1 **A turiasaurian sauropod dinosaur from the Early Cretaceous Wealden Supergroup of the**
2 **United Kingdom**
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9 RRH: EARLY CRETACEOUS UK TURIASAUR
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11
12 **ABSTRACT**
13
14 The Jurassic/Cretaceous (J/K) boundary, 145 Ma, has long been recognised as an extinction
15 event or faunal turnover for sauropod dinosaurs, with many 'basal' lineages disappearing.
16 However, recently, a number of 'extinct' groups have been recognised in the Early Cretaceous,
17 including diplodocids in Gondwana, and non-titanosauriform macronarians in Laurasia.
18 Turiasauria, a clade of non-neosauropod eusauropods, was originally thought to have been
19 restricted to the Late Jurassic of western Europe. However, its distribution has recently been
20 extended to the Late Jurassic of Tanzania (*Tendaguria tanzaniensis*), as well as the Early
21 Cretaceous of the USA (*Mierasaurus bobyoungi* and *Moabosaurus utahensis*), demonstrating
22 the survival of another 'basal' clade across the J/K boundary. Teeth from the Middle Jurassic–
23 Early Cretaceous of western Europe and North Africa have also tentatively been attributed to
24 turiasaurs, whilst recent phylogenetic analyses recovered Late Jurassic taxa from Argentina and
25 China as further members of Turiasauria. Here, an anterior dorsal vertebra (NHMUK 1871) from
26 the Early Cretaceous Wealden Supergroup of the UK is described for the first time. It shares
27 several synapomorphies with the turiasaurs *Moabosaurus* and *Tendaguria*, including: (1) a
28 strongly dorsoventrally compressed centrum; (2) the retention of prominent epipophyses; and
29 (3) an extremely low, non-bifid neural spine. NHMUK 1871 therefore represents the first
30 postcranial evidence for Turiasauria from European deposits of unequivocal Early Cretaceous
31 age. Although turiasaurs show clear heterodont dentition, only broad, characteristically 'heart'-
32 shaped teeth can currently be attributed to Turiasauria with confidence. As such, several
33 putative turiasaur occurrences based on isolated teeth from Europe, as well as the Middle
34 Jurassic and Early Cretaceous of Africa, cannot be confidently referred to Turiasauria.
35 Unequivocal evidence for turiasaurs is therefore restricted to the late Middle Jurassic–Early
36 Cretaceous of western Europe, the Late Jurassic of Tanzania, and the late Early Cretaceous of
37 the USA, although remains from elsewhere might ultimately demonstrate that the group had a
38 near-global distribution.
39
40 **INTRODUCTION**
41
42   The Late Jurassic is often regarded as a period of heightened sauropod dinosaur diversity,
43 prior to a precipitous decline across the Jurassic/Cretaceous (J/K) boundary (145 Ma), at which
44 point many 'basal' sauropod lineages went extinct (Bakker, 1977; Hunt *et al.*, 1994; Wilson &

45   Sereno, 1998; Upchurch & Barrett, 2005; Barrett, McGowan & Page, 2009; Mannion *et al*.,
46   2011). Increasingly, however, it is becoming apparent that any J/K extinction was not
47   instantaneous (Tennant *et al*., 2017), at least in sauropods, with representatives of several
48   'extinct' sauropod groups now recognised from Early Cretaceous deposits (Gallina *et al*., 2014;
49   Royo-Torres *et al*., 2014, 2017a,b; Upchurch, Mannion & Taylor, 2015; D'Emic & Foster, 2016;
50   McPhee *et al*., 2016).
51   The non-neosauropod eusauropod clade Turiasauria was first recognised by Royo-Torres,
52   Cobos & Alcalá (2006) for three genera (*Turiasaurus riodevensis*, *Losillasaurus giganteus*,
53   *Galveosaurus herreroi*) from either the latest Jurassic (late Tithonian) or earliest Cretaceous
54   (early Berriasian) of Spain. Although *Galveosaurus* has subsequently been demonstrated to
55   more likely represent a macronarian neosauropod (e.g. Barco, Canudo & Cuenca-Bescós, 2006;
56   Carballido *et al*., 2011; D'Emic, 2012; Mannion *et al*., 2013), the western European record of
57   named turiasaurs has since been expanded to include the Late Jurassic Portuguese taxon *Zby*
58   *atlanticus* (Mateus, Mannion & Upchurch, 2014). In addition to postcranial remains, both
59   *Turiasaurus* and *Zby* preserve teeth. These tooth crowns are mesiodistally broad relative to
60   their apicobasal length, and have a distinctive 'heart'-shaped outline (Royo-Torres, Cobos &
61   Alcalá, 2006), narrowing mesiodistally along their apical halves (Mateus, Mannion & Upchurch,
62   2014). Primarily consisting of isolated teeth, additional remains have been referred to
63   Turiasauria from contemporaneous Iberian deposits (Royo-Torres, Cobos & Alcalá, 2006; Royo-
64   Torres *et al*., 2009; Mocho *et al*., 2016). Several authors have suggested that 'heart'-shaped
65   teeth from the Middle Jurassic–Early Cretaceous of the UK and France might also be
66   attributable to turiasaurs (Royo-Torres, Cobos & Alcalá, 2006; Néraudeau *et al*., 2012; Royo-
67   Torres & Upchurch, 2012; Mocho *et al*., 2016).
68   The distribution of turiasaurs was recently expanded to include the Early Cretaceous of the
69   western USA (Royo-Torres *et al*., 2017a), based on relatively complete skeletons of two taxa,
70   *Mierasaurus bobyoungi* (Royo-Torres *et al*., 2017a) and *Moabosaurus utahensis* (Britt *et al*.,
71   2017), and thus confirming the group's survival across the J/K boundary. Finally, several
72   remains from Africa have been suggested to represent turiasaurs. Mocho *et al*. (2016)
73   commented upon similarities of two fragmentary Middle Jurassic teeth from Madagascar and
74   Morocco, as well as a partial tooth from the Early Cretaceous of Libya, with European
75   turiasaurs. Xing *et al*. (2015) also recovered the Middle Jurassic Moroccan sauropod *Atlasaurus*
76   *imelakei* in a polytomy with *Losillasaurus* and *Turiasaurus*. Royo-Torres & Cobos (2009)
77   suggested that several postcranial remains from the Late Jurassic Tendaguru Formation of
78   Tanzania might also belong to Turiasauria. Most recently, Mannion *et al*. (in press) presented
79   new anatomical data and phylogenetic analyses linking the enigmatic Tendaguru sauropod
80   *Tendaguria tanzaniensis* with the turiasaur *Moabosaurus*. These authors recovered additional
81   Late Jurassic taxa as possible turiasaurs: in some of their analyses, the Tendaguru sauropod
82   *Janenschia robusta* and the Argentinean taxon *Tehuelchesaurus benitezii* were also placed in
83   Turiasauria, whilst the Chinese sauropod *Bellusaurus sui* was consistently positioned as a
84   turiasaur too.
85   Here, a previously undescribed anterior dorsal vertebra (NHMUK 1871) of a turiasaur from
86   the Early Cretaceous Wealden Supergroup of the UK is presented. The putative turiasaurian
87   affinities of several African and European occurrences are also discussed, including the utility of
88   tooth morphology for identifying turiasaurs.

89

90 **HISTORY AND PROVENANCE OF NHMUK 1871**

91

92   NHMUK 1871 is a relatively complete, but poorly preserved, anterior dorsal vertebra from an
93 unknown Early Cretaceous 'Wealden' locality of the UK. Purchased by the NHMUK in 1891 as
94 part of the Samuel H. Beckles collection, this specimen does not seem to have ever been
95 mentioned in the published literature. Correspondence between Beckles and the NHMUK also
96 does not provide any information on the provenance of NHMUK 1871. Most of the dinosaur
97 specimens collected by Beckles (e.g. the sauropod *Haestasaurus* ['*Pelorosaurus*'] *becklesii*
98 [Upchurch, Mannion & Taylor, 2015]) came from the late Berriasian–Valanginian Hastings
99 Group, in Hastings, East Sussex, southeastern England (Woodhams, 1990), and so this is the
100 most likely source of NHMUK 1871. However, Beckles also collected material from elsewhere in
101 the southeast of England, including the Isle of Wight (Woodhams, 1990), and so the specimen
102 could conceivably have come from another Wealden locality. As such, although NHMUK 1871 is
103 most likely to be late Berriasian–Valanginian, it could conceivably have come from any section
104 in the Wealden Supergroup, and thus its stratigraphic age could be anywhere from late
105 Berriasian–early Aptian (Batten, 2011).
106   NHMUK 1871 comprises the centrum (including neural arch pedicels) and unfused neural
107 arch. It is not possible to re-articulate the centrum and neural arch. Although this might be a
108 result of missing material through erosion, it remains possible that these elements do not
109 belong together. In particular, whereas the neural arch is primarily black in colour, only a few
110 small areas of the centrum display a similar colour. As such, although the available information
111 indicates that they came from the same locality, and their relative sizes are consistent, it is
112 possible that the centrum and neural arch come from separate beds.

113

114 **Institutional Abbreviations**

115

116 **NHMUK**, Natural History Museum, London, UK

117

118 **SYSTEMATIC PALAEONTOLOGY**

119

120 Sauropoda Marsh, 1878
121 Eusauropoda Upchurch, 1995
122 Turiasauria Royo-Torres, Cobos & Alcalá, 2006
123 Turiasauria indet.

124

125 **Material:** NHMUK 1871, a relatively complete, but poorly preserved, anterior dorsal vertebra
126 (Figs 1, 2).

127

128 **Locality and stratigraphic position:** Unknown locality, southeastern England, United Kingdom;
129 Wealden Supergroup; late Berriasian–early Aptian (Early Cretaceous).

130

131 **DESCRIPTION**

132

133   The centrum is poorly preserved and incomplete, especially around the ventrolateral
134   margins of its posterior cotyle (Fig. 1; see Table 1 for measurements). It is strongly
135   opisthocoelous, and much wider mediolaterally than it is dorsoventrally tall (ratio = 1.44). The
136   ventral surface is transversely convex, lacking ridges or excavations. Each lateral surface is too
137   poorly preserved to determine whether the parapophyses were situated on the centrum or on
138   the neural arch pedicels, although they are definitely absent from the preserved neural arch.
139   Based on the right side of the centrum, a lateral pneumatic foramen is present (Fig. 1), but poor
140   preservation and infilling by matrix mean that little of its morphology can be discerned. There is
141   evidence for several poorly preserved laminae, comprising the anterior centrodiapophyseal
142   lamina (ACDL), posterior centrodiapophyseal lamina (PCDL), centroprezygapophyseal lamina
143   (CPRL), and centropostzygapophyseal lamina (CPOL) (Fig. 1). The neural arch pedicels terminate
144   a short distance from the posterior margin of the centrum.
145   Erosion of the centrum in places reveals that it was pneumatised, with rounded camerae of
146   ~15 mm in diameter. No evidence for pneumaticity is visible in the neural arch. Unfortunately,
147   attempts to CT scan the vertebra, to examine its internal tissue structure, were unsuccessful, as
148   a result of its high density. As such, we cannot be sure whether the centrum was pneumatised
149   by small camerae throughout, or if these were primarily restricted to near the outer bone
150   surface.
151   In general, the neural arch is better preserved than the centrum (Fig. 2; see Table 1 for
152   measurements). The flat articular surfaces of the widely separated prezygapophyses face
153   dorsomedially and slightly anteriorly. They also expand anteroposteriorly towards their lateral
154   tips. There is evidence for a V-shaped interprezygapophyseal lamina (TPRL), but this has been
155   largely worn away (Fig. 2). The postzygapophyses are situated more dorsally than the
156   prezygapophyses, and their articular surfaces face ventrolaterally and posteriorly. Overall, the
157   zygapophyseal table is oriented at approximately 40° to the horizontal. There is no hyposphene,
158   which is consistent with this being an anterior dorsal vertebra, and the postzygapophyses are
159   connected by a horizontal interpostzygapophyseal lamina (TPOL). A prominent epipophysis is
160   present on the dorsal surface of each postzygapophysis (Fig. 2).
161   The diapophyses project laterally and slightly ventrally, and there is evidence for a poorly
162   preserved PCDL. The anterior and posterior surfaces of the diapophyses are unexcavated. A
163   poorly preserved, near-horizontal postzygodiapophyseal lamina (PODL) is present. A shallow,
164   dorsally-facing, elliptical spinodiapophyseal fossa (SDF) is situated anterior to the PODL,
165   bounded anteriorly by the spinoprezygapophyseal lamina (SPRL) (Fig. 2).
166   SPRLs run dorsomedially from the middle of the posterior margin of the prezygapophyses.
167   The anterior surface of the neural spine is transversely concave between the two SPRLs, and
168   becomes rugose towards the midline, although there is no clearly defined prespinal ridge. The
169   posterior surface of the neural spine is transversely concave, but poor preservation obscures
170   whether a postspinal ridge or rugosity was present. Dorsomedially oriented, undivided
171   spinopostzygapophyseal laminae (SPOLs) contribute to the posterolateral margins of the neural
172   spine, but there are no spinodiapophyseal laminae (SPDLs). The dorsoventrally low,
173   unbifurcated neural spine projects only very slightly above the level of the postzygapophyses,
174   and is anteroposteriorly narrow, especially towards the midline (Fig. 2).
175
176   **DISCUSSION**

177

Taxonomic affinities of NHMUK 1871

179

180 A strongly dorsoventrally compressed centrum (mediolateral width to dorsoventral height
181 ratio of > 1.3) characterises the anterior dorsal vertebrae of several somphospondylan
182 titanosauriforms (Mannion *et al.*, 2013), the basal macronarian *Lourinhasaurus* (Mocho *et al.*,
183 2014), *Apatosaurus* (Gilmore, 1936), and Turiasauria ((Mannion *et al.*, in press). The presence of
184 camerae in the centrum is consistent with the anteriormost dorsal vertebrae of most
185 eusauropods more derived than *Omeisaurus*, whereas the absence of clear camellae suggests
186 that NHMUK 1871 lies outside of Titanosauriformes, and that it is not a mamenchisaurid
187 (Wedel, 2003, 2005).
188 The steeply inclined zygapophyseal table of NHMUK 1871 is most similar to the morphology
189 in the anterior dorsal vertebrate of titanosaurs and rebbachisaurids (Carballido *et al.*, 2012).
190 Whereas the cervical vertebrae of most sauropods are characterised by the presence of
191 epipophyses (Yates, 2007; Wilson & Upchurch, 2009; Mannion *et al.*, 2013), their retention in
192 anterior dorsal vertebrae is much less common, where they tend to be reduced structures
193 (Mannion *et al.*, in press). However, NHMUK 1871 shares the presence of prominent
194 epipophyses with the turiasaurs *Moabosaurus* and *Tendaguria*, as well as *Jobaria* (Mannion *et*
195 *al.*, in press). Only a small number of sauropod taxa are characterised by such a low neural
196 spine in their anterior dorsal vertebrae, in which the spine is approximately level with the
197 SPOLs. *Euhelopus* and *Mamenchisaurus* both share this feature, but the anterior dorsal neural
198 spines of those taxa are bifid (Ouyang & Ye, 2002; Wilson & Upchurch, 2009). In contrast, the
199 non-bifid anterior dorsal neural spines of *Moabosaurus* and *Tendaguria* (Britt *et al.*, 2017;
200 Mannion *et al.*, in press) strongly resemble that of NHMUK 1871.
201 In summary, the combination of: (1) a dorsoventrally compressed centrum; (2) the retention
202 of prominent epipophyses; (3) the low, non-bifid neural spine; and (4) the overall morphology
203 of NHMUK 1871, more closely resembles the holotypic dorsal vertebrae of the turiasaurs
204 *Moabosaurus* and *Tendaguria* than any other sauropods. The anterior and posterior surfaces of
205 the diapophyses of NHMUK 1871 are unexcavated though, contrasting with those two taxa
206 (Mannion *et al.*, in press). Despite the incomplete and fragmentary nature of NHMUK 1871, it
207 appears to be readily referable to Turiasauria, more closely related to *Moabosaurus* +
208 *Tendaguria* than to other turiasaurs. The lack of fusion between the centrum and neural arch
209 indicates that this individual was not fully grown at the time of death.

210

Possible implications for turiasaurs from the Late Jurassic Tendaguru Formation of Tanzania

212

213 Upchurch, Mannion & Taylor (2015) recovered a sister taxon relationship between
214 *Janenschia* and *Haestasaurus* (see also Mannion *et al.*, in press), which are sympatric with
215 *Tendaguria* and (probably) NHMUK 1871, respectively. Such close affinities might indicate a
216 close faunal relationship between the latest Jurassic Tendaguru Formation and the Early
217 Cretaceous Wealden Supergroup. Furthermore, this could conceivably be regarded as
218 circumstantial evidence that *Tendaguria* is a junior synonym of *Janenschia* if NHMUK 1871 was
219 recovered from the same area and stratigraphic bed as *Haestasaurus*. Given that both
220 *Janenschia* and *Tendaguria* are recovered as turiasaurs in some of the phylogenetic analyses of

221   Mannion *et al*. (in press), synonymy remains a possibility. However, until we find limb material
222   associated with anterior dorsal vertebrae that can be referred to any of these taxa, such
223   synonymisation cannot be justified.
224
225   **Turiasaurian sauropod biogeography and evolutionary history**
226
227   In addition to the named taxa *Turiasaurus*, *Losillasaurus*, *Zby*, *Mierasaurus*, *Moabosaurus*,
228   and *Tendaguria*, several remains have been referred to Turiasauria (see Introduction). Most of
229   these referrals are based on isolated teeth. Although the 'heart'-shape is quite distinctive in
230   most of the referred western European teeth, this is not the case in all instances (e.g. the type
231   specimen of *Oplosaurus armatus*, from the Early Cretaceous of the UK), and especially not for
232   the African specimens (two of which preserve only half of the crown). Mocho *et al*. (2016)
233   identified three morphotypes of putative turiasaur teeth, which they suggested could be
234   explained in two ways: either they represent different taxa, potentially including non-
235   turiasaurs, or they are indicative of variation along the tooth row. The North American
236   turiasaurs *Mierasaurus* and *Moabosaurus* show a clear heterodont dentition (Britt *et al*., 2017;
237   Royo-Torres *et al*., 2017a), with subtle heterdonty present in *Turiasaurus* too (Royo-Torres &
238   Upchurch, 2012). As such, the second hypothesis of Mocho *et al*. (2016) might well be correct.
239   However, two of their morphotypes overlap with the teeth of other non-neosauropods, and
240   thus only broad, 'heart'-shaped teeth can currently be attributed to Turiasauria with
241   confidence. As such, the isolated teeth from the Middle Jurassic and Early Cretaceous of Africa
242   cannot unambiguously be referred to Turiasauria, and are herein regarded as indeterminate
243   eusauropods.
244   Xing *et al*. (2015) recovered the Middle Jurassic Moroccan sauropod *Atlasaurus* as a
245   turiasaur in their phylogenetic analysis, but this result was not supported in recent studies that
246   scored turiasaurian taxa based on firsthand observations (Mannion, Allain & Moine, 2017;
247   Royo-Torres *et al*. 2017a; Mannion *et al*., in press). Very little published information is currently
248   available for *Atlasaurus*, and it is in need of revision. As such, its phylogenetic affinities are
249   uncertain (see Mannion *et al*., in press), but there is currently no evidence to support a
250   turiasaurian placement. Finally, Mannion *et al*. (in press) recovered two Late Jurassic taxa
251   within Turiasauria that would greatly extend the group's distribution: the Argentinean
252   sauropod *Tehuelchesaurus*, and the Chinese taxon *Bellusaurus*. However, those placements
253   should be treated with caution: *Tehuelchesaurus* was placed outside of Turiasauria when
254   extended implied weighting was applied, and *Bellusaurus* is known only from juvenile remains,
255   which might affect its phylogenetic position (Moore *et al*., 2018). Furthermore, these positions
256   have not been recovered in independent analyses (e.g. D'Emic, 2012; Royo-Torres & Upchurch,
257   2012; Carballido *et al*., 2017).
258   In summary, there is currently only unequivocal evidence for Turiasauria in the late Middle
259   Jurassic–Early Cretaceous of western Europe (UK, France, Spain and Portugal), the Late Jurassic
260   of Tanzania, and the late Early Cretaceous of the USA, but other remains suggest the possibility
261   that the clade was more widespread, at least in the Late Jurassic.
262
263   **CONCLUSIONS**
264

265   A previously undescribed anterior dorsal vertebra (NHMUK 1871) from the Early Cretaceous
266   Wealden Supergroup of the UK is recognised as a turiasaurian eusauropod dinosaur. It shares
267   several synapomorphies with the Late Jurassic Tanzanian sauropod *Tendaguria*, as well as with
268   *Moabosaurus*, from the Early Cretaceous of the USA. NHMUK 1871 represents the first
269   postcranial evidence for Turiasauria from European deposits of unequivocal Early Cretaceous
270   age. Unambiguous evidence for the non-neosauropod eusauropod clade Turiasauria is
271   restricted to the late Middle Jurassic–Early Cretaceous of western Europe, the Late Jurassic of
272   Tanzania, and the late Early Cretaceous of the USA, although remains from the Late Jurassic of
273   Argentina and China might mean that the group had a near-global distribution.
274
275   **ACKNOWLEDGEMENTS**
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281

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400

401 ==Figure 1.== Photographs of the anterior dorsal centum NHMUK 1871 in (A) anterior, (B) posterior,
402 (C) left lateral, (D) right lateral, (E) dorsal, and (F) ventral views. Abbreviations: ACDL, anterior
403 centrodiapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL,
404 centroprezygapophyseal lamina; lpf, lateral pneumatic foramen; nc, neural canal; PCDL,
405 posterior centrodiapophyseal lamina. Scale bar equals 100 mm.

406

407 **Figure 2.** Photographs of the anterior dorsal neural arch NHMUK 1871 in (A) anterior, (B)
408 posterior, (C) right lateral, and (D) dorsal views. Abbreviations: dia, diapophysis; epi,
409 epipophysis; PCDL, posterior centrodiapophyseal lamina; PODL, postzygapophysis; poz,
410 postzygapophysis; prz, prezygapophysis; SDF, spinodiapophyseal fossa; SPOL,
411 spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPOL,
412 interpostzygapophyseal lamina; TPRL, interprezygapophyseal lamina. Scale bar equals 200 mm.

413

414 **Table 1.** Measurements of the anterior dorsal vertebra NHMUK 1871. All measurements in
415 millimetres.

416

Dimension	Measurement
Centrum length (including condyle)	229
Centrum length (excluding condyle)	170
Anterior centrum dorsoventral height	158
Anterior centrum mediolateral width	228
Total preserved dorsoventral height of neural arch and spine	205
Neural arch height	167
Transverse width from midline to distal tip of right diapophysis	248

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Figure 1

Photographs of the anterior dorsal centum NHMUK 1871.

(A) anterior, (B) posterior, (C) left lateral, (D) right lateral, (E) dorsal, and (F) ventral views. Abbreviations: ACDL, anterior centrodiapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; lpf, lateral pneumatic foramen; nc, neural canal; PCDL, posterior centrodiapophyseal lamina. Scale bar equals 100 mm.
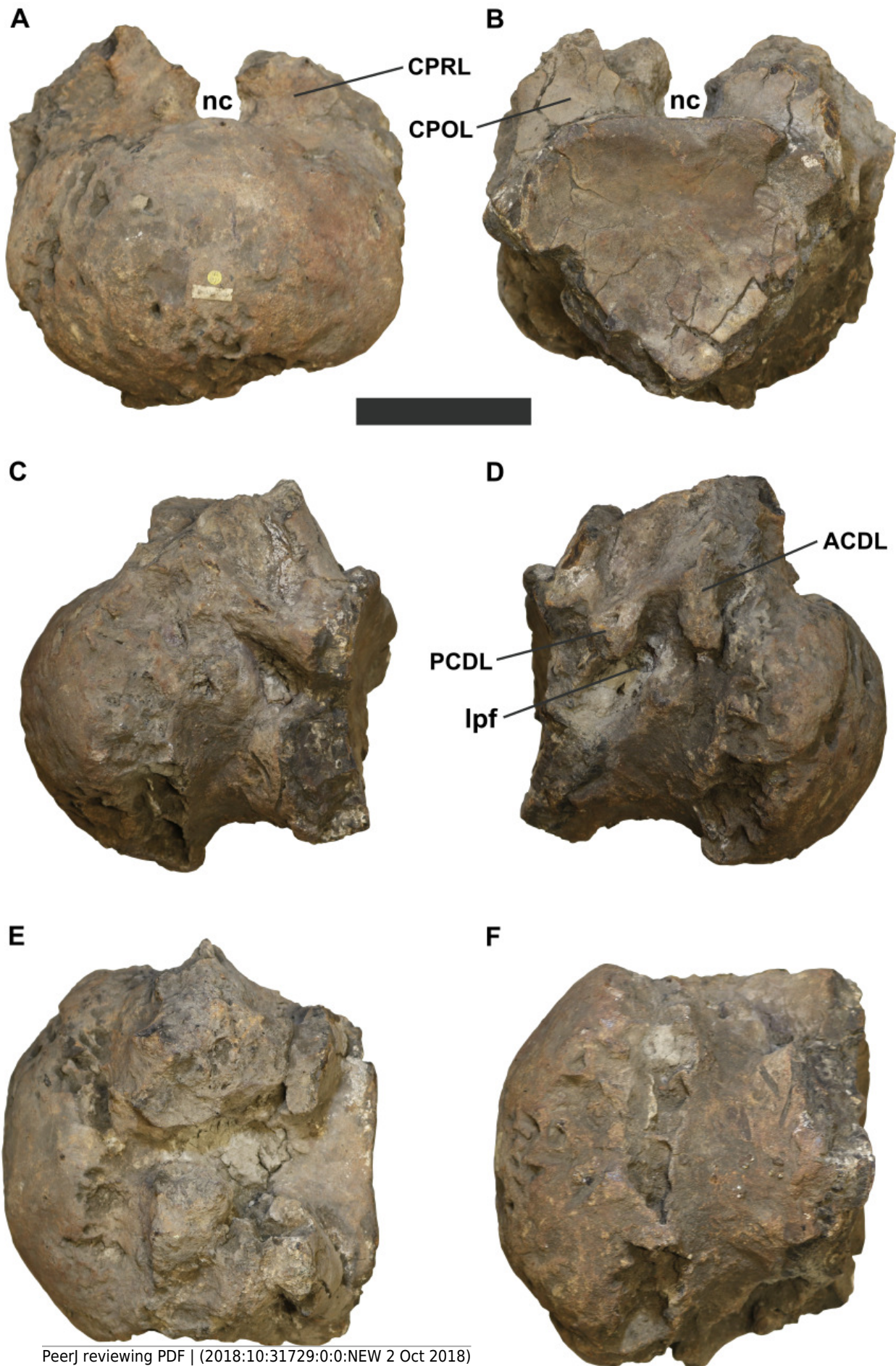
Figure 2

Photographs of the anterior dorsal neural arch NHMUK 1871.

(A) anterior, (B) posterior, (C) right lateral, and (D) dorsal views. Abbreviations: dia, diapophysis; epi, epipophysis; PCDL, posterior centrodiapophyseal lamina; PODL, postzygapophysis; poz, postzygapophysis; prz, prezygapophysis; SDF, spinodiapophyseal fossa; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPOL, interpostzygapophyseal lamina; TPRL, interprezygapophyseal lamina. Scale bar equals 200 mm.
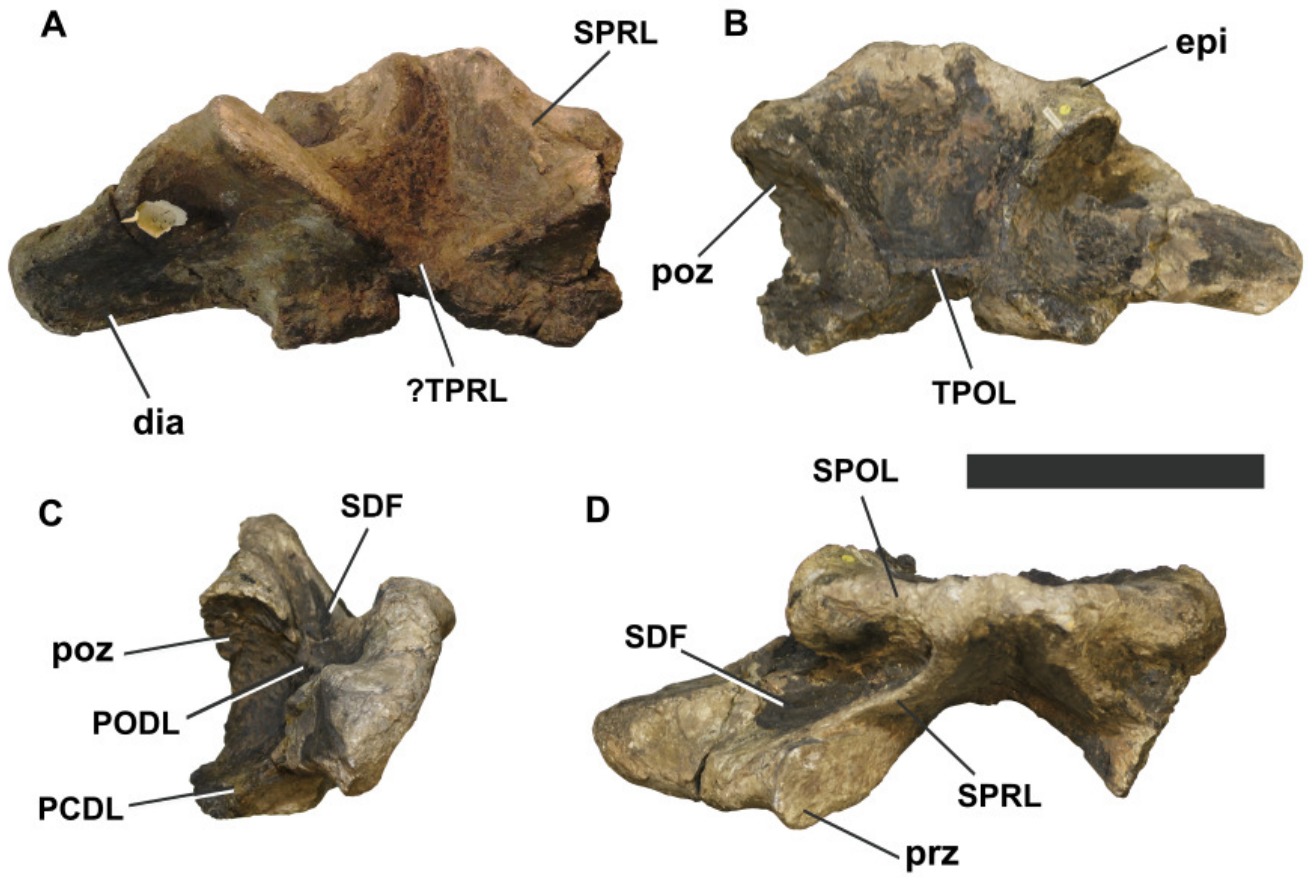
Table 1(on next page)

Measurements of the anterior dorsal vertebra NHMUK 1871.

All measurements in millimetres.

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