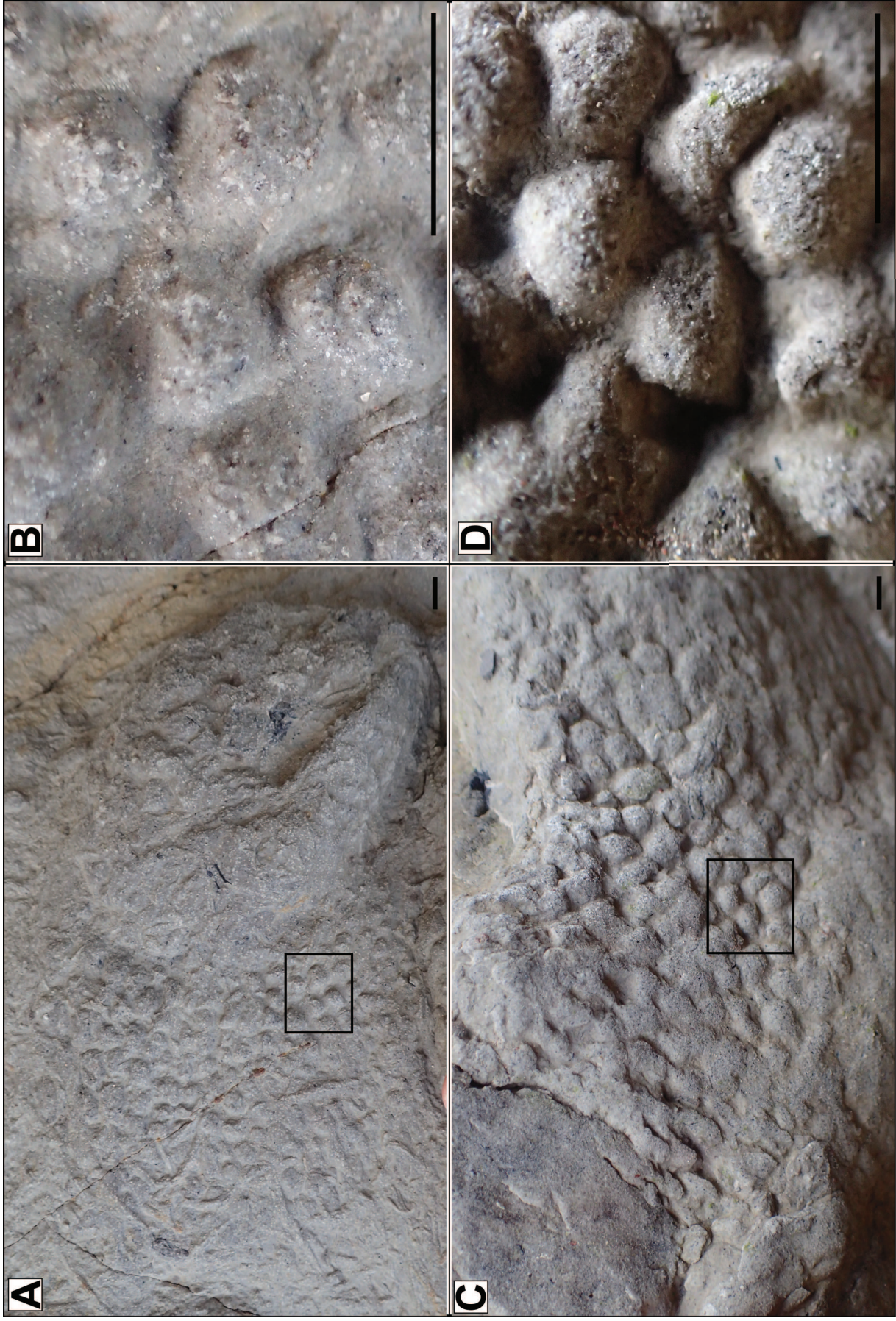


Figure 12

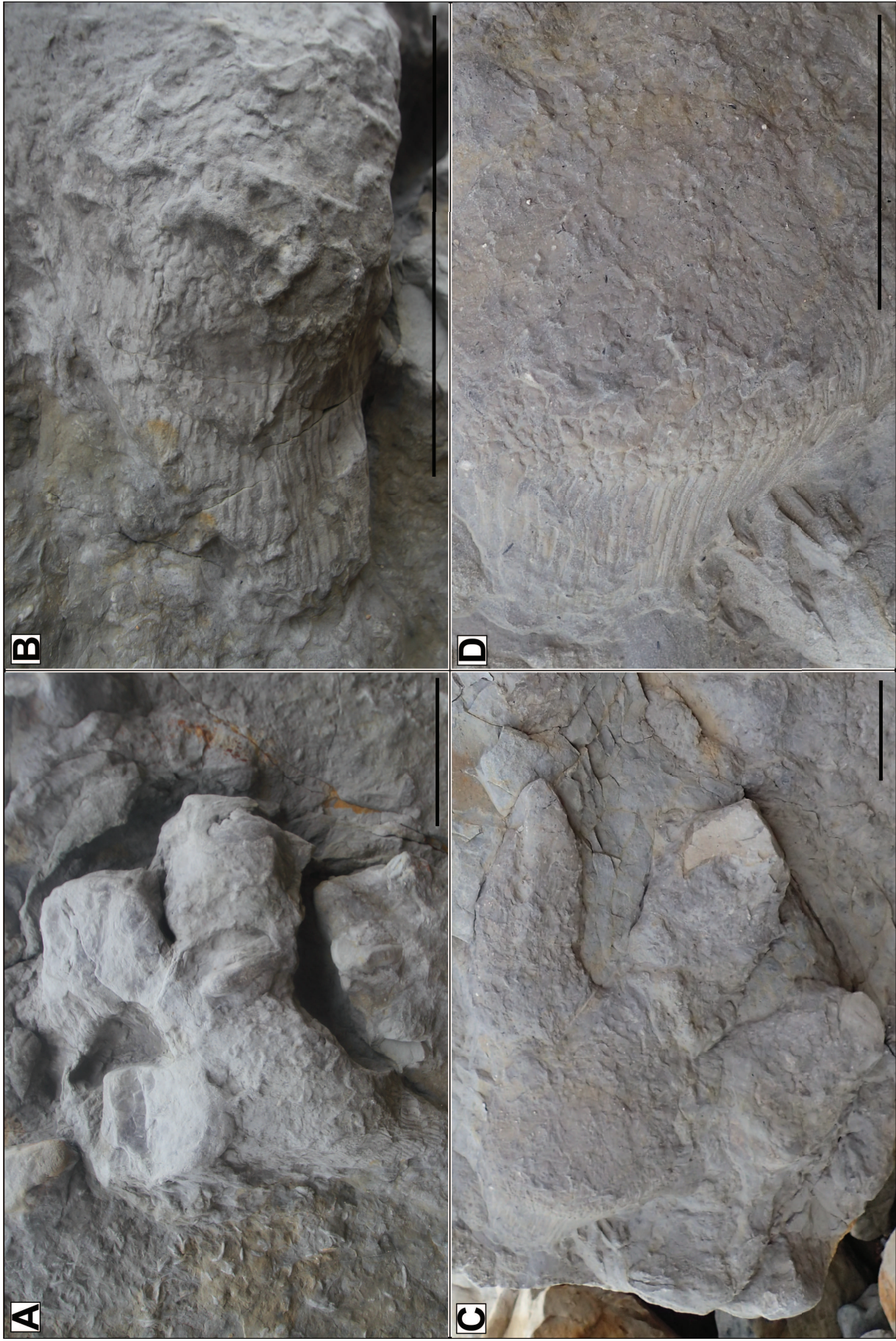


Figure 13

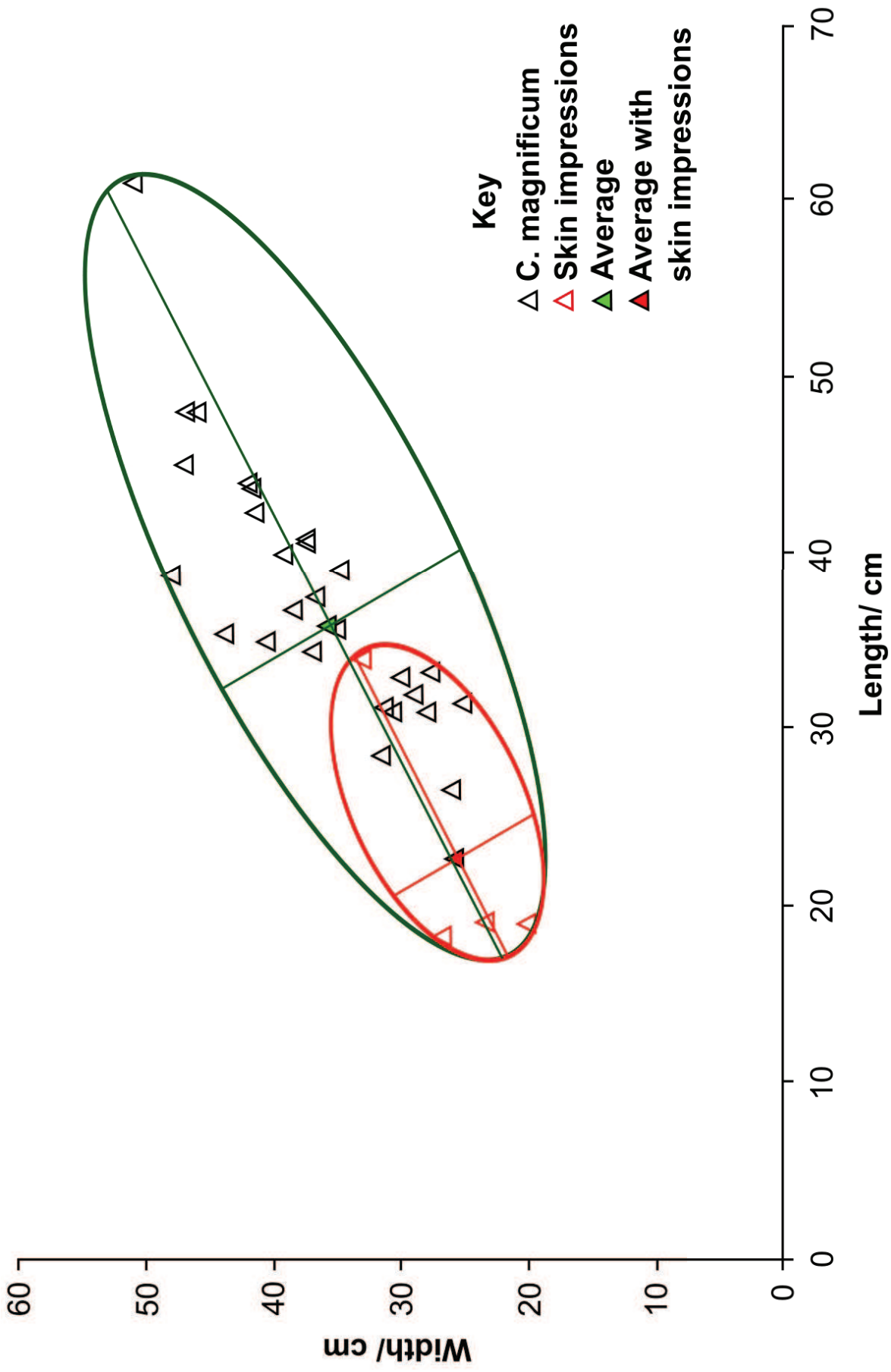


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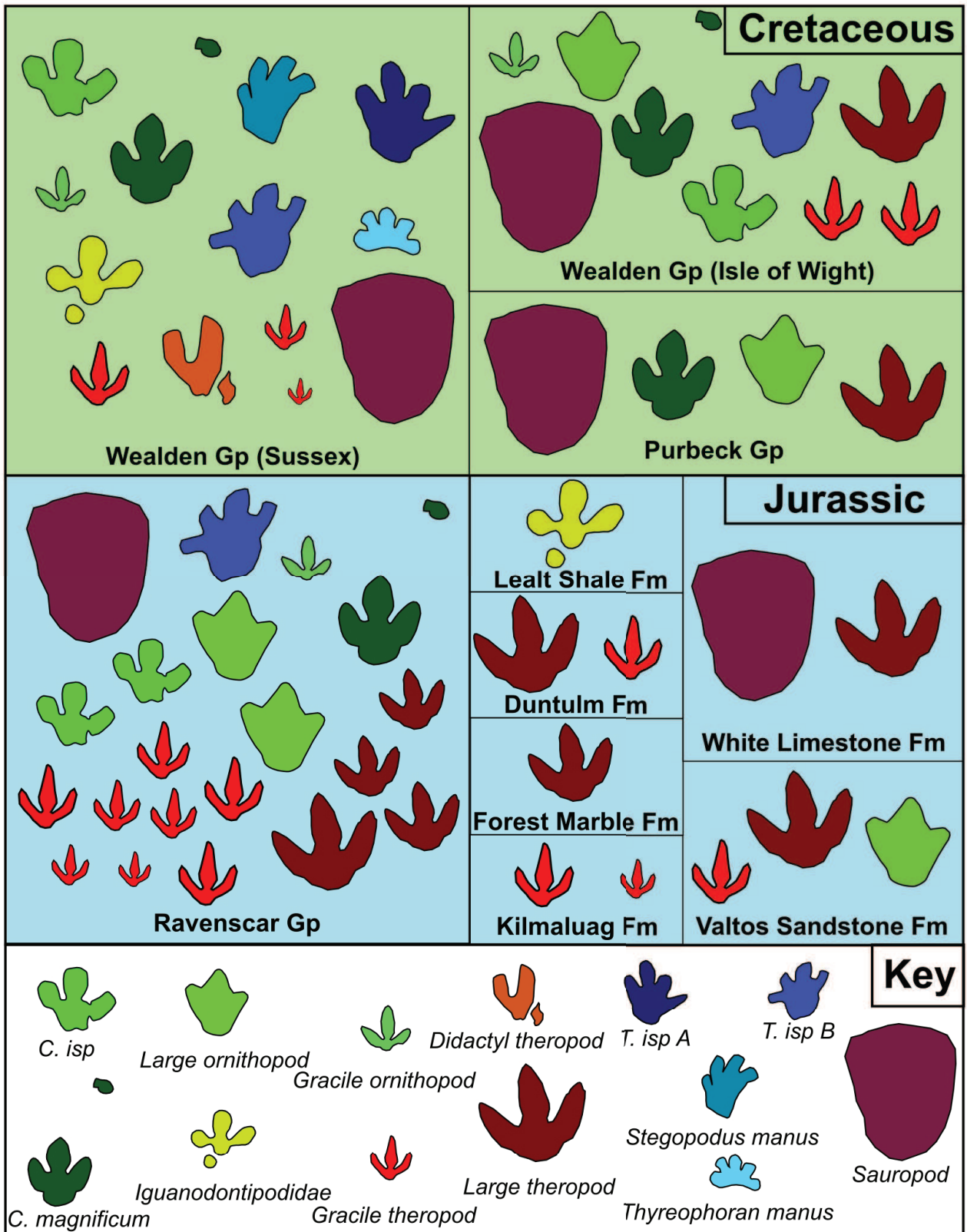


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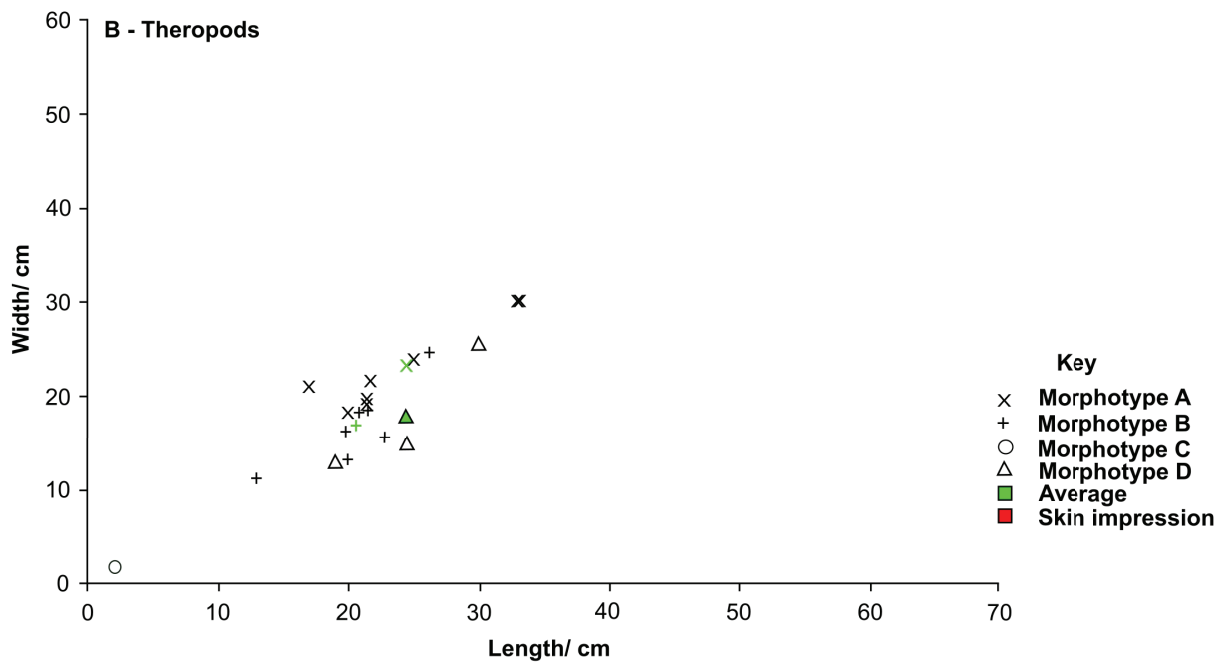
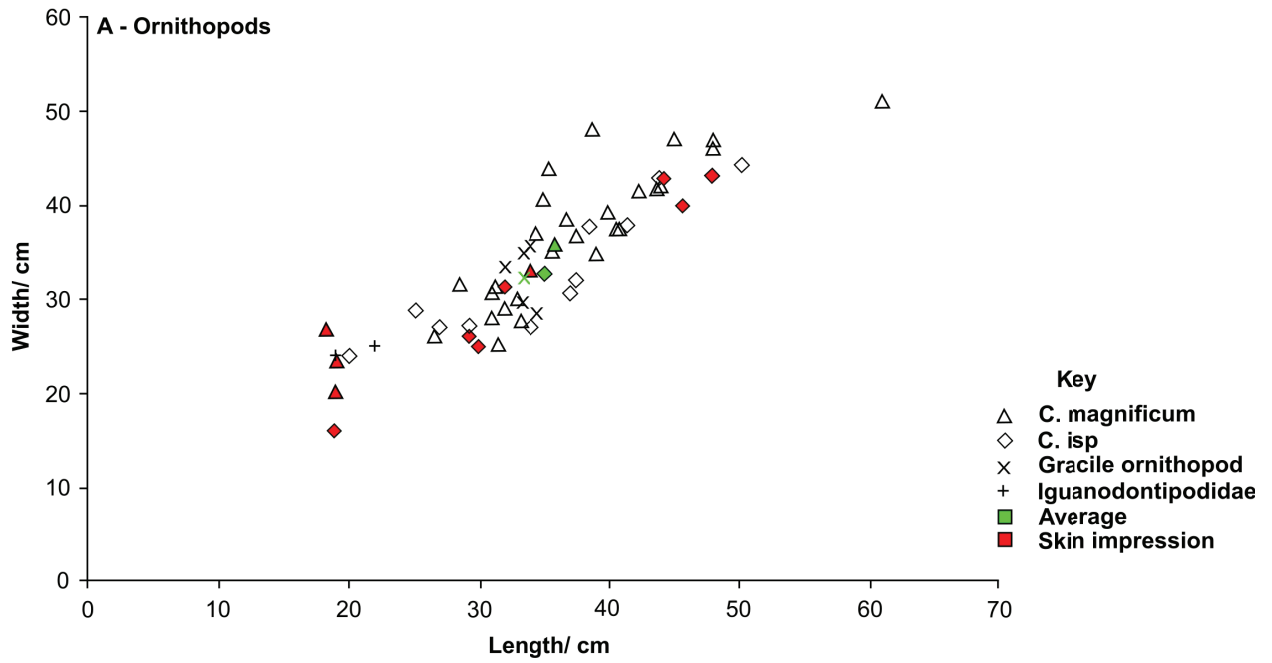


Figure 16

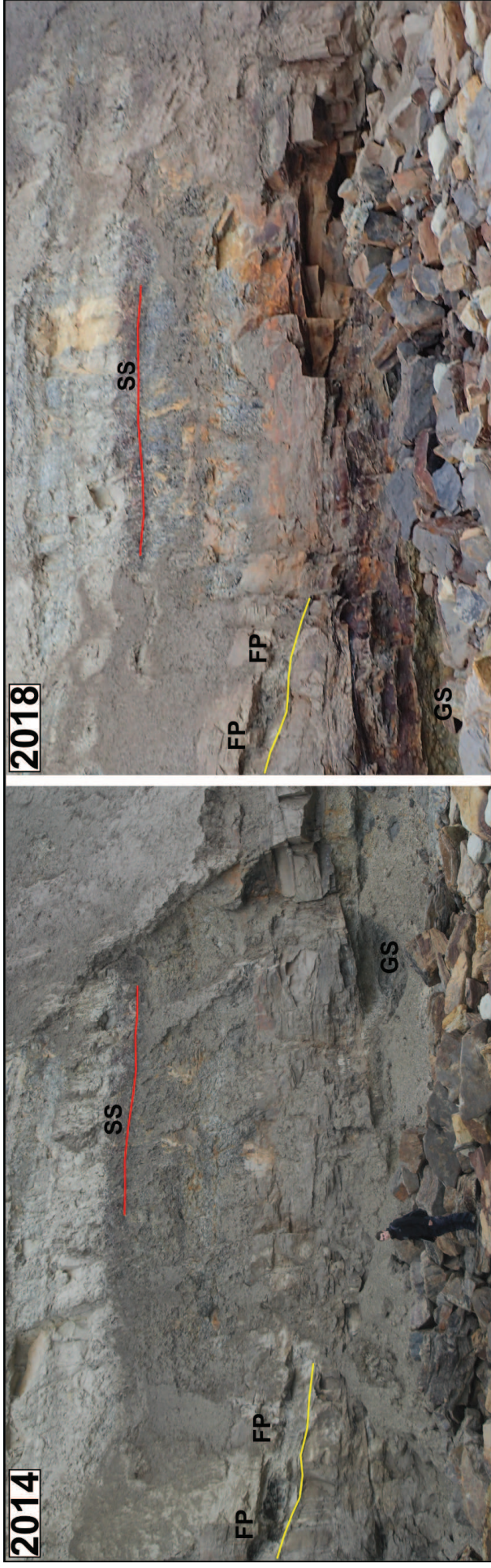
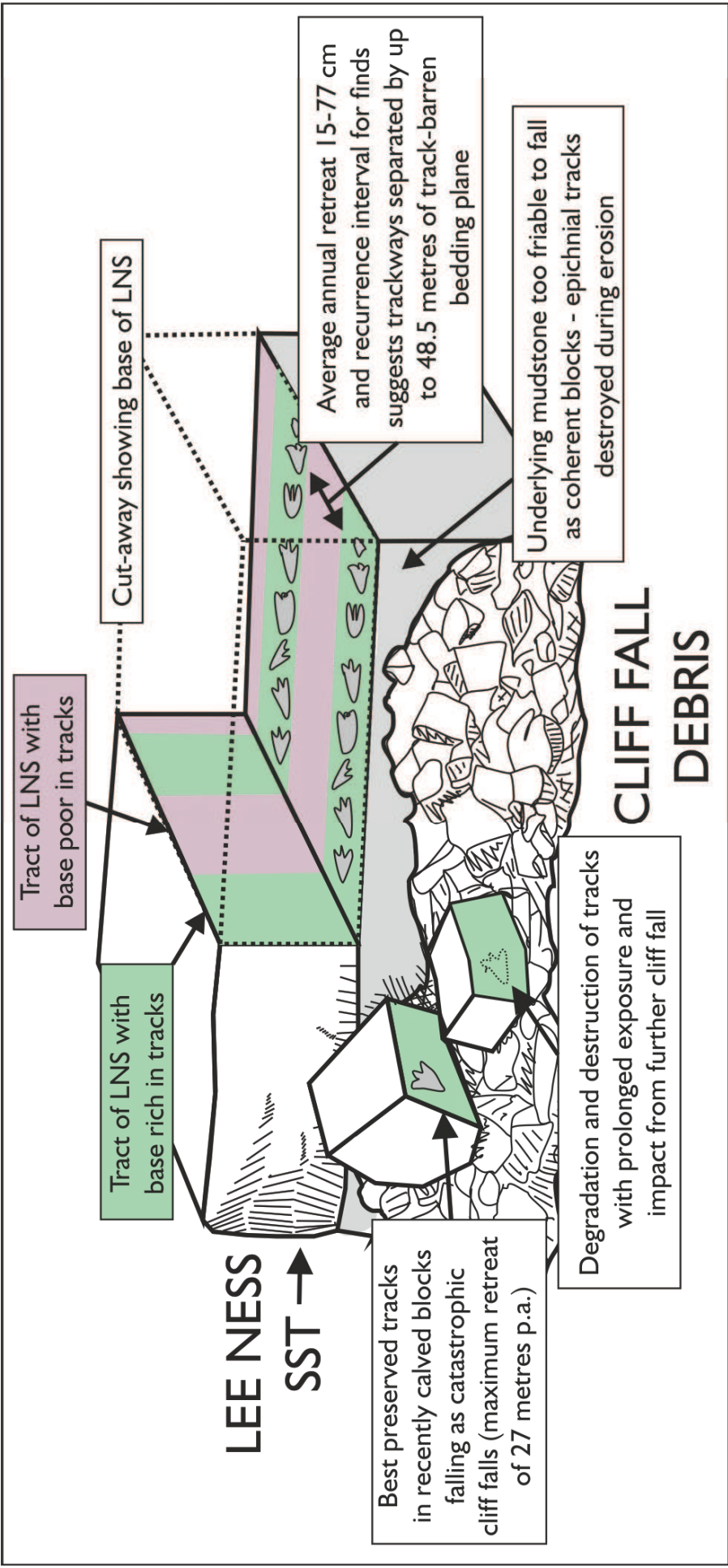


Figure 17



Figure 18



LEE NESS
SST →

Tract of LNS with base rich in tracks

Tract of LNS with base poor in tracks

Cut-away showing base of LNS

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

Underlying mudstone too friable to fall as coherent blocks - epichnial tracks destroyed during erosion

Best preserved tracks in recently calved blocks falling as catastrophic cliff falls (maximum retreat of 27 metres p.a.)

Degradation and destruction of tracks with prolonged exposure and impact from further cliff fall

CLIFF FALL DEBRIS

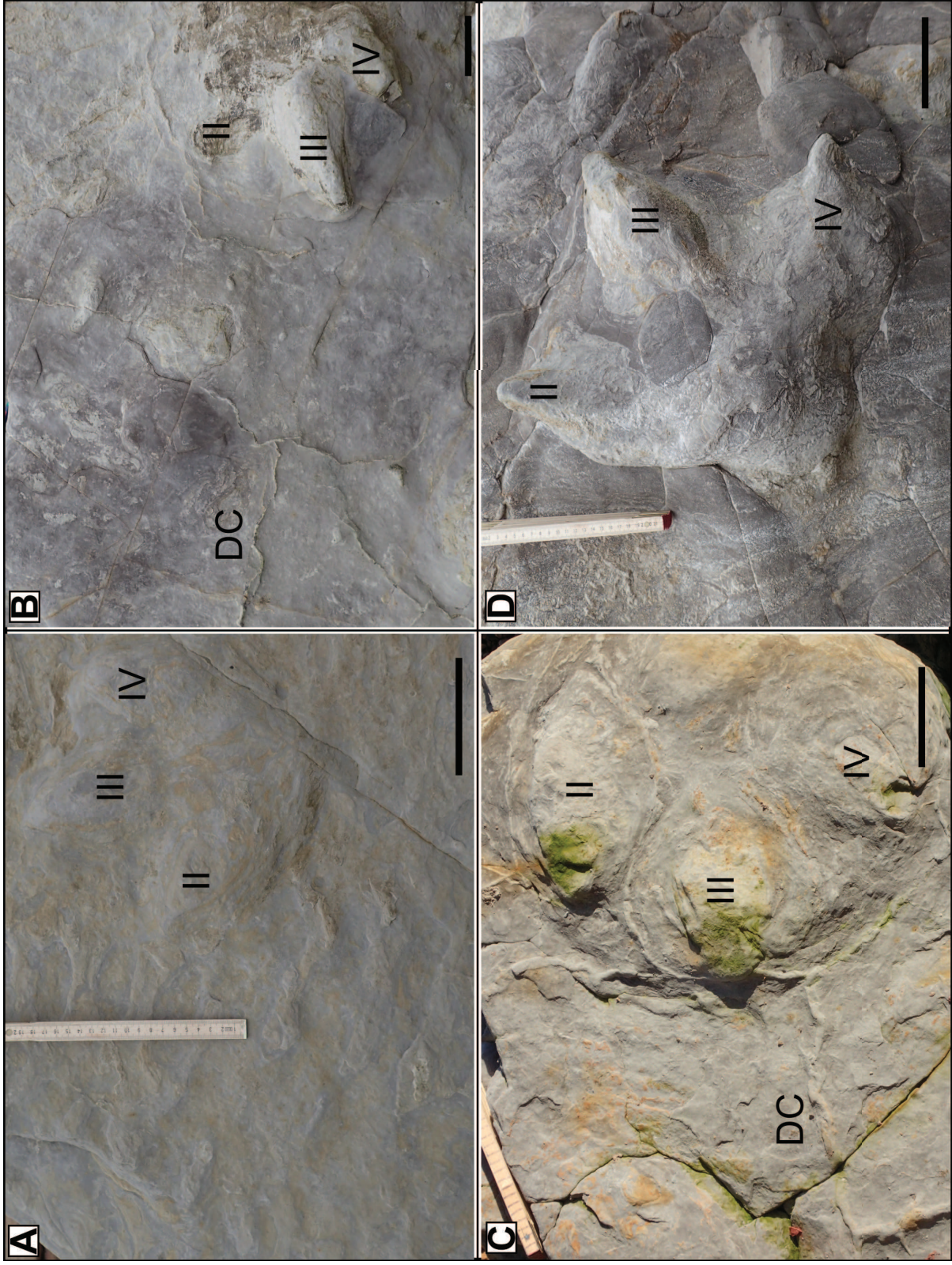


Figure 20

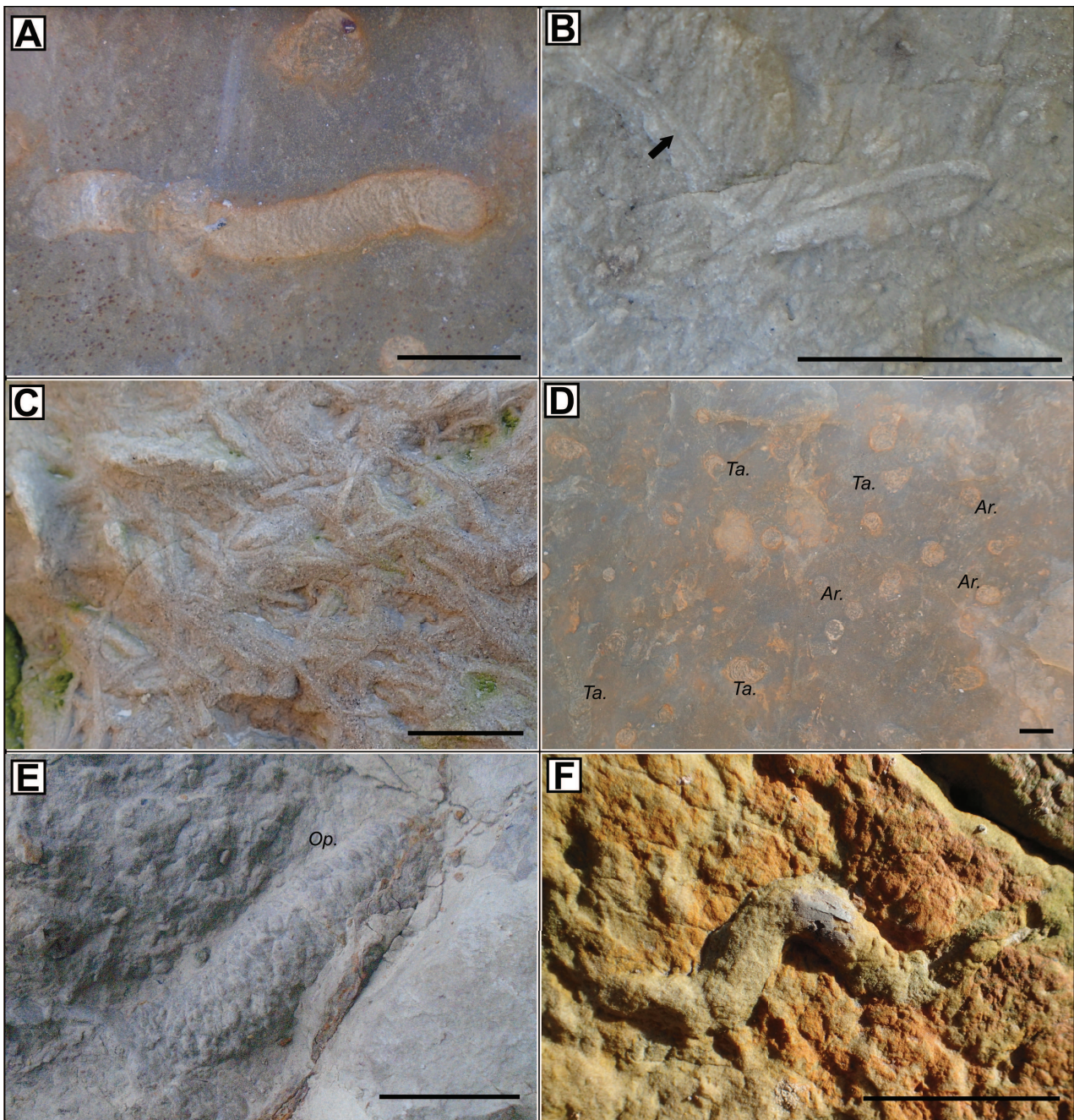


Figure 21

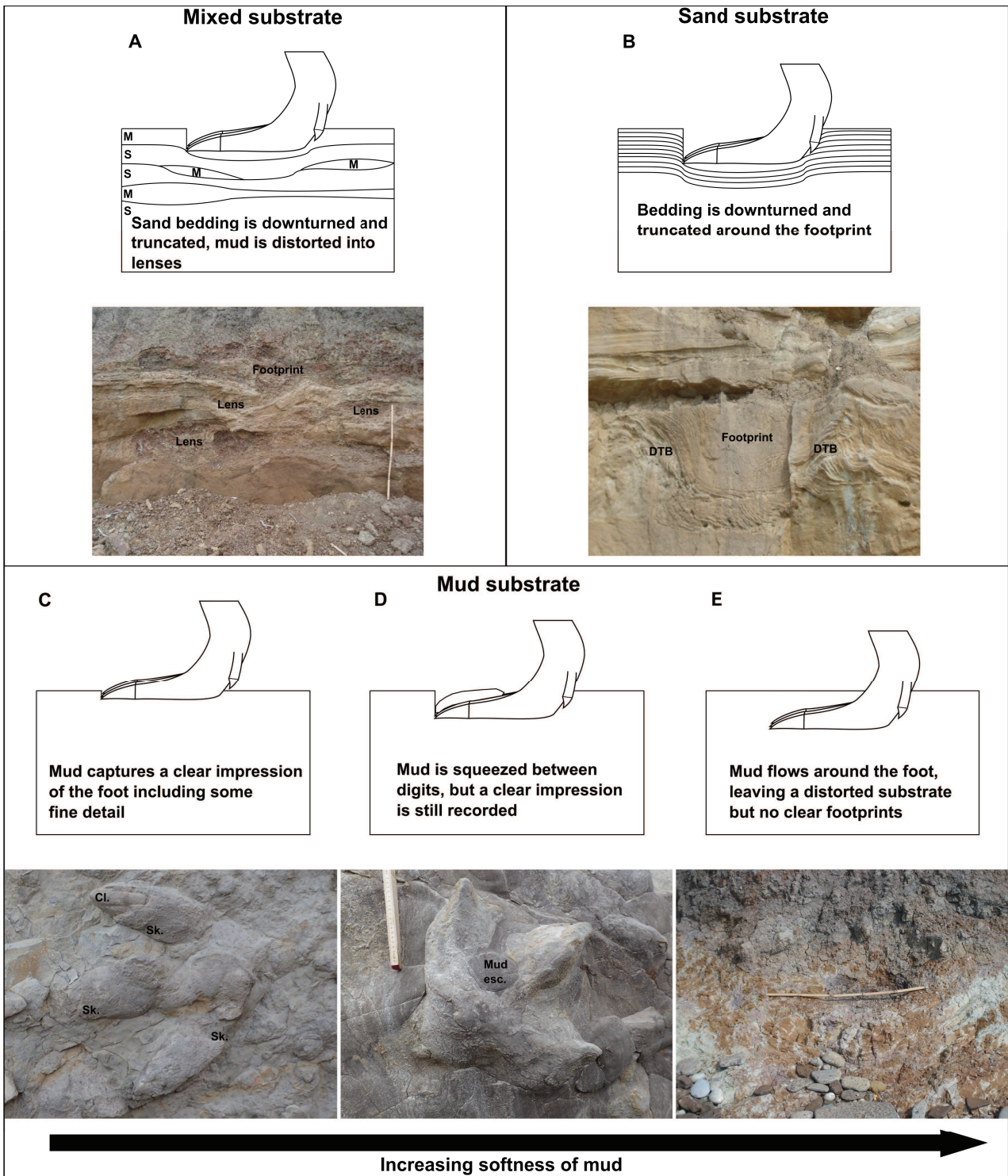


Figure 22

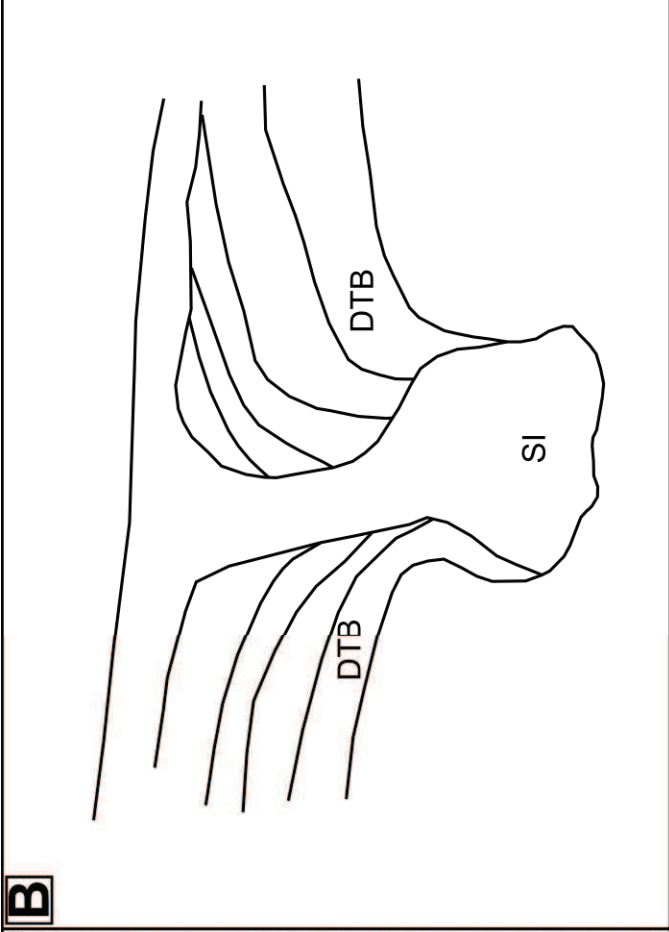


Figure 23

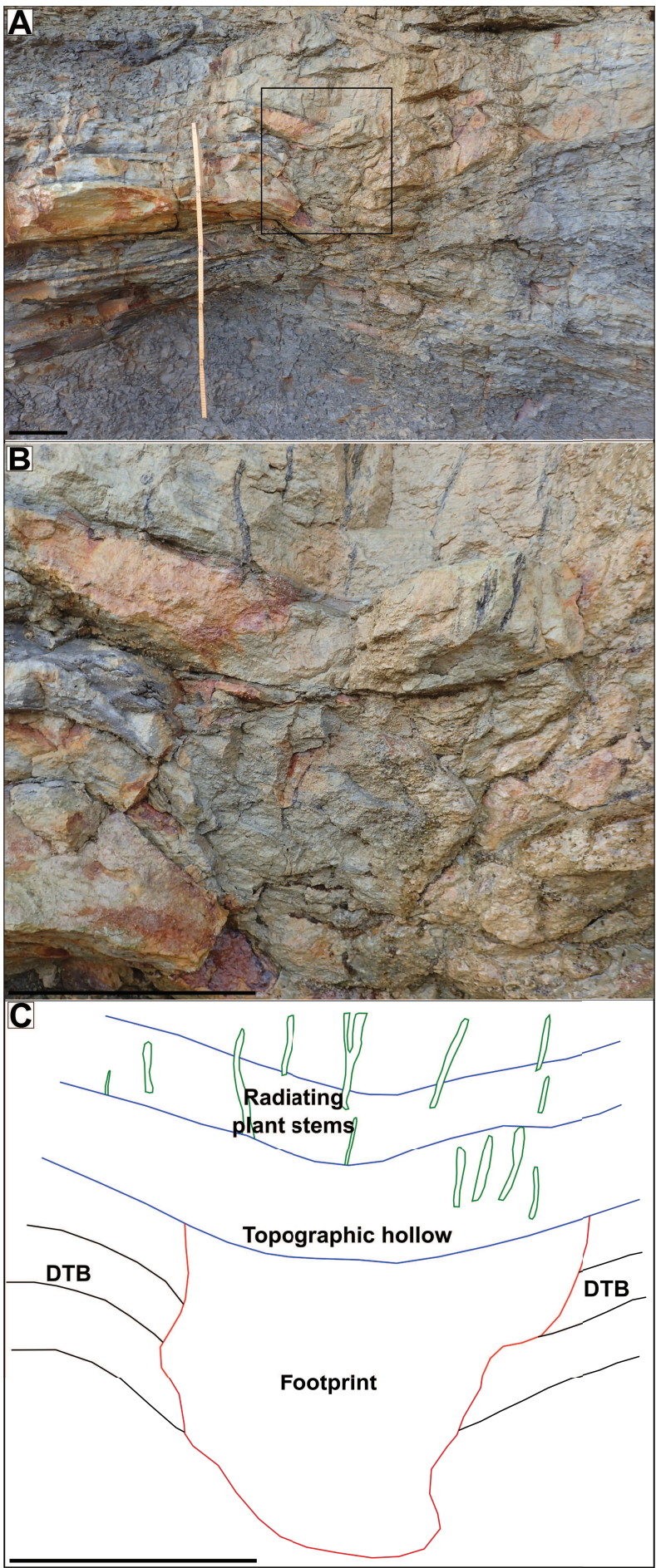


Figure 24

Morphotype	Abundance	Abundance of skin impressions	Length/ cm	Width/ cm
Ornithopod	56	11	18.3 – 61 average 34.7	16 – 51 average 33.8
<i>Caririchnium magnificum</i>	31	4	18.3 – 61 average 36	20.1 – 51 average 35.7
<i>Caririchnium isp.</i>	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
<i>Tetrapodosaurus isp.</i> (A)	2	2	25 – 27 average 26	26 – 28.8 average 27.4
<i>Tetrapodosaurus isp.</i> (B)	1	0	30	33
<i>Stegopodus manus</i>	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	<i>Arenicolites isp.</i>	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
	<i>Taenidium barretti</i>	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	<i>Cochlichnus cochi</i>	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
	<i>Ophiomorpha nodosa</i>	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
	<i>Palaeophycus striatus</i>	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
	<i>T. barretti</i>	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.