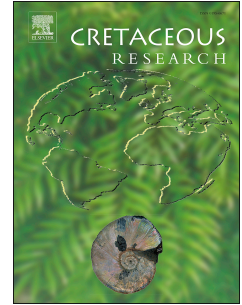


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A new dromaeosaurid dinosaur from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, and implications for European palaeobiogeography

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1 A new dromaeosaurid dinosaur from the Wessex
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4 palaeobiogeography

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18 Kingdom

19

20 A B S T R A C T

21

22

23 The Lower Cretaceous of England has produced a diverse assemblage of dinosaurs, including
24 ornithischians, sauropods, and theropods. The origins of this assemblage are poorly
25 understood. Here, we describe a new dromaeosaurid, *Vectiraptor greeni* gen. et sp. nov., from
26 the Barremian Wessex Formation of the Isle of Wight. The animal is represented by associated
27 dorsal vertebrae and a partial sacrum. Dorsal vertebrae are short, with pleurocoels, camellate
28 pneumatization, stalked parapophyses and enlarged neural canals. Neural spines are tall, with
29 large ligament scars. Sacral centra lack pleurocoels but have large neural canals and foramina
30 suggesting pneumatization. These characters suggest affinities with Dromaeosauridae and
31 specifically the derived, large-bodied Eudromaeosauria. *Vectiraptor* resembles Early
32 Cretaceous eudromaeosaurs from North America, suggesting a faunal exchange between
33 Europe and North America. The diverse Early Cretaceous dinosaur assemblage found in
34 England and Europe resulted from dispersal from North America, Asia, and West Gondwana,
35 likely involving both land bridges and oceanic dispersal. Europe served as a biotic crossroads
36 in the Early Cretaceous, allowing faunal interchange between landmasses.

37

38 1. Introduction

39

40 During the Early Cretaceous, England supported a highly diverse dinosaur assemblage
41 (Weishampel et al., 2004). Perhaps the most diverse assemblage comes from the Wessex
42 Formation of the Wealden Group, on the Isle of Wight (Martill et al., 2001). While complete
43 remains are rare, the fauna has been sampled and studied for over a century, and includes both
44 fossils (Martill et al., 2001) and footprints (Pond et al., 2014; Lockwood, 2016), with around
45 20 dinosaur species now known (Table 1). This high diversity is surprising because Europe
46 was isolated from the rest of the world by seas for much of the Cretaceous (Smith et al., 2004).

47 The Wessex Formation primarily outcrops along the Isle of Wight's southwest coast (Fig.
48 1A), with smaller outcrops at Sandown and on the Isle of Purbeck, in Dorset. On the Isle of
49 Wight, the Wessex Formation comprises a thick sequence— up to 180 metres (Gale, 2019)—
50 of sandstones and variegated mudstones representing floodplain and fluvial deposits. Plant
51 debris beds (*sensu* Sweetman and Insole 2010) within the Wessex Formation yield a high
52 diversity of vertebrates, including theropod dinosaurs. At least nine taxa are recognized (Table
53 1), including basal tetanurans (Benson et al., 2009), spinosaurids (Martill and Hutt, 1996)
54 (Barker et al., 2021), allosauroids (Brusatte et al., 2008), tyrannosauroids (Hutt et al., 2001), a
55 probable ornithomimosaur (Allain et al., 2014), and bird-like maniraptorans (Howse and
56 Milner, 1993; Sweetman, 2004).

57 The Dromaeosauridae, a clade of birdlike, predatory maniraptorans, appear to be present,
58 but are poorly represented. *Ornithodesmus cluniculus*, known from a sacrum (Howse and
59 Milner, 1993) likely represents a dromaeosaur (Norell and Makovicky, 2004; Hartman et al.,
60 2019). Several isolated teeth, varying in size and morphology, have been referred to
61 Dromaeosauridae (Sweetman, 2004). Another possible dromaeosaur, *Nuthetes destructor*, has
62 been reported from older, Berriasian beds of the Lulworth Formation of the Purbeck Limestone

63 Group (Owen, 1854; Milner, 2002), which would tend to support the presence of
64 dromaeosaurids in the Lower Cretaceous of England.

65 Here we describe two associated vertebrae and a partial sacrum of a small theropod,
66 collected from the Wessex Formation at Compton Bay, Isle of Wight, by Mr Mick Green of
67 Brighstone, IOW, and Mr Nick Chase (deceased). Study of this material reveals that it
68 represents a new species of dromaeosaurid (Fig. 2).

69

70 Abbreviations. IWCMS, Isle of Wight County Museum Service, Isle of Wight, Sandown, Isle
71 of Wight; MIWG Museum of Isle of Wight Geology, Sandown, Isle of Wight; TMP, Royal
72 Tyrrell Museum of Palaeontology, Drumheller, Alberta; YPM, Yale Peabody Museum, New
73 Haven, Connecticut.

74

75

76 **2. Geology**

77

78 The specimen described here comprises two bones (IWCMS. 2021.31.1-3) collected by Mr.
79 Mick Green in 2004 from the foreshore at Compton Bay on the Isle of Wight (Fig. 1A), and a
80 third collected by Mr. Nick Chase. The attached matrix indicates they derive from a pyrite-rich
81 plant debris bed exposed on the foreshore (National Grid Reference SZ 372 846:
82 Latitude/Longitude 50° 39' 36.6"N, 01° 28' 26.5"W). The fossils can be identified as part of a
83 single animal because they were collected over a short time period, and each find was located
84 within several metres of the others. They also resemble each other in preservation and pyrite
85 rich matrix initially coating the specimens, which is characteristic of the PDB exposed close to
86 the finds, as well as the colour and texture of the bones. Furthermore, the relative size of the

87 bones is consistent with them belonging to a single animal (Fig. 2B). Finally, the bones share
88 features such as enlarged neural canals and, in the dorsals, pleurocoels with camellate
89 pneumaticity (see description below).

90

91 At this locality, the upper Wessex Formation of the Wealden Group is exposed above a small
92 fault, down throwing the younger and overlying Vectis Formation against the Wessex
93 Formation. The plant debris bed yielding the specimens lies west of the fault and occurs below
94 the boundary of the Wessex-Vectis formations.

95 The non-marine Wessex Formation is comprised of a succession of variegated and
96 oxidized overbank mudstones, some having undergone long periods of pedogenesis (Wright et
97 al., 2000; Robinson et al., 2002). They represent riparian seasonal wetlands (Wright et al.,
98 2000). Alluvial sandstones and plant debris beds (PDBs) are intermittent throughout the
99 sequence (Stewart, 1981; Radley, 1994; Sweetman et al., 2014). Plant debris beds (PDBs)
100 occur as laterally discrete and well-defined beds with abundant plant material and irregular
101 nodules of siderite and pyrite. PDBs are thought to represent locally generated debris flows,
102 collecting in depressions on the floodplain (Sweetman and Insole, 2010). Wright et al. (2000)
103 conclude they are a result of stagnant to periodically oxygenated ponds, or billabongs, acting
104 as local refugia for animals during droughts. The rapid burial of the PDBs, and the development
105 of reducing conditions within the sediment, created favourable environments for the
106 preservation of vertebrates (Batten, 2011; Austen and Batten, 2018), from microvertebrates
107 (Sweetman, 2007) to giant dinosaurs (Naish et al., 2004). Vertebrates from the Wessex include
108 elasmobranchs (Sweetman and Underwood, 2006), freshwater osteichthyans (Sweetman et al.,
109 2014), mammaliaforms (Sweetman, 2006, 2008, 2009), lizards, crocodyliforms (Ristevski et
110 al., 2018), turtles (Joyce et al., 2011; Pérez-García, 2012), and pterosaurs (Steel et al., 2005;

111 Sweetman and Martill, 2010; Martill, 2015; Martill et al., 2020). Dinosaurs are diverse, with
112 around 20 recognized species (Table 1).

113

114 **3. Systematic palaeontology**

115

116 Dinosauria Owen 1842

117 Saurischia Seeley 1887

118 Theropoda Marsh 1881

119 Dromaeosauridae Matthew and Brown 1922

120 Eudromaeosauria Longrich and Currie 2009

121

122 Genus *Vectiraptor* gen. nov.

123

124 *Etymology.* *Vectis*, Latin name for the Isle of Wight + Greek *raptor*, ‘thief’

125

126 *Diagnosis.* As for type and only species *V. greeni* (see below)

127

128 *Vectiraptor greeni*, gen. et sp. nov.

129

130 *Etymology.* *greeni*, after Mr Mick Green of Brighstone, Isle of Wight, who discovered and
131 prepared the type material.

132

133 *Holotype.* IWCMS 2021.31.1-3 (Figs. 3-10); IWCMS 2021.31.2, anterior dorsal vertebra
134 (Figs. 3,4), IWCMS 2021.31.1, posterior dorsal vertebra (Figs. 5-7), and IWCMS 2021.31.3
135 partial sacrum (Figs. 8,9).

136

137 *Type Locality:* Compton Bay, Isle of Wight, United Kingdom (Fig. 1).

138 *Type horizon.* Wessex Formation (Lower Cretaceous, Barremian) (Batten, 2011).

139

140 *Diagnosis.* Large dromaeosaur (2.5 - 3 m) characterized by the following character
141 combination (* = autapomorphy). Dorsal vertebrae with deep, triangular infradiapophyseal
142 fossae, divided by accessory lamina* in anterior dorsals, deep infrapostzygapophyseal fossae;
143 extensive pneumatization of vertebral column including dorsal centra, with small pleurocoels
144 anteriorly, large, elliptical pleurocoels posteriorly, and camellate internal architecture; massive
145 neural spines with broad ligament scars*; dorsals with large neural canals; sacrum with a
146 massive neural canal; ventral groove not extending the full length of the sacrum; sacral centra
147 not pneumatized.

148

149 *Description.* The holotype comprises an anterior dorsal vertebra (Figs. 3,4), a posterior dorsal
150 (Figs. 5-7), and parts of three fused sacral vertebrae (Figs. 8, 9). The bone is dark and encrusted
151 and infilled with pyrite. The anterior dorsal and sacrum have rounded edges resulting from
152 weathering in the surf.

153

154 *Anterior dorsal.* The centrum of the anterior dorsal (IWCMS 2021.31.2) is short and robust
155 (Figs. 3,4). As preserved the anterior face measures 33 mm high by 31 mm wide; the centrum
156 measures 45 mm long. The anterior articular face is slightly concave, and is strongly angled
157 downward (Fig. 4), as in anterior dorsals of other dromaeosaurs (Ostrom, 1969; Sues and
158 Averianov, 2014; Turner et al., 2021), as well as tyrannosaurs (Brusatte et al., 2016) and
159 ornithomimosaurs (Sues and Averianov, 2016). The centrum's lateral surfaces bear large,
160 shallow depressions. Anteriorly, these depressions bear a large (5 mm diameter) pneumatic

161 foramen. The centrum is relatively broad ventrally, in contrast to that of Troodontidae, where
162 the anterior dorsal centra are narrow ventrally (Zanno et al., 2011).

163 Posteriorly, the centrum is broken, revealing its interior structure. The bone has a dense
164 cortex, and inside this a series of bony laminae that divide the centrum into air-filled chambers,
165 or camellae. This internal structure is similar to that reported for unenlagiine dromaeosaurs,
166 including *Unenlagia comahuensis* (Gianechini and Zurriaguz, 2021) and *Rahonavis ostromi*
167 (Forster et al., 2020). In other dromaeosaurs, including *Itemirus medullaris* (Sues and
168 Averianov, 2014) and *Saurornitholestes langstoni* (Sues, 1978) breakage of the cortex reveals
169 that the centrum's internal architecture has a spongy texture, but the structure in the center of
170 the vertebra is not visible. The tyrannosauroid *Vectaerovenator inopinatus* (Barker et al., 2020)
171 has large camerae inside the centrum. The camellate internal structure seen here instead
172 resembles that of some sauropods, such as the contemporary *Chondrosteosaurus gigas* (Owen,
173 1876).

174 The neural arch is fused to the centrum, but a suture remains visible. Prominent anterior
175 centrodiapophyseal laminae and posterior centrodiapophyseal laminae extend dorsally to the
176 diapophyses. These laminae define a deep, triangular infradiapophyseal fossa, as in other
177 dromaeosaurids (Ostrom, 1969; Sues and Averianov, 2014). These fossae deeply excavate the
178 neural arch and would have extended above the neural canal. Inside the fossa is a thin, vertical
179 lamina, dividing the infradiapophyseal fossa into two distinct chambers; this lamina appears to
180 be unique to *Vectiraptor*.

181 The neural canal is large, as in other Paraves (Ostrom, 1969; Zanno et al., 2011) and
182 slightly taller than wide. Inside the neural arch, the canal becomes narrower and deeper,
183 becoming teardrop-shaped and extending downwards into the centrum. The neural canal also
184 becomes larger inside the vertebrae in *Rahonavis*; this condition is not known for other taxa.

185 The neural spine is largely eroded away, but its base preserves a deep, broad excavation
186 anteriorly. Here a large interspinous ligament attached, as in eudromaeosaurs (Ostrom, 1969;
187 Sues and Averianov, 2014). The eroded surfaces of the neural spine expose the hollow interior,
188 showing that the camellate architecture extends into the neural arch.

189

190

191 *Posterior dorsal.* The centrum is short and robust (Figs. 5,6). As preserved, it measures 36 mm
192 long, 35 mm wide, and 30 mm tall, but anterior and posterior articular surfaces are broken.

193 The articular surface is damaged but the centrum's proportions suggest it was wider
194 than tall, as typical of dromaeosaurids (Norell and Makovicky, 2004), including *Unenlagia*
195 *comahuensis* (Novas et al., 2021), *Deinonychus antirrhopus* (Ostrom, 1969), *Sauromitholestes*
196 *langstoni* (Sues, 1978) and *Ornithodesmus cluniculus* (Seeley, 1887a). By contrast, the
197 articular surfaces of *Utahraptor ostrommayisi* (NRL, pers obs.) and *Itemirus medullaris* (Sues
198 and Averianov, 2014) are at least as tall as wide. In Troodontidae the faces of the centra are
199 subequal in height and width (Averianov and Sues, 2016), or narrower than tall (Zanno et al.,
200 2011).

201 The centrum is broken but it appears to have been short, and yet somewhat more
202 elongate than is typical of eudromaeosaurids (Fig. 10), e.g. *Deinonychus* (Ostrom, 1969)
203 *Sauromitholestes* (Sues, 1978), and *Velociraptor* (Norell and Makovicky; 1999) where the
204 centrum is distinctly shorter than tall. In this respect, it is more similar to *Unenlagia* (Novas et
205 al., 2021) and troodontids (Zanno et al., 2011; Averianov and Sues, 2016).

206 The centrum is broken to expose the interior, and the bone's inside is filled with the
207 same camellae seen in the anterior dorsal vertebra (Fig. 7). The cortices and septa dividing the
208 camellae are relatively thick given the animals relatively small size and extensive pneumaticity:
209 cortices measure up to 2 mm in thickness, the bony septa are up to 1 mm thick. In the pneumatic

210 cervicals of ornithomimids, for example, both the cortices and septa dividing the pneumatized
211 interior of the bone are very thin-walled; cortices are 1 mm thick or less, and septa are less than
212 0.5 mm thick (Watanabe et al. 2015).

213 The centrum sides bear deep, elliptical depressions, the floors of which are pierced by
214 pneumatic foramina. The presence of pneumatic foramina on the dorsal vertebrae is a derived
215 feature of Eudromaeosauria (Longrich and Currie, 2009), but is also seen in some Unenlagiinae
216 (Forster et al., 2020; Novas et al., 2021); troodontids (Novas et al., 2021) and ornithomimosaur
217 (Makovicky et al., 2004) lack pneumatic foramina. Similar deep, narrow depressions surround
218 the pneumatic foramina in *Deinonychus* (Ostrom, 1969). By contrast, *Itemirus* (Sues and
219 Averianov, 2014) and *Saurornitholestes* (Sues, 1978) have deep but broad fossae here, rather
220 than narrow depressions. In the velociraptorine *Shri devi* the pneumatic foramina themselves
221 are elongate (Turner et al., 2021), but simply pierce the centrum, rather than lying in a
222 depression.

223 The neural arch is fused to the centrum. Anteriorly, the arch bears an elongate, laterally
224 projected parapophysis. Stalked parapophyses are a derived feature of dromaeosaurs (Longrich
225 and Currie, 2009), e.g. *Unenlagia comahuensis* (Novas et al., 2021), *Deinonychus* (Ostrom,
226 1969) *Itemirus* (Sues and Averianov, 2014), and *Velociraptor* (Norell and Makovicky, 1999).
227 This condition is approached in troodontids, however (Zanno et al., 2011).

228 Anterior and posterior centrodiapophyseal laminae are prominent. As in other
229 coelurosaurs, they define three fossae- a narrow infraprezygapophyseal fossa, a deep, triangular
230 infradiapophyseal fossa and a deep and triangular infrapostzygapophyseal fossa. The deep and
231 triangular shape of the infradiapophyseal fossa resembles those of other dromaeosaurids, in
232 particular *Deinonychus antirrhopus*, *Utahraptor ostrommaysi*, and *Itemirus medullaris*. This
233 infradiapophyseal fossa is obliquely oriented and elliptical in Velociraptorinae (Norell and
234 Makovicky, 1999; Turner et al., 2021), and weakly developed in Saurornitholestinae (Sues,

235 1978). Unlike the anterior dorsal vertebra, there does not appear to be a lamina dividing the
236 infradiapophyseal fossa.

237 Behind the posterior centrodiaepophyseal lamina, the infrapostzygapophyseal fossa is
238 triangular, and deeply excavates the neural arch. This shape of this fossa resembles
239 *Deinonychus*, *Utahraptor*, and *Itemirus*, but is deeper in *Vectiraptor*; this fossa is reduced
240 however in *Sauromitholestes*.

241 The diapophyses are narrow in dorsal view, as in other eudromaeosaurs (Ostrom, 1969;
242 Norell and Makovicky, 1999; Sues and Averianov, 2014; Turner et al., 2021) and troodontids
243 (Zanno et al., 2011). They are directed posteriorly and almost horizontally, which may indicate
244 that the vertebra comes from the back of the dorsal column (Ostrom, 1969). Diapophyses are
245 broken distally, and it is unclear how long they were.

246 The neural canal is large anteriorly; posteriorly it is greatly expanded. This expanded
247 neural canal is approached but less well-developed in *Deinonychus antirrhopus* (MCZ 5210),
248 where the posterior opening of the neural canal is larger than the anterior. In *Sauromitholestes*
249 *langstoni* the neural canal is greatly expanded anteriorly and posteriorly (Sues, 1978) to a
250 degree not seen in *Vectiraptor*. Inside the neural canal, the floor of the neural arch is narrow
251 and extends deep into the centrum; two matrix-filled depressions may represent pneumatic
252 foramina piercing the top of the centrum. The large neural canal in these dromaeosaurs may be
253 associated with development of pneumatic diverticula inside the neural canal, as seen in some
254 extant birds (O'Connor, 2006). Expansion of the neural canal inside the arch is also seen in the
255 dorsals of ornithomosaurs (Watanabe et al., 2015), and paravians in general appear to have large
256 neural canals (Zanno et al., 2011).

257 The neural spine is anteroposteriorly short, and very wide mediolaterally for such a
258 small theropod, to a degree not seen in other dromaeosaurids (Fig. 10). The apex is broken, but
259 it appears to have been much taller than broad anteroposteriorly (Fig. 6), as in eudromaeosaurs

260 (Ostrom, 1969; Norell and Makovicky, 1999), *Unenlagia* (Novas et al., 2021), and derived
261 troodontids (Zanno et al., 2011). Its anterior and posterior surfaces bear broad interspinous
262 ligament scars, as in eudromaeosaurs (Ostrom, 1969), but the ligament scars are much broader
263 than in other dromaeosaurs, except perhaps *Sauornitholestes*. The ligament scars are narrow
264 in *Unenlagia* (Novas et al., 2021) and Troodontidae (Zanno et al., 2011). The interspinous
265 ligament scars extend ventrally between the postzygapophyses displacing the
266 postzygapophyses laterally.

267
268 *Sacrum*. The fragmentary sacrum (Fig. 8) preserves parts of two centra and their associated
269 neural arches (Fig. 9). Based on comparisons with *Sauornitholestes langstoni* (Howse and
270 Milner, 1993) the sacrum includes parts of the first and second sacrals, and the first, second,
271 and third neural arches (Fig. 11). Note, however, that *Ornithodesmus cluniculus* has a dorsal
272 vertebra incorporated into the sacrum for a total of 6 sacrals (Howse and Milner, 1993). The
273 number of sacrals varies in dromaeosaurs (Norell and Makovicky, 2004), so it is possible that
274 *Vectiraptor* had six as well. If so, the sacrum would correspond to centra 2 and 3, and arches
275 2, 3, and 4 of *Ornithodesmus*.

276 The first sacral has a low, broad centrum. Its ventral surface is broadly convex
277 transversely, and slightly concave in lateral view, more like *Ornithodesmus* than
278 *Sauornitholestes* in this respect. The centrum's lateral surfaces bear a pair of broad, triangular
279 depressions, as in *Sauornitholestes*, *Ornithodesmus* (Howse and Milner, 1993), and
280 *Variraptor* (Le Loeuff and Buffetaut, 1998; Chanthasit and Buffetaut, 2009). However, this
281 lateral fossa lacks the pneumatic foramen seen in *Ornithodesmus* (Howse and Milner, 1993).
282 The centrum does not appear to have been pneumatized. Its internal structure is cancellous and
283 formed of many small trabeculae, showing no trace of the camellate pneumaticity of the
284 dorsals.

285 The neural arch is broadly arched to form a massive neural canal, with a maximum
286 diameter of up to 20 mm anteriorly and 25 mm more posteriorly. This expanded neural canal
287 is seen in *Sauromitholestes langstoni* (TMP 1967.20.36), *Rahonavis ostromi* (Forster et al.,
288 2020), and judging by the shape of the neural arch, also in *Ornithodesmus*. It is unclear how
289 widely distributed this feature is in Dromaeosauridae, but it is absent in ornithomimosaur
290 (Watanabe et al., 2015).

291 Large intervertebral foramina, formed between adjacent sacral neural arches, pierce the
292 neural canal laterally. This feature is seen in other dromaeosaurids, including *Sauromitholestes*
293 *Ornithodesmus*, *Rahonavis* and *Unenlagia* (Novas et al., 2021). Small intervertebral foramina
294 are present in *Variraptor* (Le Loeuff and Buffetaut, 1998; Chanthasit and Buffetaut, 2009).
295 Ornithomimosaur lack this feature (Watanabe et al., 2015), but it occurs convergently in the
296 abelisaurids (O'Connor, 2006). The floor of the neural canal is irregular, with small, paired
297 depressions atop the posterior end of the first sacral.

298 The second sacral was much narrower than the first. It bears a massive transverse
299 process, and atop this transverse process, a narrow ridge that extends to the neural spine. The
300 neural arch of the second sacral is broadly arched, and narrower than the arch of the first sacral.
301 Posteriorly, the neural arch of the third sacral is fused to the second. It bears traces of a narrow
302 neural spine, but the height of the neural spine cannot be determined.

303 The size of the neural canal in *Vectiraptor* is extraordinary; this feature is not unique to
304 *Vectiraptor*, and occurs in other dromaeosaurids including *Sauromitholestes* and *Rahonavis*.
305 It is unlikely the enlarged neural canal simply accommodated neurons, as the volume of
306 neurons required to fill it would have been comparable to the volume of the brain. Instead, it
307 seems likely this cavernous canal contained a large air-sac system. The large intervertebral
308 foramina of the sacrum, seen convergently in abelisaurids (O'Connor, 2006), may
309 accommodate diverticula of this air-sac system.

310

311

312 *Histology.* A natural break of the posterior dorsal revealed a number of well-defined growth
313 lines (Erickson, 2005), or lines of arrested growth (LAGs) which are readily visible in
314 photographs (Fig. 12).

315 The LAGs are seen in the unworked outer cortex of the centrum. Two millimetres of
316 cortex preserve at least six and perhaps eight LAGs: a thin outer layer appears to exist but is
317 difficult to trace due to damage, and two closely spaced inner LAGs appear to be present, but
318 cannot be traced to confirm this due to remodelling of the cortex.

319 The innermost layer is largely destroyed by resorption and remodelling of the bone. It
320 may be followed by a very thin layer, >0.1 mm in thickness. This is followed by a thick layer,
321 around 0.5 mm in thickness, then a thin layer, ~ 0.1 mm in thickness, and four layers around
322 0.2 mm in thickness. The final, outermost layer is very thin, about 0.1 mm thick, and
323 presumably was growing just before the animal died. Based on the relatively thin growth lines,
324 the texture of the bone, and the fusion of skeletal elements, including the fusion of neural arches
325 to the centra, and sacra to one another, the animal was probably fully grown and a mature or
326 even old individual.

327 Assuming that the LAGs correspond to seasonal growth, the LAGs would correspond
328 to between seven and nine years of life. It is impossible to precisely determine the age of the
329 animal, but assuming the final 7-9 years correspond to roughly the final third of the animal's
330 life, when growth slows dramatically (Erickson et al., 2004), it may have died at around 20-30
331 years of age.

332

333

334 **4. Discussion**

335
336 *Systematics of Vectiraptor*. The affinities of *Vectiraptor* are, like many other Isle of Wight
337 theropods, complicated by the fragmentary nature of the material. Furthermore, many of the
338 potentially informative characters seen in the specimen occur in several different theropod
339 groups. All these characters, however, are seen in Dromaeosauridae.

340

341 Features supporting dromaeosaurid affinities:

342

343 (1) Parapophyses borne on stalks

344 (2) Dorsal centra wider than tall

345

346 Features specific to dromaeosaurid subclades:

347 (3) Dorsal centra short relative to diameter (Eudromaeosauria, *Unenlagia*)

348 (4) Pleurocoels in posterior dorsals (Eudromaeosauria, *Unenlagia*, *Rahonavis*)

349 (5) Dorsal neural spines tall, anteroposteriorly narrow (Eudromaeosauria, *Unenlagia*)

350 (6) Broad interspinous ligament scars (Eudromaeosauria)

351

352 Some of these characters occur in other theropods, but dromaeosaurs are the only group
353 that possesses all of them.

354 Within Dromaeosauridae, the affinities are uncertain. In most respects, the vertebrae
355 resemble the large-bodied Eudromaeosauria, particularly in terms of the broad neural spine.
356 However, the dorsal centra, while approaching the short, stout condition seen in
357 Eudromaeosauria are more elongate than is typical of e.g. *Saurornitholestes* or *Deinonychus*,
358 here showing a more primitive condition. A similar suite of features are seen in the Late
359 Cretaceous *Unenlagiia* (Novas et al., 2021) as well as the enigmatic *Variraptor* from the

360 Maastrichtian of France (Le Loeuff and Buffetaut, 1998). Overall, the morphology and age of
361 the material suggest affinities with Eudromaeosauria, perhaps as a primitive member of the
362 group or sister to it. However, more complete material is required to understand the
363 relationships of *Vectiraptor* with other dromaeosaurs.

364 The anatomy of the vertebrae argues against referral to another theropod group. The
365 separation of the postzygapophyses and hyposphenes by the interspinous ligament scars is
366 typical of dromaeosaurs and Alvarezsauridae but would preclude referral to ornithomimosaur,
367 tyrannosaurs, or a basal theropod (Gianechini et al., 2018). *Vectiraptor* can be excluded from
368 Tyrannosauridae on the basis of the stalked parapophyses, and from Ornithomimosauria on the
369 basis of the short centra, presence of pleurocoels, and stalked parapophyses (Makovicky et al.,
370 2004). It can be excluded from Oviraptorosauria by the stalked parapophyses. *Vectiraptor* can
371 be excluded from Troodontidae by the stalked parapophyses, and presence of pleurocoels
372 (Makovicky and Norell, 2004).

373

374 *Comparisons of Vectiraptor to other Wessex Formation theropods*

375 Many theropods have been reported from the Wessex Formation (Fig. 13). Most of are
376 based on material that is incomplete, non-overlapping, and of uncertain affinities (Martill et
377 al., 2001) which complicates attempts to understand the diversity of the Wessex. Several teeth
378 (Sweetman, 2004: Fig 3) may pertain to *Vectiraptor*, but a review of the Isle of Wight theropods
379 suggests that *Vectiraptor* cannot be referred to any of the previously described theropod
380 species.

381 The isolated teeth identified by Sweetman (2004) are consistent with the presence of a
382 large dromaeosaurid in the assemblage. These teeth (including IWCMS.2002.1,
383 IWCMS.2002.3, and IWCMS.2002.4, and BMNH R 16510) are typical of dromaeosaurids in
384 having small anterior denticles and large anterior denticles, and in some specimens

385 (IWCMS.2002.1; BMNH R 16510) strongly recurved crowns. They resemble other
386 dromaeosaurs (Longrich, 2008) in terms of the shape of the basal cross-section, although the
387 crowns are much wider mediolaterally than is typical of dromaeosaurids, and the basal pinching
388 and fluting of the crown that characterizes dromaeosaurs (seen e.g. in *Nuthetes destructor*:
389 Milner, 2002) is highly reduced. Finally, in terms of size, with a basal length of 6.5-10 mm,
390 the teeth compare well with *Deinonychus antirrhopus* (up to 9 mm: Ostrom, 1969,) and are
391 therefore likely to pertain to *Vectiraptor*, which is similar to *Deinonychus* in size. If these teeth
392 do belong to *Vectiraptor*, then their morphology would tend to support the idea that the animal
393 is related to the Eudromaeosauria. At the same time, the small anterior denticles and basal
394 fluting of the teeth are also seen in some tyrannosauroids (Rauhut et al., 2010); suggesting
395 caution in referring the Isle of Wight teeth to dromaeosaurids.

396 Another tooth, IWCMS.2002.2, is smaller and exhibits a more classic dromaeosaur
397 cross-section, with a flattened and pinched base, suggesting it represents a distinct taxon. It
398 may pertain to another dromaeosaurid species, perhaps *Ornithodesmus cluniculus*.

399 Aside from these teeth, none of the coelurosaur fossils previously described from the
400 Wessex Formation (Table 1) appear to pertain to *Vectiraptor*.

401 *Ornithodesmus cluniculus* (Howse and Milner, 1993) closely resembles dromaeosaurs
402 in a number of features (Norell and Makovicky, 1997). Its anterior sacrals are pneumatized
403 suggesting pleurocoels extended into the posterior dorsals, a eudromaeosaur feature. However,
404 *Ornithodesmus* appears to be distinct from *Vectiraptor*. It considerably smaller than
405 *Vectiraptor*, perhaps a little more than half its size, but appears to be mature based on the fusion
406 of the sacrals to each other, and fusion of the last dorsal into the sacrum. *Ornithodesmus* also
407 has pleurocoels in the sacral centra, which *Vectiraptor* lacks. This argues against synonymy
408 of *Ornithodesmus* and *Vectiraptor*, but it remains possible that they are related. A small,
409 isolated tibia (Lydekker, 1891) may represent *Ornithodesmus*: it resembles dromaeosaurids

410 (Ostrom, 1969; Norell and Makovicky, 2004) in having a triangular fibular crest, a broad distal
411 end of the tibia an astragalar suture that is straight in posterior view, and a relatively low
412 ascending process of the astragalus. The affinities of *Ornithodesmus* itself are uncertain. It
413 appears to represent a dromaeosaurid. To date, the only phylogenetic analysis to include it
414 recovered it as an unenlagiine (Hartman et al., 2019), although some of the features (e.g.
415 pneumatic foramina in the posterior dorsals) seem similar to eudromaeosaurs. The dorsosacral
416 is shorter than is typical of basal dromaeosaurs such as Microraptorinae, but not as short as in
417 Eudromaeosauria; in this feature the animal is reminiscent of *Vectiraptor*.

418 The small theropod *Aristosuchus pusillus* also preserves a sacrum (Naish, 2002). The
419 sacra are elongate and spool-shaped, unlike in *Vectiraptor*. The S-shaped curvature of the
420 pubis, along with the spool-shaped centra, resembles *Compsognathus* (Peyer, 2006), *Coelurus*
421 *fragilis* (Carpenter et al., 2005), and Ornithomimosauria (Ji et al., 2003), suggesting
422 compsognathid or ornithomimosaur affinities.

423 *Calamosaurus foxi*, represented by an isolated cervical (Lydekker, 1891), does not
424 overlap with *Vectiraptor*. However, the strongly convex anterior articular surface rules out
425 dromaeosaurid affinities, in which the cervicals are flat anteriorly (Norell and Makovicky,
426 2004). In overall morphology *Calamosaurus* closely resembles tyrannosauroids such as *Dilong*
427 *paradoxus* (Xu et al., 2004).

428 *Thecocoelurus daviesi* is of uncertain affinities. It has been allied with caenagnathids
429 (Naish and Martill, 2002) but may more closely resemble ornithomimosaur (Allain et al.,
430 2014); in either case it is distinct from *Vectiraptor*.

431 *Yaverlandia bitholos*, represented by a pair of fused and thickened frontals, was
432 traditionally classified as a pachycephalosaurid ornithischian (Galton, 1971). More recently, it
433 has been interpreted as a theropod, perhaps a troodontid (Naish and Martill, 2008). Either

434 assignment precludes a relationship with *Vectiraptor*; furthermore, it appears to come from a
435 much smaller animal.

436 MIWG 6214, a femur (Naish, 2000), exhibits maniraptoran features, but its small size
437 suggests that, if mature, it is distinct from *Vectiraptor*.

438 *Vectiraptor* therefore adds to the already high diversity of the Wessex Formation fauna.

439

440

441 *Implications for Wessex Formation dinosaur diversity and biogeography.*

442

443 The Early Cretaceous of England has one of the most diverse known Early Cretaceous
444 dinosaur assemblages (Table 1; Fig. 13). The high diversity of this assemblage might be
445 expected given that fossils have been collected here for almost 200 years (Naish and Martill,
446 2007). However, this high diversity is surprising considering the biogeography. For much of
447 the Early Cretaceous, Europe was isolated from other land masses by epicontinental seas
448 (Smith et al., 2004; Scotese, 2016). Europe was separated from North America by the North
449 Atlantic, from Asia by the Turgai Strait, and from West Gondwana (Africa and South America)
450 by the Tethys Sea (Smith et al., 2004; Scotese, 2016). As a result of the small area and isolation,
451 British and European dinosaurs might be expected to show low diversity, and high endemism.
452 Instead, diversity is high, with many lineages found in the UK and mainland Europe occurring
453 elsewhere. These faunal connections imply extensive dispersal between Europe and other land
454 masses in the Early Cretaceous.

455 The European dinosaur assemblage's origins remain unclear. The iguanodontids of
456 Britain and Europe appear to be related to species from North America (McDonald et al., 2010;
457 McDonald, 2012), suggesting a possible origin there. Similarly, European polacanthines show
458 affinities with North American nodosaurs (Jingtao et al., 2013). The tyrannosauroids

459 meanwhile suggest affinities with Asia (Brusatte et al., 2016). A rebbachisaurid vertebra from
460 the Wessex Formation (Mannion et al., 2011) nests within species found in West Gondwana
461 (Averianov and Sues, 2021), suggesting a West Gondwanan origin for Rebbachisauridae.

462 *Vectiraptor* itself appears most similar to eudromaeosaurs from the Early Cretaceous
463 of North America, suggesting a possible North American origin for the European
464 dromaeosaurs. Although dromaeosaurs appear roughly at the same time in Europe and Asia
465 (Fig. 14); North America has a diverse fauna of eudromaeosaurs in the Early Cretaceous
466 (Pittman and Xu, 2020), including *Utahraptor* (Kirkland et al., 1993), *Yurgovuchia*, an
467 unnamed velociraptorine (Senter et al., 2012) and *Deinonychus* (Ostrom, 1969).
468 Velociraptorinae (Evans et al., 2013). The basal clade (Longrich and Currie, 2009)
469 Saurornitholestinae (Sues, 1978; Burnham et al., 2000) (Currie and Varricchio, 2004; Currie
470 and Evans, 2020) occurs in North America during the Late Cretaceous, suggesting a North
471 American origin for Eudromaeosauria (Ding et al., 2020).

472 By comparison, dromaeosaurs from the Early Cretaceous of Asia include basal
473 lineages (Ding et al., 2020; Pittman and Xu, 2020) such as Microraptorinae (Xu et al., 2003;
474 Turner et al., 2007; Han et al., 2014) and *Tianyuraptor* (Zheng et al., 2010); *Fukuivenator*
475 (Azuma et al., 2016) may also represent a basal dromaeosaur. Eudromaeosaurs only appear
476 later in Asia (Ding et al., 2020) (Fig. 14), with the appearance of animals like *Itemirus* (Sues
477 and Averianov, 2014) and a giant, *Achillobator*-like form (Sues and Averianov, 2014: Fig. 13)
478 in the Turonian, and diverse velociraptorines in the latest Cretaceous (Norell et al., 2006;
479 Godefroit et al., 2008; Xu et al., 2010; Turner et al., 2021).

480 These patterns suggest that the dromaeosaurs originated in North America or Asia, then
481 dispersed to Europe. The presence of *Nuthetes* in the Purbeck Group (Milner, 2002) suggests
482 that this dispersal occurred no later than the Berriasian. *Dromaeosauroides bornholmensis*

483 from the Berriasian of Denmark (Bonde and Christiansen, 2003) may also represent an early
484 eudromaeosaur.

485 Since no biogeographic signal dominates, it seems likely that European faunas result
486 from a dinosaur influx from North America, Asia, and West Gondwana. This might explain
487 how this relatively small landmass nevertheless achieved high diversity.

488 Rather than simply accumulating lineages, however, Europe may have been an
489 important source of dinosaur diversity for other landmasses (Fig. 15). The Anglo-European
490 landmasses may have acted as a sort of crossroads between North America, Asia, and Africa.
491 Polacanthine phylogeny (Jingtao et al., 2013) suggests polacanthines originated in North
492 America, then colonized Asia via Europe. Rebbachisaurids (Averianov and Sues, 2021) and
493 hadrosauroids (McDonald, 2012) may have colonized Asia the same way.

494 The presence of the iguanodontian *Ouranosaurus* (McDonald et al., 2010) and the
495 dryosaurid *Elrhazosaurus* (McDonald, 2012) in Africa suggests two separate dispersals of
496 ornithopods into Gondwana. Likewise, basal spinosaurids occur in Europe (Arden et al., 2019)
497 (Charig and Milner, 1997; Mateus et al., 2011) and more derived forms later appear in Africa
498 (Serenio et al., 1998) and South America (Sues et al., 2002), suggesting dispersal from Europe
499 into North Africa (Barker et al., 2021), and beyond to South America (Sues et al., 2002);
500 spinosaurs also appear to colonize Asia (Allain et al., 2012) from Europe.

501 While large continents such as Asia, North America, and West Gondwana were
502 important in terms of generating diversity, England and Europe may have played a critical role
503 in facilitating faunal interchange between these larger landmasses. It should be kept in mind
504 that the origins of clades and their direction of dispersal can easily be changed by either the
505 discovery of new species in poorly sampled areas, changes in tree structure, or both. Dispersal
506 scenarios are therefore speculative and subject to change with an improved understanding of
507 dinosaur diversity, distribution, and phylogeny. Regardless of which evolutionary scenario one

508 invokes, multiple dispersals are needed to explain the widespread distribution of these
509 dinosaurs in the Early Cretaceous (Fig. 15).

510 Dispersal could have involved land bridges or oceanic dispersal. Many of the seas
511 surrounding Europe were shallow, so land bridges may have intermittently linked Great Britain
512 and mainland Europe to other landmasses. Greenland likely acted as a land bridge between
513 North America and Europe in the earliest Cretaceous (Smith et al., 2004), which could explain
514 their faunal similarities. Another land bridge may have subsequently linked Europe to Asia in
515 the Aptian and Albian (Smith et al., 2004). This might explain later, eastward dispersals of
516 groups such as polacanthines and rebbachisaurids into Asia.

517 It may be that some dinosaurs could cross the narrow marine barriers separating Europe
518 and other land masses, via swimming or rafting, as likely happened in Late Cretaceous
519 hadrosaurs and titanosaurs (Longrich et al., 2021). In particular, the deep, persistent ocean
520 channels separating Europe from West Gondwana (Smith et al., 2004) seem to preclude a land
521 bridge; if so, faunal exchange between Europe and Gondwana must have been via swimming,
522 or rafting. The rare, intermittent dispersal between the two seems consistent with oceanic
523 dispersal.

524 Finally, in the latest Cretaceous, the widening Atlantic limited dispersal between
525 Europe and North America, and faunal turnover eliminates the endemic Early Cretaceous
526 lineage. The dinosaurs are therefore low in diversity, with only a handful of lineages, mostly
527 from Gondwana and Asia (Longrich et al., 2021). These include lambeosaurine hadrosaurids
528 and telmatosaurs from Asia (Longrich et al., 2021), and titanosaurs and abelisaurids from Africa.

529 Strikingly, although dromaeosaurs are known from the latest Cretaceous of Europe
530 (Allain and Taquet, 2000; Chanthasit and Buffetaut, 2009), they may not be related to
531 *Vectiraptor* or even to Eudromaeosauria, but instead may represent unenlagiines (Hartman et
532 al., 2019), an hypothesis supported here. The ilium of *Variraptor* (Chanthasit and Buffetaut,

533 2009) resembles that of Unenlagiinae. Features shared include the enlarged cuppedicus fossa,
534 arched dorsal margin of the ilium and deep anterior blade, short posterior blade, concave
535 posterodorsal margin of the blade, and a brevis fossa that is reduced anteriorly (Novas et al.,
536 2021). Similarly, the short heel of pes phalanx II-2 in *Pyroraptor olympianus* (Allain and
537 Taquet, 2000) is more consistent with Unenlagiinae than Eudromaeosauria. These animals may
538 be related to Gondwanan dromaeosaurs, including dromaeosaurs from Africa (Rauhut and
539 Werner, 1995) and the South American Unenlagiinae. Further study and more fossils are
540 needed to resolve their relationships and patterns of dispersal. Finally *Balaur bondoc*,
541 previously interpreted as a dromaeosaur (Csiki et al., 2010), may represent a distinct lineage of
542 theropod, perhaps a bird (Lee et al., 2014) possibly related to the enigmatic *Gargantuavis*
543 (Mayr et al., 2020).

544

545 **5. Conclusions**

546

547 Associated skeletal remains from the Wessex Formation, of the Isle of Wight, document the
548 existence of a new dromaeosaur, *Vectiraptor greeni*. It appears to be a member of the
549 Eudromaeosauria, a group otherwise restricted to North America in the Early Cretaceous. The
550 presence of *Vectiraptor* on the Isle of Wight underscores the remarkable diversity of dinosaurs
551 in the Early Cretaceous of Europe. Extensive faunal interchange with the North America, Asia,
552 and Africa, may have allowed Europe achieve high diversity in a small region.

553

554

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556

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- 882

TABLES

883

884

885 **Table 1.** Dinosaurs of the Early Cretaceous (Hauterivian—Barremian) Wessex Formation,

886 Isle of Wight, United Kingdom.

887

888 **Table 2.** Dromaeosauridae from Europe.

889

890

FIGURE CAPTIONS

891

892

893 **Figure 1.** Type of locality of *Vectiraptor greeni*. A, Map of the Isle of Wight with the type

894 locality indicated by a red star, modified from Gale (2019). B, Stratigraphic column of the

895 Wessex Formation, modified from Sweetman and Insole Sweetman and Insole (2010). C,

896 Compton Bay showing exposed section containing the upper most 50m of the Wessex

897 Formation on the foreshore

898

899 **Fig. 2.** Relative size of *Vectiraptor greeni* (top) and position of recovered elements (below)

900

901 **Fig. 3.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.2 , anterior dorsal. In **A**, left lateral, **B**,

902 right lateral, **C**, anterior, **D**, posterior, and **E**, dorsal views. Abbreviations: aaf, anterior

903 articular face; idf, infradiapophyseal fossa; ils, interspinous ligament scar; fos, lateral fossa;

904 nec, neural canal; plc, pleurocoel. Scale = 5 cm.

905

906 **Fig. 4.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.2 , anterior dorsal, interpretive

907 drawing. **A**, lateral view; **B**, anterior view; **C**, dorsal view (anterior to right). Scale = 5 cm.

908

909 **Fig. 5.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.1, posterior dorsal. In **A**, anterior, **B**,
910 posterior, **C**, left latera, **D**, right lateral and **E**, dorsal views. Abbreviations: adl, anterior
911 diapophyseal laminal; dia, diapophysis; ils, interspinous ligament scar; ipf,
912 infraprezygapophyseal fossa; par, parapophysis; pdl, posterior diapophyseal lamina, ple,
913 pleurocoel. Scale = 5 cm.

914
915 **Fig. 6.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.1, posterior dorsal, interpretive
916 drawings. **A**, anterior view; **B**, posterior view; **C**, lateral view; **D**, dorsal view. Scale = 5 cm.

917
918 **Fig. 7.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.1, posterior dorsal, showing camellate
919 pneumaticity. **A**, anterior view; **B**, posterior view. Scale = 1 cm.

920
921 **Fig. 8.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.3, sacrum. **A**, left lateral; **B**, ventral, **C**,
922 dorsal, **D**, right lateral, **E**, anterior, and **F**, posterior views. Abbreviations: fe, intervertebral
923 fenestra; fos, lateral fossa; nec, neural canal; nsp, neural spine, s1, sacral 1, s2, sacral 2, tp,
924 transverse process. Scale = 5 cm.

925
926 **Fig. 9.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.3 sacrum, interpretive drawings. **A**,
927 left lateral view; **B**, dorsal view; **C**, ventral view. Numbers 1-5 correspond to sacra 1
928 through 5; ivf = intervertebral foramen; nec = neural canal. Scale = 5 cm.

929
930 **Fig. 10.** Posterior dorsal vertebra of *Vectiraptor greeni* IWCMS. 2021.33.1 compared to the
931 holotype of *Unenlagia comahuensis* (Novas et al. 2021) and to *Deinonychus antirrhopus*
932 YPM 5210. Top: lateral view; bottom: anterior view.

933

934 **Fig. 11.** Sacra of (top to bottom) *Vectiraptor greeni* IWCMS. 2021.33.3, *Ornithodesmus*
935 *cluniculus* (Seeley, 1887) *Sauromitholestes langstoni* TMP 12439 and *Variraptor*
936 *mechanorum* (Chanthasit and Buffetaut, 2009).

937

938

939 **Fig. 12.** *Vectiraptor greeni*, holotype IWCMS. 2021.33.3. **A**, cortical bone and air chambers
940 in posterior dorsal, **B**, closeup showing lines of arrested growth (LAGs). At least six and
941 perhaps eight closely-spaced LAGs are visible, representing 7-9 growth rings and likely,
942 years of life.

943

944 **Fig. 13.** Diversity of Wessex Formation theropods (see Table 1).

945

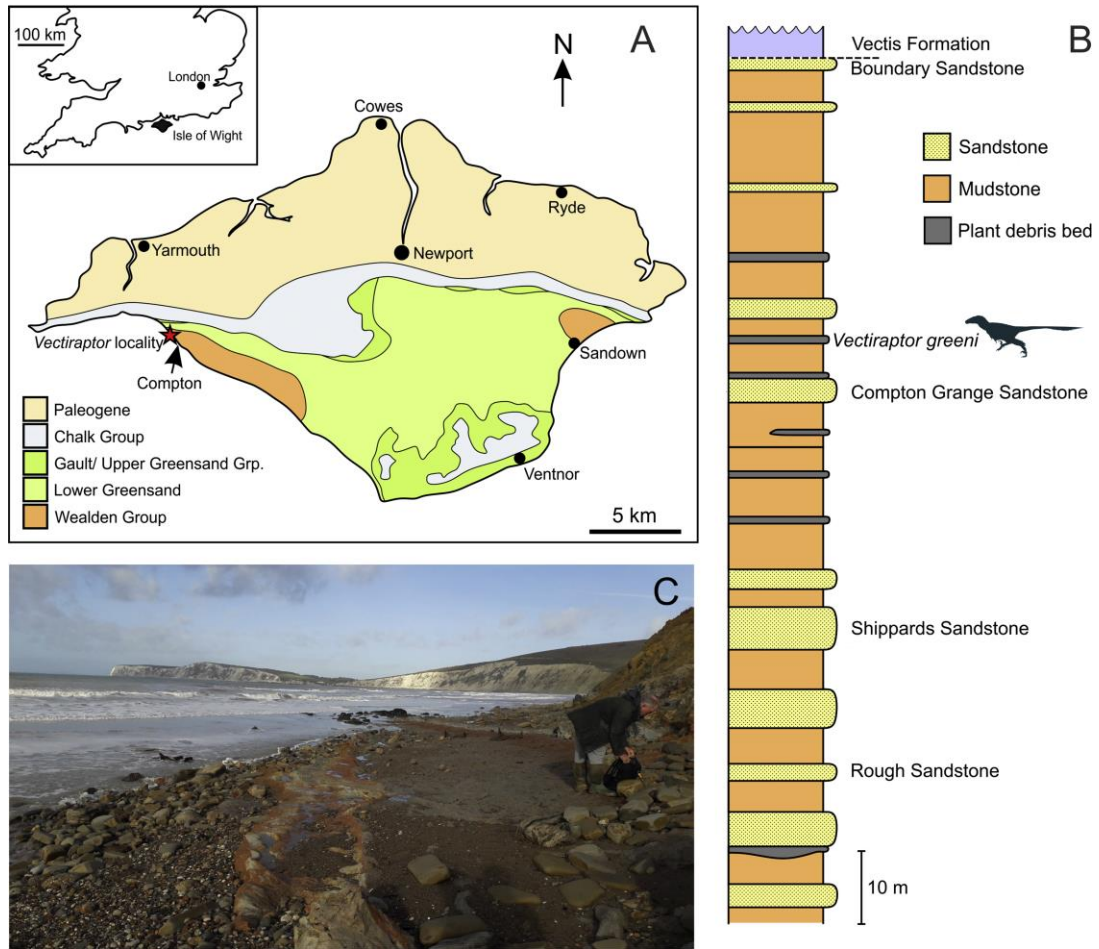
946 **Fig. 14.** Geographic and stratigraphic distribution of Eudromaeosauria in Europe (blue),
947 North America (red), and Asia (yellow), and Unenlagiinae (?) in Europe (light blue).

948

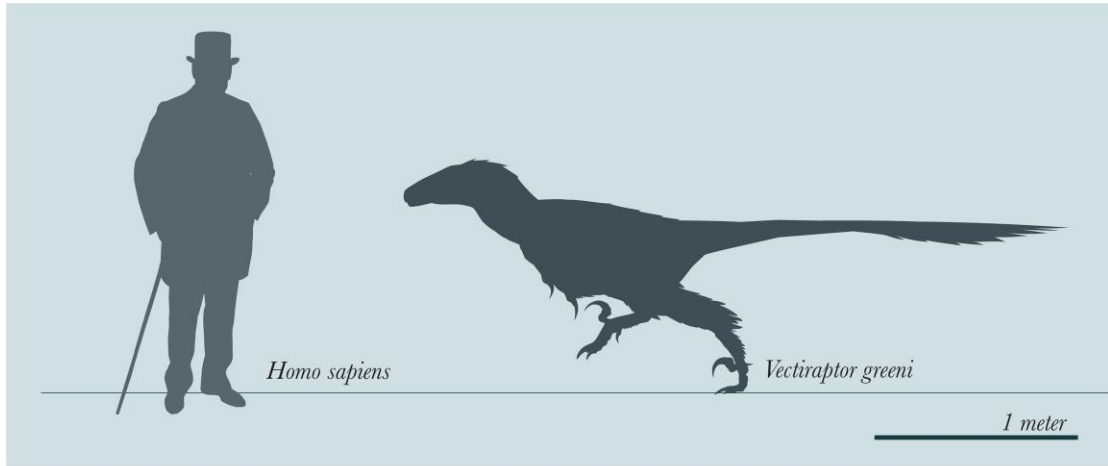
949 **Fig. 15.** Paleogeographic map showing potential dispersal routes in the Early Cretaceous. (1),
950 Iguanodontia; (2) Polacanthinae; (3) Dromaeosauridae; (4) Rebbachisauridae; (5)
951 Abelisauridae; (6) Dryosauridae; (7) Spinosauridae; (8) Tyrannosauroidae. Note that further
952 sampling of fossils and/or revisions to phylogenetic hypotheses could easily support
953 alternative patterns of dispersal, but any scenario requires extensive dispersal between
954 Europe, North America, Asia, and West Gondwana to explain shared faunal elements.

955

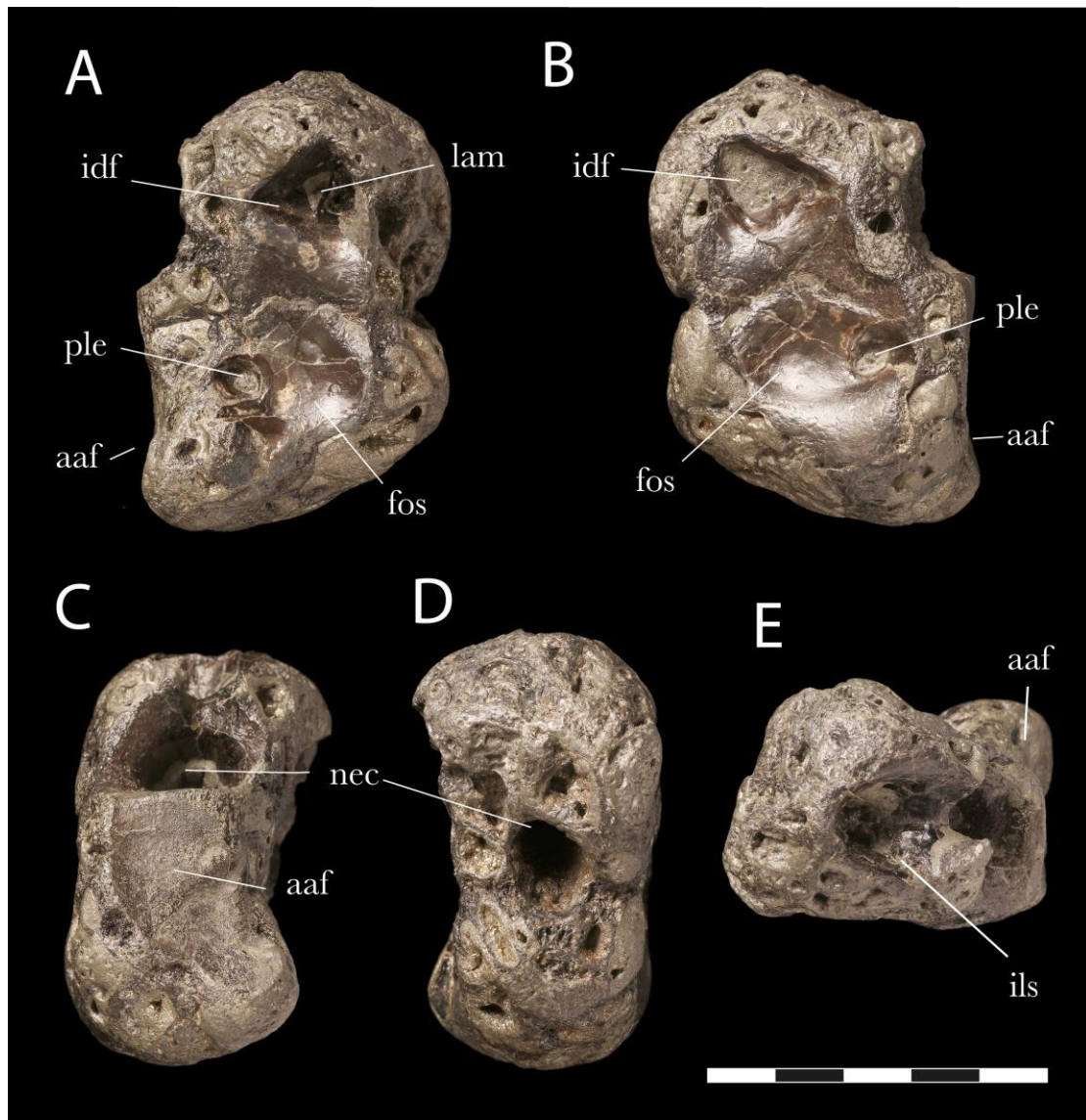
956 **Fig. 16.** Life reconstruction of *Vectiraptor greeni* by Gabriel Ugueto.

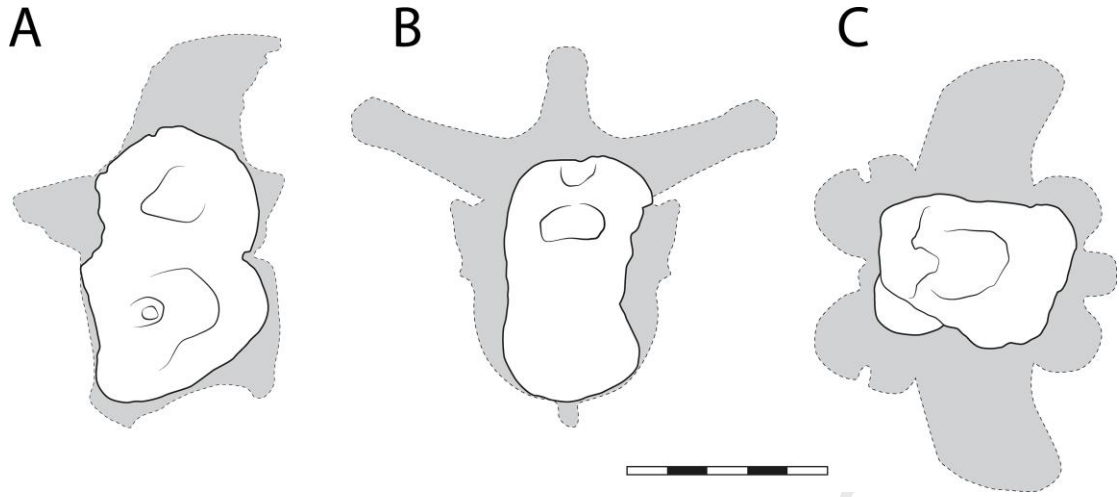


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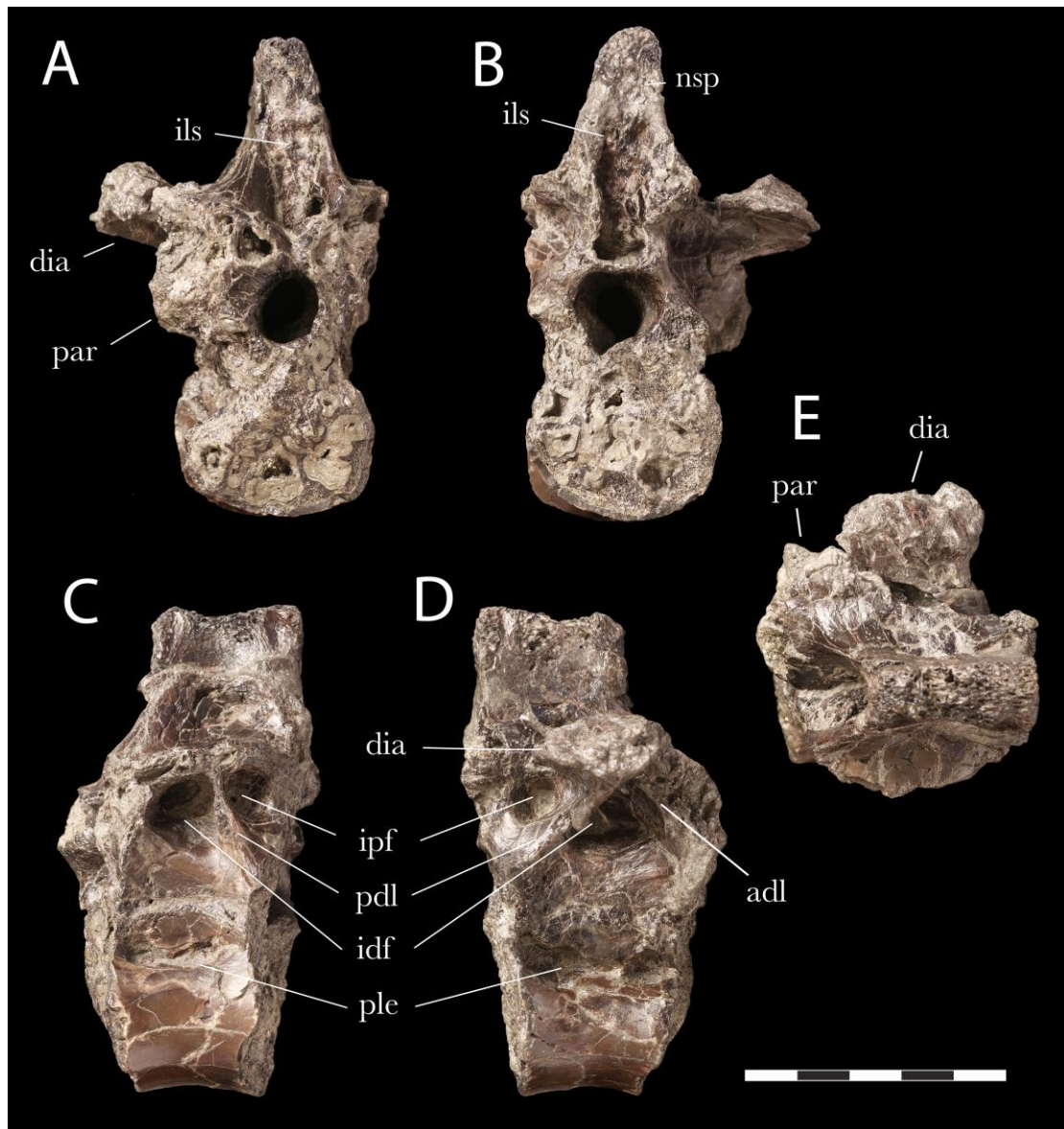


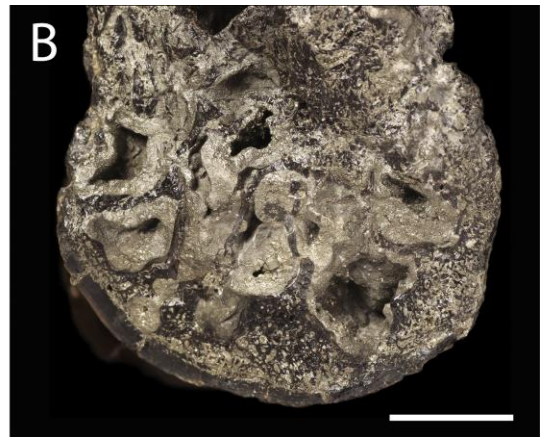
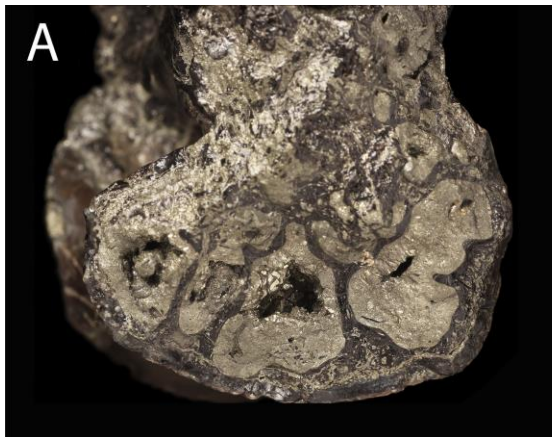
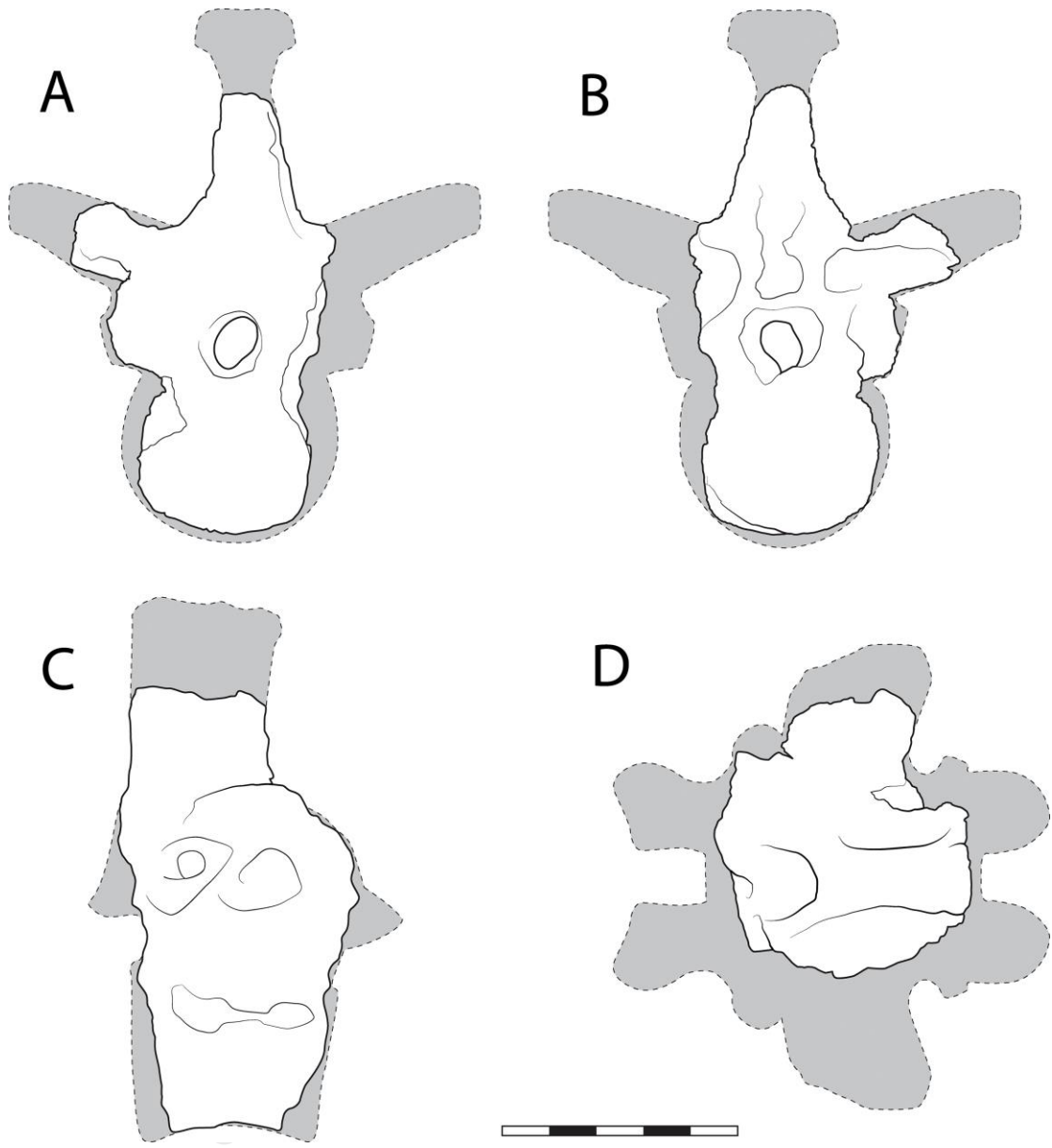
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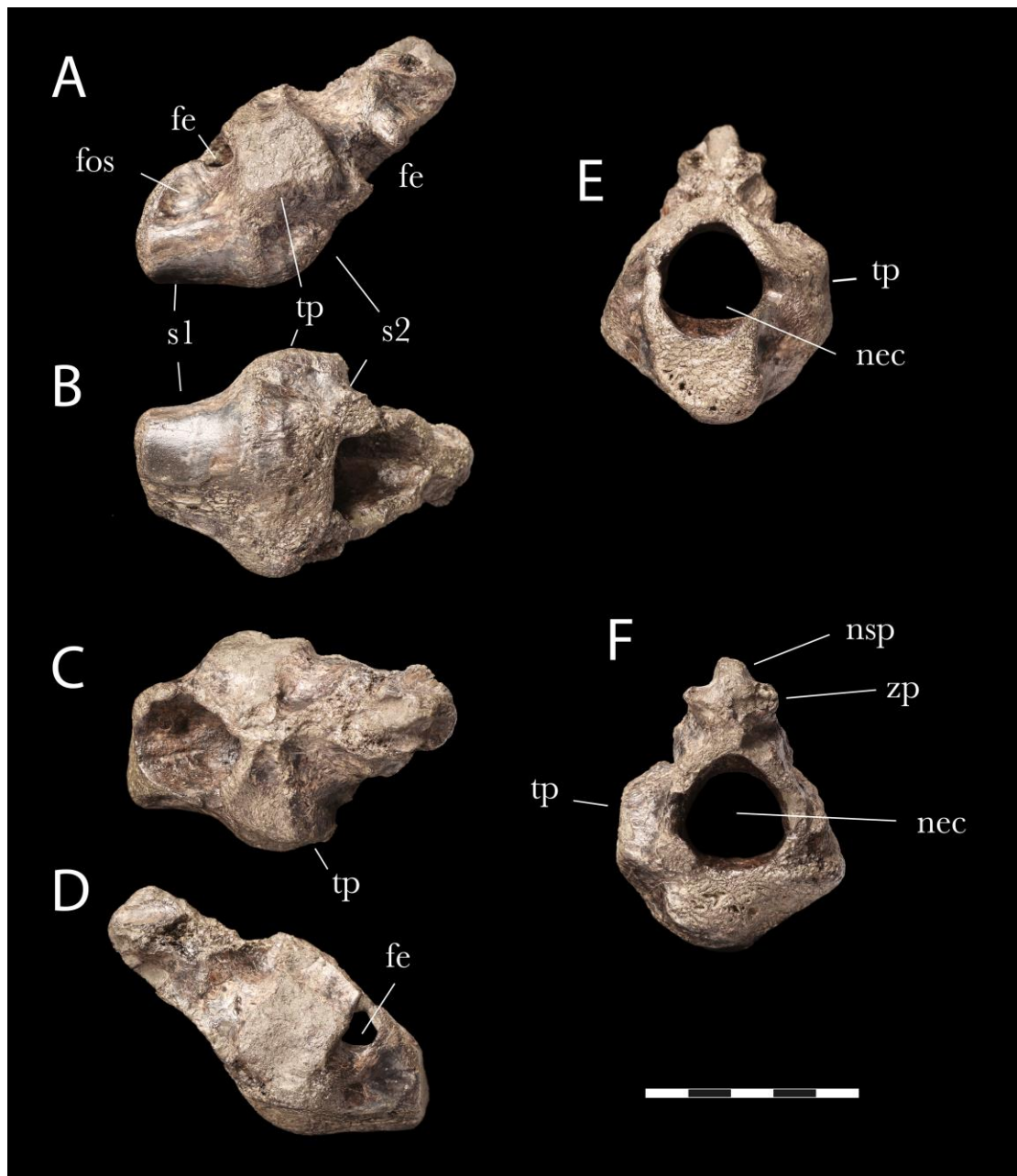


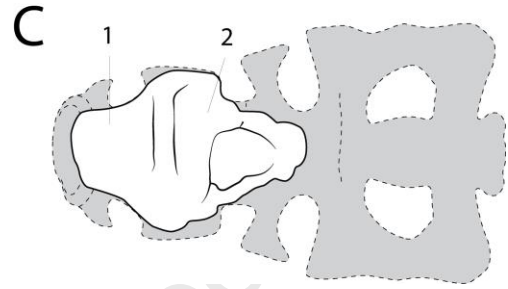
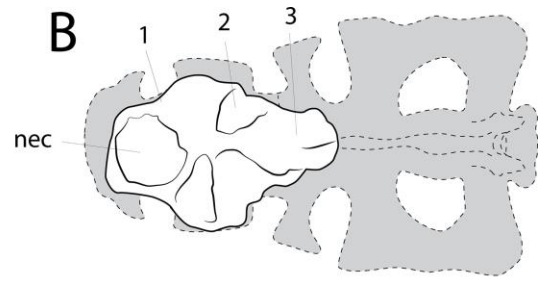
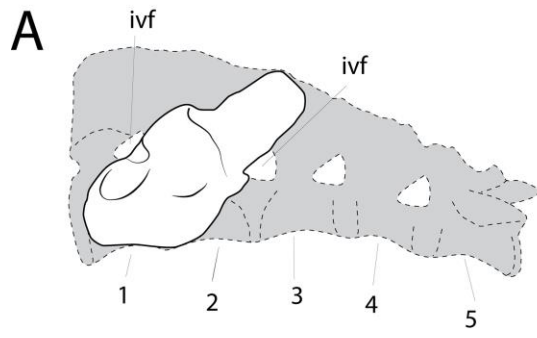


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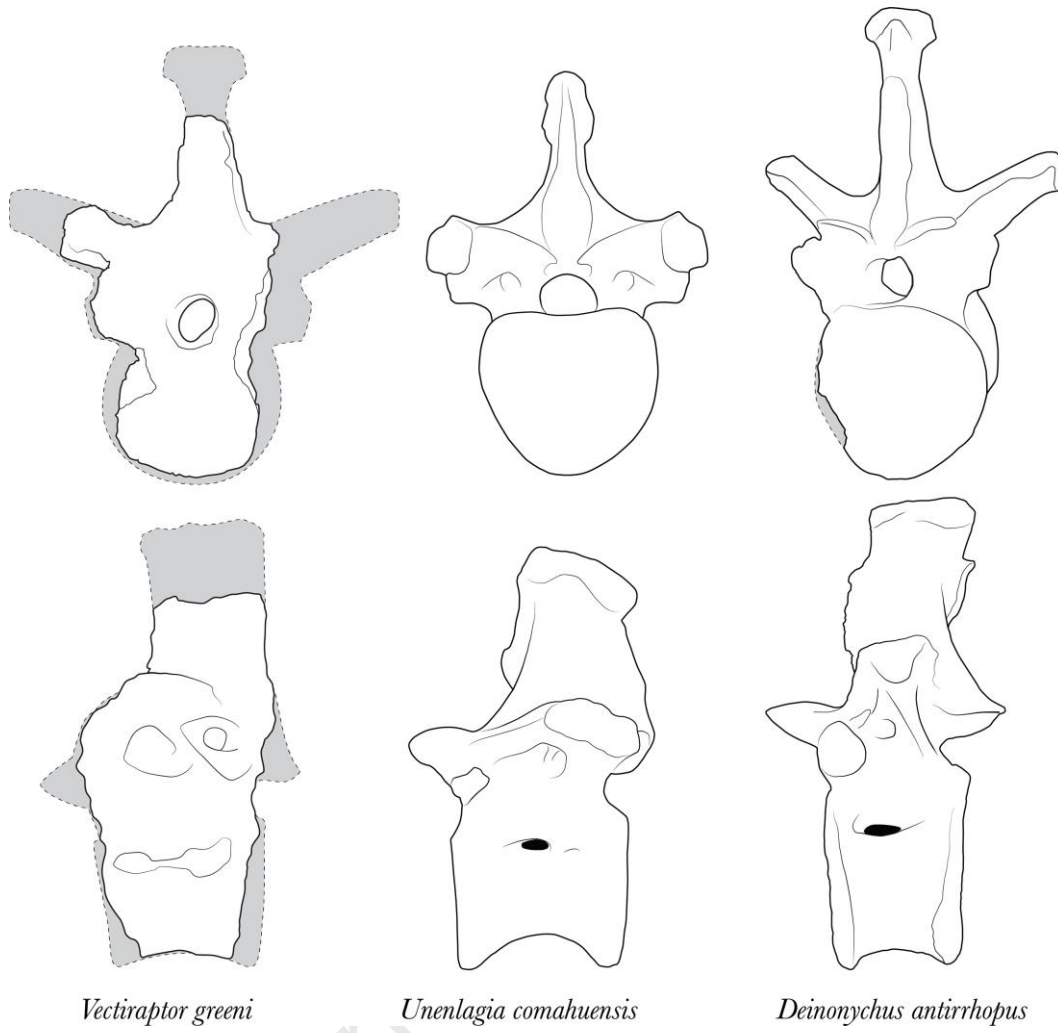


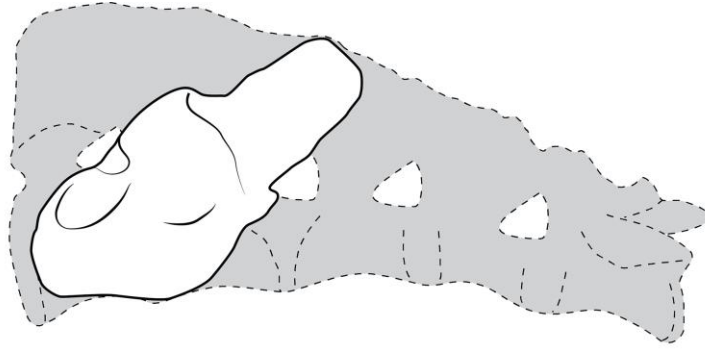




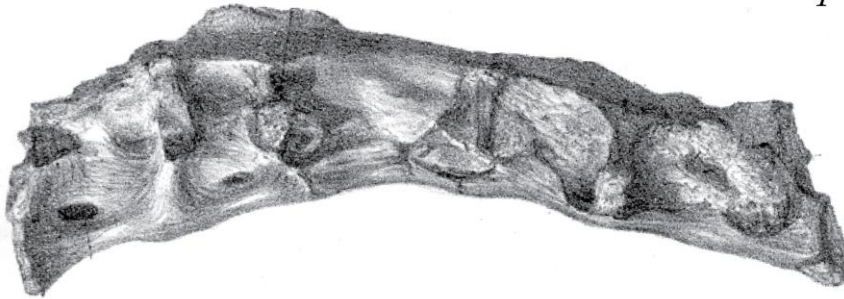


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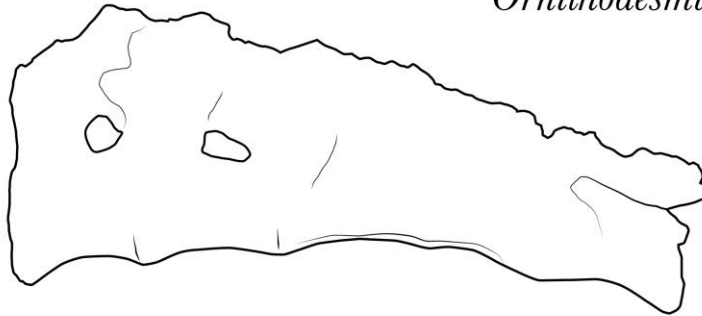




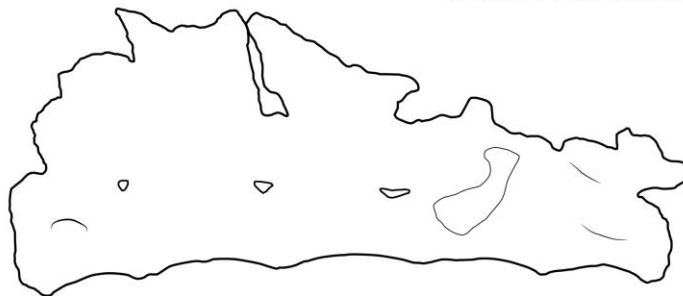
Vectiraptor greeni



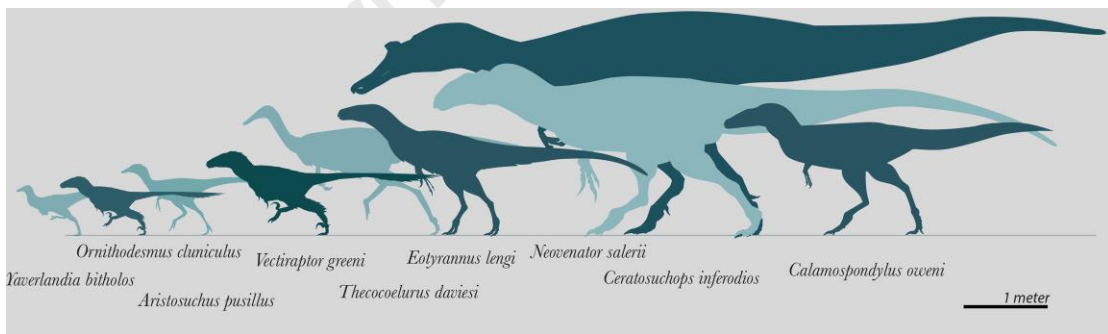
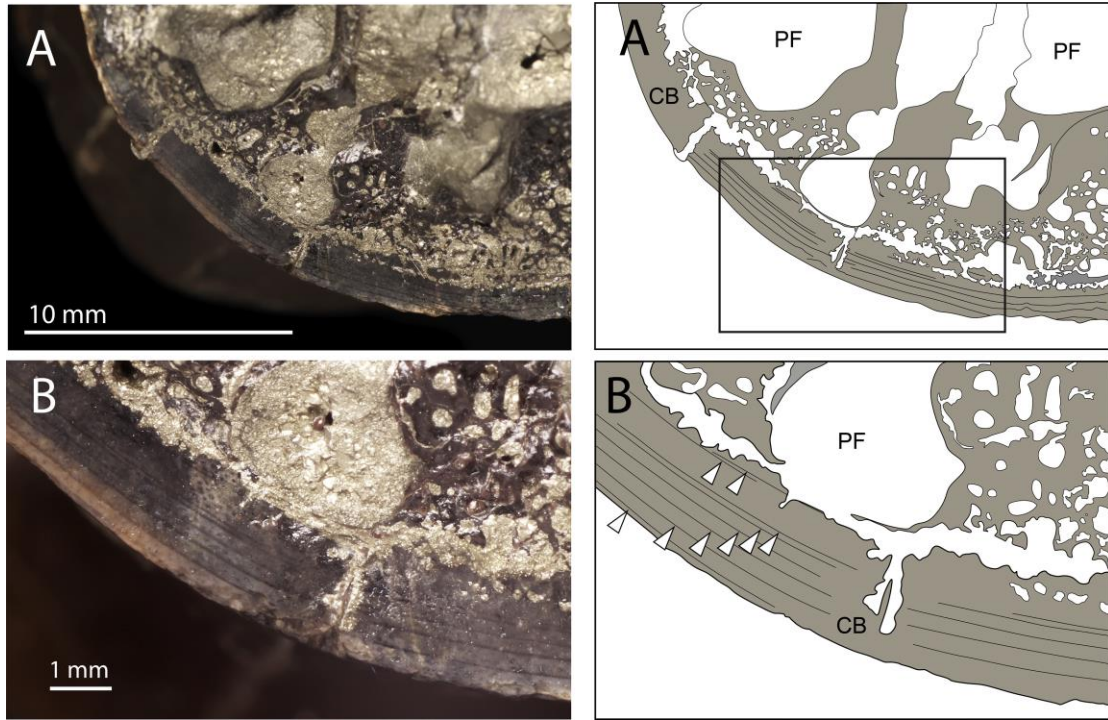
Ornithodesmus cluniculus

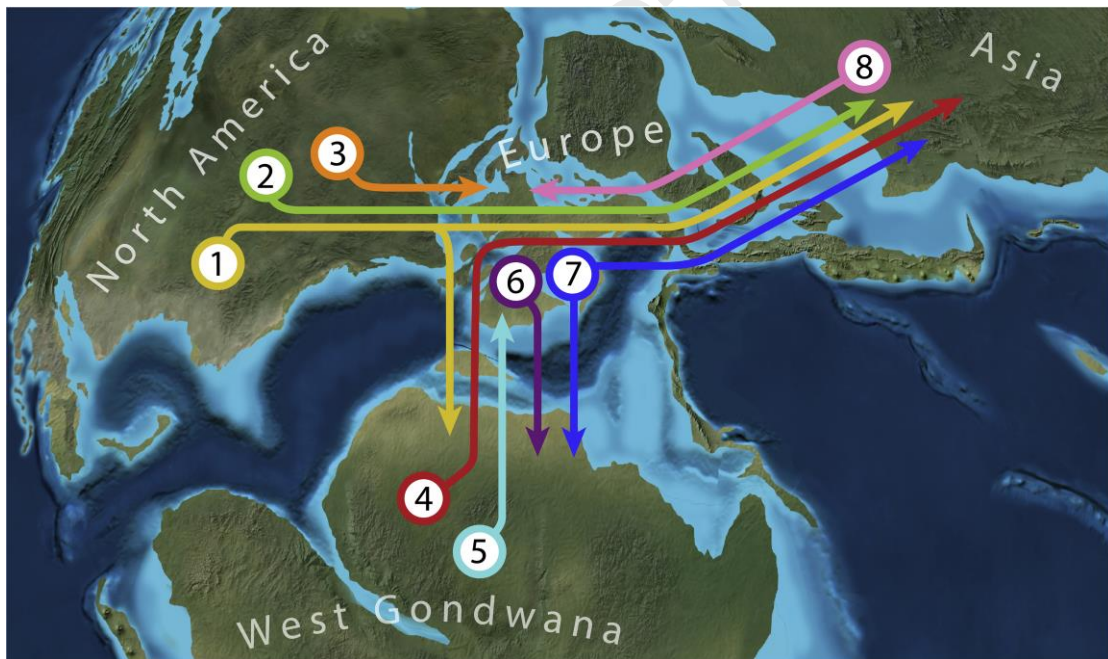
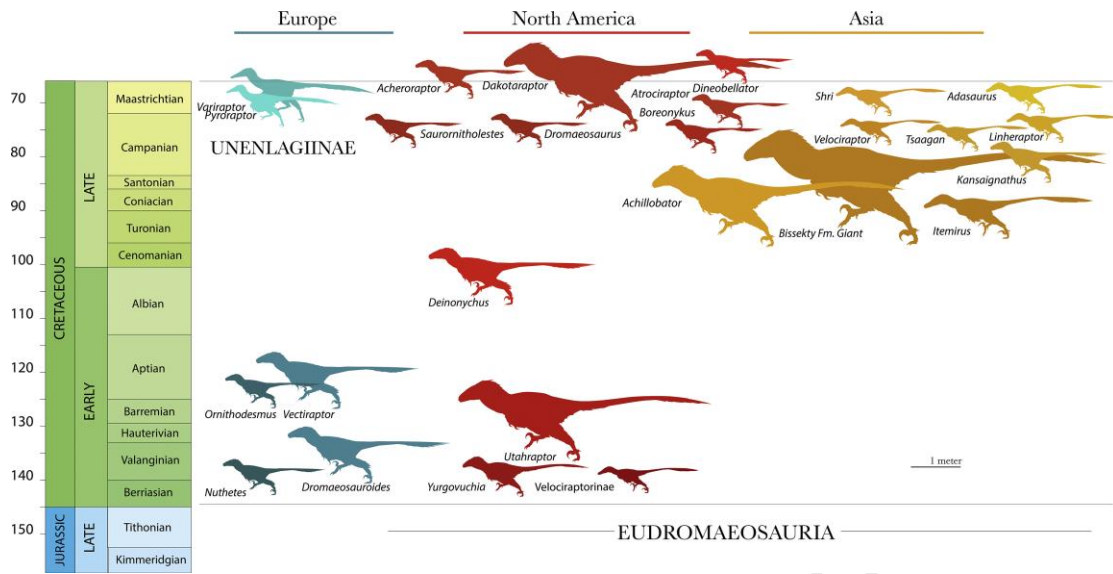


Saurornitholestes langstoni



Variraptor mechanorum







Author statement

NRL: Conceptualization, Investigation, Writing, Visualization

MJ: Investigation, Writing Original Draft & Editing

DM: Investigation, Writing Original Draft & Editing

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THEROPODA

Basal Tetanurae

MIWG 6350 (Benson et al., 2009)

Spinosauridae

Ceratosuchops inferodios (Barker et al. 2021)

Riparovenator milnerae (?)

Neovenatoridae

Neovenator salerii (Hutt et al., 1996)

Tyrannosauroidae

Eotyrannus lengi (Hutt et al., 2001)

Calamosaurus foxii (Lydekker, 1889)

?Ornithomimosauria

Thecocoelurus daviesi (Seeley, 1888)

Aristosuchus pusillus (Owen, 1876)

?Troodontidae

Yaverlandia bitholos (Galton, 1971)

Dromaeosauridae

Ornithodesmus cluniculus (Seeley, 1887a)

Vectiraptor greeni (this paper)

SAUROPODA

Eusauropoda Incertae sedis

Chondrosteosaurus gigas (Owen, 1876)

Titanosauria incertae sedis

Iuticosaurus valdensis (von Huene, 1929)

Rebbachisauridae

aff. *Demandisaurus darwini* (Mannion et al., 2011)

Brachiosauridae?

Brachiosauridae indet. (Naish et al., 2004)

Titanosauriformes

Eucamerotus foxii (Blows, 1995)

ORNITHISCHIA

Nodosauridae

Polacanthus foxii (Owen, 1865)

Iguanodontidae

Iguanodon bernissartensis (Norman, 2013)

Mantellisaurus atherfeldensis (Hooley, 1925)

Dryosauridae

Valdosaurus canaliculatus (Galton, 1975)

Hypsilophodontidae

Hypsilophodon foxii (Huxley, 1869)

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?Eudromaeosauria			
<i>Dromaeosauroides bornholmensis</i>	Berriasian	Denmark	Bonde and Christiansen, 2003
<i>Nuthetes destructor</i>	Berriasian	United Kingdom	Milner 2002
<i>Ornithodesmus cluniculus</i>	Barremian	United Kingdom	Howse and Milner, 1993
<i>Vectiraptor greeni</i>	Barremian	United Kingdom	This paper
?Unenlagiinae			
<i>Pyroraptor olympius</i>	Campanian-Maastrichtian	France	Allain and Tacquet, 2002
<i>Variraptor mechanorum</i>	Campanian-Maastrichtian	France	Le Loeuff and Buffetaut, 1998

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