Additional sauropod material from the Peterborough Oxford Clay: evidence for higher sauropod diversity (#25725)

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Additional sauropod material from the Peterborough Oxford Clay: evidence for higher sauropod diversity.

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An isolated anterior caudal vertebra of a sauropod from the Oxford Clay (Callovian, Middle Jurassic) of King's Dyke pit near Peterborough, UK, is examined. Despite post-mortem residency on the seabed, some diagnostic features are preserved, including the presence of a ventral keel, a 'shoulder' indicating a wing-like transverse process, along with a possible prespinal lamina. This, together with an overall high complexity of the anterior caudal transverse process (ACTP) complex, indicates that this caudal belonged to a derived eusauropod, most likely a neosauropod. A second isolated middle-posterior caudal from the Oxford Clay of Peterborough is also described, also showing some diagnostic features, despite the neural spine and neural arch not being preserved and the neurocentral sutures being unfused. The positioning of the neurocentral sutures on the anterior 1/3rd of the centrum indicates a middle caudal position, and the presence of faint ventrolateral crests, as well as a rhomboid anterior articulation surface, show neosauropod affinities. The presence of possible nutrient foramina are only tentative evidence of a neosauropod origin, as they are also found in Late Jurassic non-neosauropod eusauropods. As the caudals from the two other known sauropods from the Peterborough Oxford Clay, *Cetiosauriscus stewarti* and a brachiosaurid, do not show the features seen on either of the new elements described, both isolated caudals indicate a higher sauropod species diversity in the region than previously recognised. A reduced consensus tree using these caudal characters shows a diplodocoid affinity for the anterior caudal, and a diplodocid origin for the middle caudal. Together with *Cetiosauriscus*, and other material assigned to different sauropod groups, this study indicates the presence of a high sauropod biodiversity in the Oxford Clay, equivalent to that of both the classic Jurassic Morrison and Tendaguru formations. This study shows that it is still beneficial to examine isolated elements, as these may be indicators for species richness in deposits that are otherwise

poor in terrestrial fauna.

Additional sauropod material from the Peterborough Oxford Clay: evidence for higher sauropod diversity

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ABSTRACT

An isolated anterior caudal vertebra of a sauropod from the Oxford Clay (Callovian, Middle Jurassic) of King's Dyke pit near Peterborough, UK, is examined. Despite post-mortem residency on the seabed, some diagnostic features are preserved, including the presence of a ventral keel, a 'shoulder' indicating a wing-like transverse process, along with a possible prespinal lamina. This, together with an overall high complexity of the anterior caudal transverse process (ACTP) complex, indicates that this caudal belonged to a derived eusauropod, most likely a neosauropod. A second isolated middle-posterior caudal from the Oxford Clay of Peterborough is also described, also showing some diagnostic features, despite the neural spine and neural arch not being preserved and the neurocentral sutures being unfused. The positioning of the neurocentral sutures on the anterior 1/3rd of the centrum indicates a middle caudal position, and the presence of faint ventrolateral crests, as well as a rhomboid anterior articulation surface, show neosauropod affinities. The presence of possible nutrient foramina are only tentative evidence of a neosauropod origin, as they are also found in Late Jurassic non-neosauropod eusauropods. As the caudals from the two other known sauropods from the Peterborough Oxford Clay, *Cetiosauriscus stewarti* and a brachiosaurid, do not show the features seen on either of the new elements described, both isolated caudals indicate a higher sauropod species diversity in the region than previously recognised. A reduced consensus tree using these caudal characters shows a diplodocoid affinity for the anterior caudal, and a diplodocid origin for the middle caudal. Together with *Cetiosauriscus*, and other material assigned to different sauropod groups, this study indicates the presence of a high sauropod biodiversity in the Oxford Clay, equivalent to that of both the classic Jurassic Morrison and Tendaguru formations. This study shows that it is still beneficial to examine isolated elements, as these may be indicators for species richness in deposits that are otherwise poor in terrestrial fauna.

Keywords: Sauropoda, Eusauropoda, Neosauropoda, Oxford Clay, caudal

INTRODUCTION

The Middle Jurassic Oxford Clay has yielded many marine vertebrates (ichthyosaurs, plesiosaurs, pliosaurs, marine crocodiles, sharks, and fishes (Andrews, 1910, 1913)), as well as invertebrates (Leeds, 1956). Land-dwelling vertebrates, however, are rare from this marine setting. The Jurassic Gallery of the Vivacity-Peterborough Museum in Peterborough, and the New Walk Museum and Art Gallery in Leicester, however, house some dinosaur specimens from the Oxford Clay of Peterborough. The material consists of isolated partial elements of a stegosaur, and several isolated sauropod fossils, including a partial anterior caudal and a partial middle caudal. The caudals have been submerged in seawater, however, they do display some characters which may be used for diagnosis.

Sauropods are represented in the Middle Jurassic of the UK by two species thus far: the Bajocian-Bathonian *Cetiosaurus oxoniensis* (Phillips, 1871; Owen, 1875) and the Callovian *Cetiosauriscus stewarti* (Charig, 1980, 1993). *Cetiosauriscus* is known from material found in the Peterborough Oxford Clay, and has thus far not been encountered from other localities (Woodward, 1905; Heathcote & Upchurch, 2003; Noè, Liston & Chapman, 2010). The type material comprises of a partial caudal axial column, a femur, and a partial pelvic girdle (Woodward, 1905). Another *Cetiosauriscus*, *Cetiosauriscus greppini*, is known from Switzerland, however, this specimen is from the Late Jurassic, and moreover, has recently been reidentified as a basal titanosauriform (Schwarz, Wings & Meyer, 2007).

Next to *Cetiosauriscus*, four anterior caudal vertebrae (NHMUK R1984), ascribed to a brachiosaurid (Upchurch & Martin, 2003, Noè, Liston & Chapman, 2010, Fig.6), as well as a

partial distal tail segment including eight posterior(most) caudals, ascribed to a diplodocid (Upchurch, 1995), are described from the Oxford Clay material (Noè, Liston & Chapman, 2010). Finally, three undiagnosed 'camarasaurid' sauropod teeth are known from the Oxford Clay (Martill, 1988), which might tentatively be turiasaurid (Royo Torres & Upchurch, 2012; Mocho et al., 2015).

Despite the locality being a classic site for fossils, and many historical finds of marine reptiles having been described and redescribed, the sauropod fauna from the Oxford Clay has not received much attention thus far. Though associated material such as *Cetiosauriscus* is scarce, isolated material can be studied in detail and reveal information on both morphology and species diversity. This is especially important for material which has its provenance in the Middle Jurassic, as major sauropod radiation and evolution events happened during the Early and Middle Jurassic, with most major clades firmly established worldwide at the late Middle Jurassic, while sauropod material remains rare from this time, and not all evolutionary patterns are well understood. Moreover, caudal vertebrae have rarely been given appropriate attention, as only recently have caudal characters begun to be recognized as taxonomically diagnostic (e.g. Mocho et al., 2017; Holwerda & Liston, 2017). Therefore, we here describe two isolated sauropod caudal vertebrae from the collections of the Vivacity-Peterborough Museum and of the New Walk Museum of Leicester, both from the Oxford Clay of Peterborough, (and both previously indexed in collections under '*Cetiosaurus*'), and compare them to contemporaneous and other sauropod remains.

MATERIALS & METHODS

Institutional abbreviations

PETMG R.= Vivacity-Peterborough Museum, UK

LEICT G.= New Walk Museum, Leicester, UK

NHMUK = Natural History Museum, London, UK

Systematic Palaeontology

Dinosauria (Owen, 1842)

Saurischia (Seeley, 1888)

Sauropoda (Marsh, 1878)

Eusauropoda (Upchurch, 1995)

?Cetiosauridae (Lydekker, 1888) sensu (Upchurch, Barrett & Dodson, 2004)

?Neosauropoda (Bonaparte, 1986a)

Geological setting

Details on the provenance of the caudal specimen PETMG PETMG R272 are sparse, save that it is recorded as being from the King‘s Dyke pit (see Figure 1). The LEICT G. 418.1956.21.0 is from the Peterborough Oxford Clay formation, however, its precise provenance is unknown. The original label on the specimen dates back to 1956, however, a number of brick pits were open at that stage. The strata of King’s Dyke pit extend from the Kellaways Formation up to the Stewartby Member of the Peterborough Formation (see Hudson & Martill, 1994, for a more detailed geological setting), therefore date exclusively to the Callovian (Middle Jurassic, ~155 Ma).

RESULTS

Morphology

The anterior caudal PETMG R272 (See Figure 2) measures a maximum of 27,2 cm dorsoventrally and 26,5 cm transversely. It is covered in bivalves which are embedded in the bone matrix (see Figure 2), demonstrating long-term submersion in seawater. The neural spine is missing, as well as the entire left transverse process; the right transverse process is partially preserved at its base. The centrum is wider at its dorsal side than at the ventral side, and the anterior side protrudes further ventrally than the posterior side. The relative axial compression of the centrum, together with the apparent connection between the neural arch and base of the transverse processes (as far as can be seen) shows this vertebra to be one of the anterior-most caudals.

In anterior view (Figure 2A), the articular surface of the centrum is oval to round, and is transversely wider than dorsoventrally high. The outer surface of the articular surface is convex and displays circular striations, as is common for weightbearing bones in sauropods. The internal ±1/3rd of the anterior articular surface is mildly concave. The entire articular surface is

'cupped' by a thick rim, which mostly follows the oval to round contour of the articular surface, however, it is flattened ventrally, and on the dorsal rim it shows a slight indent, rendering the dorsal rim heart-shaped. This rim is also seen in lateral view (Figure 2C). In posterior view (Figure 2B), the articular surface is heart-shaped to triangular: the ventral rim ends in a transversely pointed shape, whereas the dorsal rim shows a rounded depression on the midline, flanked by parallel convex bulges. The articular surface itself is concave, with an additional depression in the mid ±1/3rd part of the surface. The posterior articular surface is less rugosely 'cupped' by its rim than the anterior one.

In ventral view (Figure 2D), the anterior rim of the centrum shows rudimentary semilunar shaped chevron facets, which are not seen on the posterior side. The transverse processes are visible as triangular protrusions that project laterally. Below each is a small oval depression. The lateral sides of the centrum are constricted, and flare out towards the anterior and posterior sides. A keel-like structure can be seen on the ventral axial midline of this vertebra. This keel is not visible as a thin protruding line, but more as a broad band protruding slightly ventrally from the ventral part of the centrum. It is possible this keel is formed by the close spacing of the ventrolateral rims of the centrum (Harris, 2006).

The anterior side of the neural canal and the base of the neural arch are set in a dorsoventrally high, anteroposteriorly flattened sheet of bone, consisting of the spinodiapophyseal/prezygodiapophyseal and centrodiapophyseal laminae, which give the neural arch (without transverse processes and neural spine) a roughly triangular shape (Figure 2A). In particular, the high projection on the neural arch of the diapophyseal laminae suggest the existence of a ‘shoulder’, which would make the transverse processes wing-shaped. The neural canal is broadly arched (measuring 3,3 cm by 3,8 cm). Its dorsal rim is overshadowed by a lip-like, triangular protrusion, which could be a remnant of the hypantrum (Figure 2A). Right

183 above this lip-like process, a rugosely striated lamina persists along the dorsoventral midline of
184 the neural arch, up to the dorsal-most rim of the specimen. It is not entirely clear if this is a scar
185 of a rudimentary single intraprezygapophyseal lamina or a prespinal lamina (Figure 2A). The
186 posterior side of the neural canal is more teardrop-shaped, and is set within the neural arch,
187 which displays shallow depressions on both sides of the neural canal; these could be small
188 postzygapophyseal spinodiapophyseal fossae (pocdf, sensu (Wilson et al., 2011, Figure 2B)).
189 Directly above it, the rami of the bases of the postzygapophyses are clearly visible. The
190 postzygapophyses are rounded to triangular in shape (Figure 2B). A deep oval depression is
191 seen between them; this could be the remnant of the spinopostzygapophyseal fossae (spof,
192 sensu (Wilson et al., 2011, Figure 2B). Finally, a V-shaped striated process is seen between the
193 two postzygapophyses, which could be the remnant of the hyposphene.
194
195 The transverse processes appear like rounded bulges, seen in anterior and lateral view (Figure
196 2A,C). The ventral sides of the bases of both transverse processes are concave. In lateral view,
197 the transverse process has a rounded to triangular shape, and is axially wider ventrally than
198 dorsally. It is dorsally supported by a spinodiapophyseal lamina (Figure 2E), and seems to have
199 an anterior centrodiapophyseal lamina; however, a posterior centrodiapophyseal lamina is not
200 clearly visible.
201
202 The middle caudal LEICT G.418.1956.21.0 (Figure 3) is an isolated element, and has no
203 connection to the anterior caudal. Unlike the anterior caudal, this middle caudal centrum is well-
204 preserved, with minute details clearly visible. The neural arch and neural spine are not
205 preserved, and as the unfused neurocentral sutures show, the animal this caudal belonged to,
206 was not fully grown (Brochu, 1996) and probably in Morphological Ontogenetic Stage 2 (MOS
207 2), rather than MOS 1, given the large size (sensu Carballido & Sander, 2014).
208

The centrum is 12,9 cm long axially, its anterior tranverse width is 21,7 cm and its posterior width 18,6 cm, with posterior height at 15,2 cm. The centrum is rectangular in shape, seen in dorsal (Figure 3E) and ventral view (Figure 3F), with mildly flaring anterior and posterior lateral ends of the articulation surfaces. In lateral view (Figure 3B,D), the posterior ventral side protrudes further ventrally than the anterior ventral side. However, the anterior dorsal side projects further dorsally than the posterior side. Transverse processes are only rudimentarily present, as oval, rugose, lateral bulges.

The anterior articular surface is rhomboid (hexagonal to almost octagonal) in shape (Figure 3A); the dorsal 1/3rd shows a wide transverse extension of the articular rim, whilst the lower 1/3rd shows a much narrower width, with sharply beveled constrictions between them. The ventral side shows a rounded indent on the midline, giving this articular surface a heart-shaped ventral rim. The rim itself is about 2-3 cm thick, shows concentric striations, and protrudes slightly anteriorly. The inner articular surface is flat to concave, however, the kernel shows a rugose rounded protrusion of bone. The morphology of the posterior articular surface (Figure 3C) is much more simple, oval in shape, and is wider transversely than dorsoventrally high. The articular rim is less thick than anteriorly; about 1-2cm. The articular surface is mildly concave, with a dorsal slightly convex bulge, which is common in non-neosauropod eusauropods (e.g. *Cetiosaurus*, *Patagosaurus*). The dorsal side of the centrum (Figure 3E) shows well-preserved and unfused neurocentral sutures, which span approximately the anterior 2/3rds of the axial length of the centrum. The ventral half of the neural canal is clearly visible, and shows four axially elongate, deep nutrient foramina embedded within the posterior half of the centrum. A further two shallow nutrient foramina are visible.

The ventral side of the centrum (Figure 3F) shows two sets of chevron facets, the posterior ones of which are more pronounced. Several rugose striations run along the axial length of the

ventral surface, probably for ligament attachments. Along the midline, a ventral hollow runs anteroposteriorly, braced on each lateral side by a rounded, slightly protruding beam. On each lateral side of these, shallow oval asymmetrical depressions are visible; these are caused by preparing away sediment and debris. Two faint ventrolateral crests are also possibly present, also visible in right lateral view (Figure 3B). The crests are not pronounced, and on the left lateral side (Figure 3D) the crest does not run for the entire anteroposterior length. The right lateral side (Figure 3B) furthermore shows a faint longitudinal ridge, however, in left lateral view (Figure 3D), this ridge does not persist on the entire lateral side of the centrum.The lateral side of the centrum further shows several small nutrient foramina. Finally, very shallow oval depressions, possibly pneumatic, are seen ventral to the bulges of the transverse processes.

Phylogenetic framework

To explore possible phylogenetic relationships, the caudals were used as separate Operational Taxonomic Units (OTU's). The morphological characters of both caudals were coded in an existing matrix in Mesquite (Maddison & Maddison, 2010) using non-neosauropod eusauropods and neosauropods, from Tschopp et al., (2015). See supplementary material for Tschopp et al. (2015), for the character matrix, explanatory notes, and references therein. Only anterior caudal characters could be coded for PETMG R272, and only anterior to middle, and middle to posterior characters could be coded for LEICT G.418.1956.21.0. Next to these codings, the anterior and middle caudals of *Cetiosauriscus stewarti* were recoded, based on the descriptions of Woodward (1905), Charig (1980) and based on pictures of NHMUK R3078 which resulted in some character changes. See Supplemental file for our character matrix, adapted from Tschopp et al., (2015).

The matrix was analysed using TNT (Goloboff, Farris & Nixon, 2008; Goloboff & Catalano, 2016) using TBR, which yielded 37156 trees with a best score of 2026. A strict consensus tree

rendered too many polytomies, therefore a 50% majority rule consensus analysis was performed. See Figure 4 for the simplified 50% majority consensus tree.

Cetiosauriscus is retrieved as a non-neosauropod eusauropod in this analyis, basal to *Jobaria* and more derived than Mamenchisaurids and basal non-neosauropod eusauropods, which is the same result as in Tschopp, Mateus and Benson, (2015), but see Heathcote & Upchurch (2003). The anterior caudal PETMG R272 is retrieved a a diplodocoid, more derived than *Haplocanthosaurus*, but basal to *Zapalasaurus* and all derived neosauropods. Characters that unite it with Diplodocoidea (sensu Tschopp, Mateus and Benson (2015)) are the presence of well-defined anterior diapophyseal laminae on transverse processes, as well as having an anterior neural arch base with a transverse width/anterioposterior length ratio higher than 1 (Tschopp, Benson and Mateus, 2015).

The middle caudal LEICT G.418.1956.21.0 is retrieved as more derived than *Galeomopus*, basal to *Barosaurus* and all other diplodocids, and is firmly nested within Diplodocidae. Characters that unite it with Diplodocidae (sensu Tschopp, Mateus and Benson (2015)) are having a trapezoidal articular surface, a straight ventral surface in lateral view, and articular surfaces being wider than high (Tschopp, Benson and Mateus, 2015). Furthermore, it takes 4 additional steps to force PETMG R272 outside of Neosauropoda, and it takes an additional 8 steps to force LEICT G.418.1956.21.0 outside of Neosauropoda.

DISCUSSION

Systematics

Peterborough caudal PETMG R272

287

288 The anterior caudal PETMG R272 shows characteristics shared with both non-neosauropod
289 eusauropods, as well as neosauropods.
290 The slightly more rounded shape of the centrum in lateral view is shared with *Apatosaurus*.
291 Anterior caudals of *Cetiosauriscus* are strongly axially compressed, as also seen in non-
292 neosauropod eusauropods such as *Cetiosaurus* and *Patagosaurus* (Woodward, 1905; Charig,
293 1980; Bonaparte, 1986b; Upchurch & Martin, 2003).
294 The flat anterior articular surface and the mildly concave posterior articular surface of the
295 centrum is a common feature, shared with non-neosauropod eusauropods (e.g. *Cetiosaurus*,
296 *Patagosaurus* (Bonaparte, 1986b; Upchurch & Martin, 2003). The thick rim cupping the anterior
297 surface is found in early Middle Jurassic non-neosauropod eusauropods (*Cetiosaurus*) but also
298 in the (non-neosauropod eusauropod/potentially basal neosauropod) Callovian *Cetiosauriscus*
299 (Woodward, 1905; Charig, 1980; Heathcote & Upchurch, 2003) and in the Oxfordian-
300 Kimmeridgian basal titanosauriform *Vouivria damparisensis* (Mannion, Allain & Moine, 2017).
301 The morphology of the ventrally offset anterior articular surface, together with pronounced
302 chevron facets, is seen in non-neosauropod eusauropods from the Late Jurassic of Portugal
303 (Mocho et al., 2017), however, this type of assymmetry is also seen in *Apatosaurus louisae*
304 (Harris 2006).
305
306 The ventral keel is found in an Early Jurassic indeterminate sauropod caudal from York, UK
307 (Manning, Egerton & Romano, 2015), however, it is also found in neosauropods, specifically in
308 flagellicaudates and diplodocids *Apatosaurus ajax*, *Apatosaurus louisae*, and *Suuwassea*
309 (Harris, 2006; Tschopp, Mateus & Benson, 2015). The former has a ventral keel which results
310 from a transverse constriction of the ventral side of the centrum, forming a triangular protrusion
311 on the ventral articular surface. This is also seen in non-neosauropod cervicals (such as
312 *Cetiosaurus*, *Patagosaurus*, *Spinophorosaurus*, *Amygdalodon*, *Tazoudasaurus* (Bonaparte,

313 1986c; Rauhut, 2003; Upchurch & Martin, 2003; Allain & Aquesbi, 2008; Remes et al., 2009)).
314 The latter keel-like form, which seems to match more the morphology of PETMG R272, forms
315 when there is a very close association of the two ventrolateral ridges that run along the
316 ventralmost side of the centrum, and is only seen in neosauropods. No keel-like structure is
317 seen in *Cetiosauriscus* anterior caudals, nor on the 'brachiosaurid' caudals from the Oxford Clay
318 (Upchurch & Martin, 2003, Noè, Liston & Chapman, 2010, Fig.6); the ventral surface of these
319 anterior caudal vertebrae appearing to be smooth.
320
321 The triangular shape of the anterior caudal transverse process (ACTP) complex in PETMG
322 R272 is seen to a lesser extent in non-neosauropod eusauropods, such as *Tazoudasaurus*, but
323 also in an unnamed anterior caudal from a titanosauriform from the Bajocian of Normandie,
324 France, and in indeterminate non-neosauropod sauropods from the Late Jurassic of Portugal
325 (Allain & Aquesbi, 2008; Läng, 2008; Mocho et al.). The pronounced shape, however, is more
326 suggestive of 'wing'-shaped transverse processes, due to the possible existence of a 'shoulder'
327 (see Figure 2). This is used as a caudal character to define diplodocids (Whitlock, 2011;
328 Tschopp, Mateus & Benson, 2015), and is found neither in non-neosauropod eusauropods nor
329 the Bajocian French titanosauriform. However, it is also seen in other neosauropods, such as
330 *Camarasaurus* and titanosauriforms (Gallina & Otero, 2009). To a lesser extent, a triangular,
331 sheet-like ACTP is seen in *Cetiosauriscus*, as well as the 'brachiosaurid' caudals from the
332 Oxford Clay, however, the anterior caudals of *Cetiosauriscus* do not show a pronounced
333 'shoulder'. Moreover, the transverse processes of PETMG R272 are robust, and rounded to
334 triangular in cross-section, whereas those of *Cetiosauriscus* are gracile, dorsoventrally
335 elongated and axially compressed, providing a more oval cross-section.
336 Furthermore, the presence of clearly defined anterior centrodiapophyseal laminae (acdl) is
337 considered to be an autapomorphy in the Late Jurassic titanosauriform *Vouivria*, together with

posterior centrodiapophyseal laminae (pcdl). Unfortunately, in PETMG R272 no pcdl is clearly visible, however, the acdl shows a possible derived state.

If the rugosity dorsal to the prezygapophyses is indeed a prespinal lamina (prsl) and not the single intraprezygapophyseal lamina (stpol), then this is yet another neosauropod feature on PETMG R272 (Wilson, 1999; Gallina & Otero, 2009; Tschopp, Mateus & Benson, 2015). *Cetiosauriscus* has both a prespinal and postspinal lamina (prsl and psl), however, the prsl in *Cetiosauriscus* is not rugose, but rather thin and gracile.

To summarize, more characters indicative of a neosauropod origin of this caudal are present, than those indicative of a non-neosauropod (eu)sauropod origin. However, due to the lack of complete transverse processes and neural spine, several morphological characters remain ambiguous.

Leicester caudal LEICT G.418.1956.21.0

The middle caudal LEICT G.418.1956.21.0 also shows characters both shared with non-neosauropod eusauropods, as well as neosauropods.

The rhomboid, hexagonal to octagonal shape of the anterior articular surface is not seen in *Cetiosauriscus*; the middle caudal articular surfaces of the latter are rather round to oval in shape. Hexagonal articular surfaces are a derived condition found in neosauropods, such as *Apatosaurus ajax*, *Suuwassea*, but also in *Camarasaurus*, *Demandasaurus* and *Dicraeosaurus* (Upchurch & Martin, 2002; Tschopp, Mateus & Benson, 2015). Octagonal articular surfaces are also a derived feature seen in *Dicraeosaurus* and the potential neosauropod *Cetiosaurus glymptoniensis* (Upchurch & Martin, 2003; Harris, 2006).

The ventrolateral crests seen on the ventral side of this caudal are a neosauropod feature, found in many Late Jurassic neosauropods (Harris, 2006; Mocho et al., 2017). The ventral hollow seen in LEICT G.418.1956.21.0 is also found in several neosauropods, such as *Tornieria*, *Diplodocus*, *Supersaurus*, but also *Demandasaurus* and *Isisaurus* (Tschopp et al., 2017). However, it is also seen in an unnamed caudal vertebra from the Bajocian-Bathonian of Skye, UK (Liston, 2004). The ventral hollow is also present in *Cetiosauriscus*, though not as pronounced as in LEICT G.418.1956.21.0.

The longitudinal ridge is another neosauropod feature, though it may also have been present in non-neosauropod eusauropods. A longitudinal ridge is seen on both *Cetiosauriscus* and LEICT G.418.1956.21.0, as are the lateral pneumatic foramina on the centra, and the ventrolateral crests.

Nutrient foramina are seen on the Late Jurassic diplodocid *Suuwassea*, but also on Late Jurassic Portuguese non-neosauropod eusauropods; small foramina on the ventral surface of the centrum are also seen in the anterior caudals of non-neosauropod eusauropods from Late Jurassic of Portugal (Mocho et al., 2017).

Phylogenetic signal and implications for biodiversity

As shown in Figure 4, the phylogeny retrieves the Peterborough caudal PETMG R272 as a diplodocoid, and the Leicester caudal LEICT G.418.1956.21.0 as a diplodocid. The adding of these two elements as OTU's did change some of the original relationships of the Tschopp et al. (2015) analysis, and the extremely simplified tree might not be a projection of real evolutionary trends. The strict consensus tree resulted in a great polytomy, as with Tschopp et al. (2015), therefore, a 50% majority rule consensus tree was recovered instead. However, the caudal characters that could be scored for the material from Peterborough and Leicester gave enough

information for a placement within Neosauropoda, whereas others (e.g. *Barosaurus affinis*) were unstable taxa. In Tschopp et al. (2015), however, a pruned tree is preferred. Though in this current analysis not many steps were needed to force the caudals outside of Neosauropoda (4 and 8, respectively), the characters that unite them with diplodocoids and diplodocids are characters that are clearly visible on the caudals. This analysis shows, therefore, that in addition to *Cetiosauriscus,* a diplodocoid and a diplodocid were present in the Oxford Clay Formation. Neosauropods were already reported from the Callovian of Europe (e.g. Alifanov & Averianov, 2003; Mocho et al., 2017) and also tentatively known from the UK (e.g. Noè, Liston & Chapman, 2010). Therefore, this analysis confirms the presence of neosauropods in the Callovian of the UK. Though not as species-rich as the later Kimmeridgian-Tithonian Tendaguru beds (Remes, 2007, 2009) or the Morrison Formation (Foster, 2003) or the Lourinhã Formation (Mannion et al., 2012, 2013; Mocho, Royo-Torres & Ortega, 2014; Mocho et al., 2016), the Peterborough Oxford Clay material thus far has hinted at a high diversity in sauropods: a non-neosauropod eusauropod (Heathcote & Upchurch, 2003), a diplodocoid, a diplodocid (this research) a possible brachiosaurid (Upchurch & Martin, 2003), possible diplodocid posterior caudals (Noè, Liston & Chapman, 2010) and a possible camarasaurid (Martill, 1988) or turiasaurid (Royo Torres & Upchurch, 2012; Mocho et al., 2015). This indicates an equivalent richness of sauropod groups from this Middle Jurassic marine formation, to the classic Late Jurassic terrestrial Morrison, Lourinhã and Tendaguru formations. In the future, more material can be added to this list. This shows the importance of paying close attention to caudal characters, as phylogenetic information might otherwise be missed which would indicate the range of fauna present in a given environment.

CONCLUSIONS

In summary, the anterior isolated caudal shares few morphological features with non-neosauropod eusauropods, and most morphological features with neosauropods. The middle isolated caudal shares few features with non-neosauropod eusauropods, and more with neosauropods. It is therefore most likely that these caudals belong to a neosauropod dinosaurs, and are different from *Cetiosauriscus*. Phylogenetic analysis tentatively retrieves these caudals as a diplodocoid, and diplodocid, respectively. Therefore, these caudals give a higher sauropod species diversity to the Peterborough Oxford Clay Formation than previously assumed. This diversity may be as high as the Late Jurassic Morrison, Tendaguru or Lourinhã Formations.

ACKNOWLEDGEMENTS

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Figure captions

Figure 1: Geological setting - geographical setting of King's Dyke and Star Pit, Whittlesey (adapted after Hudson & Martill (1994) with notes from Liston (2006)).

Figure 2: Anterior caudal PETMG PETMG R272 in anterior (A), posterior (B), lateral (C), ventral (D), and dorsal (E) views. Scalebar is 10 cm.

Figure 3: Middle caudal Leict LEICT G.418.1956.21.0 in anterior (A) right lateral (B), posterior (C), left lateral (D), dorsal (E), ventral (F) views. Scalebar 10 cm.

Figure 4: 50% Reduced consensus tree based on Tschopp et al., (2015) with revised *Cetiosauriscus* (purple) coding, and additionally PETMG R272 (blue) and LEICT G.418.1956.21.0 (red) as OTU's.

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Figure 1(on next page)

Geographical position of King’s Dyke and Star Pit, Whittlesey, UK.

(adapted after Hudson & Martill (1994), with notes from Liston, (2006)).

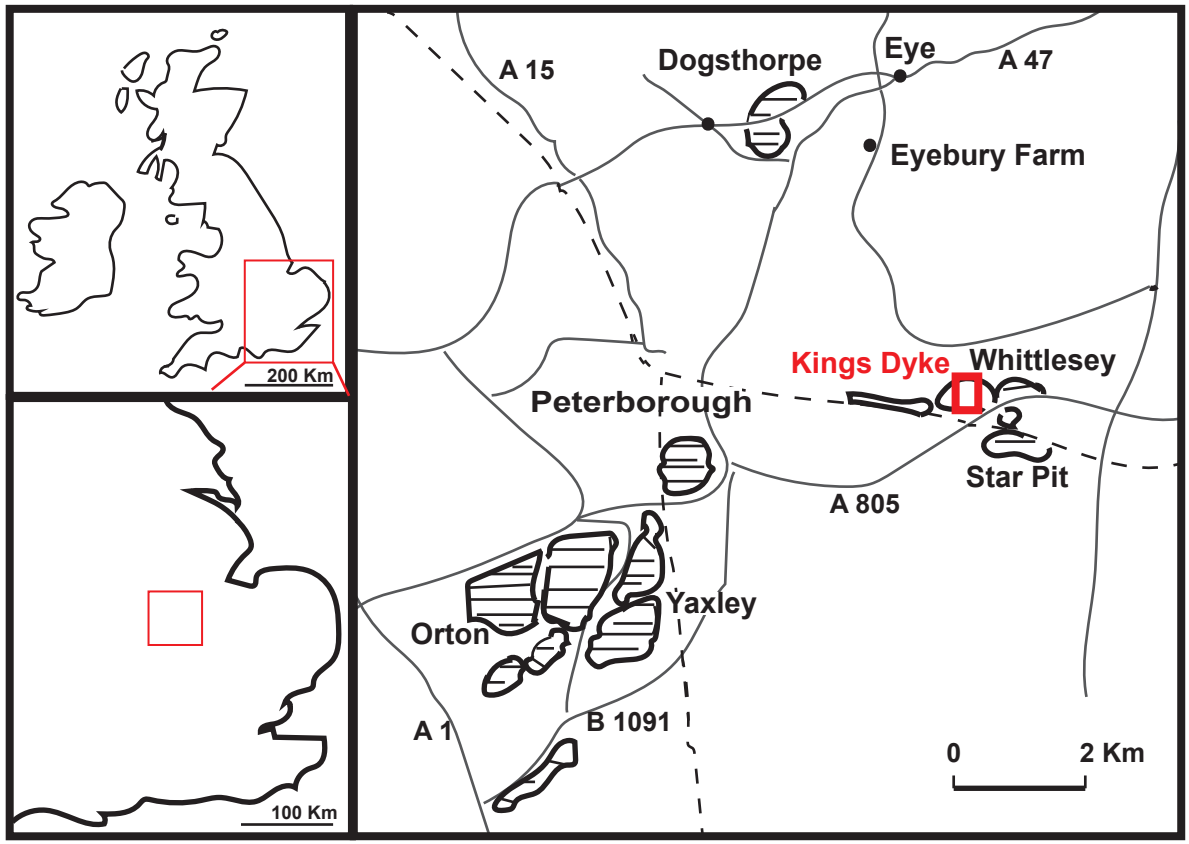
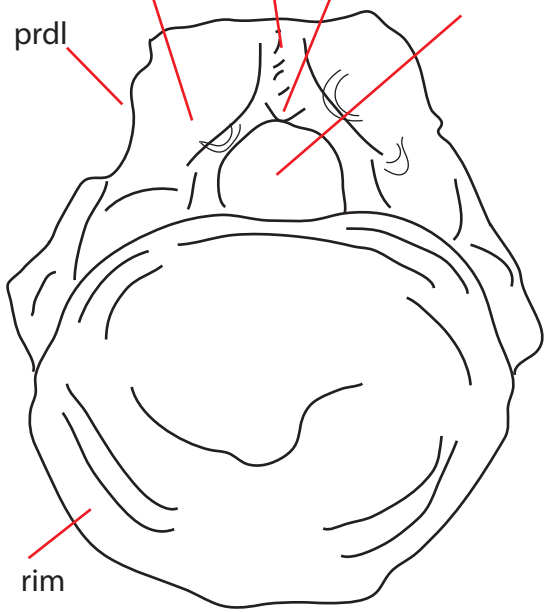

200 Km
100 Km
A 15
Dogsthorpe
Eye
A 47
Eyebury Farm
Kings Dyke
Whittlesey
Peterborough
Star Pit
A 805
Yaxley
Orton
A 1
B 1091
0
2 Km

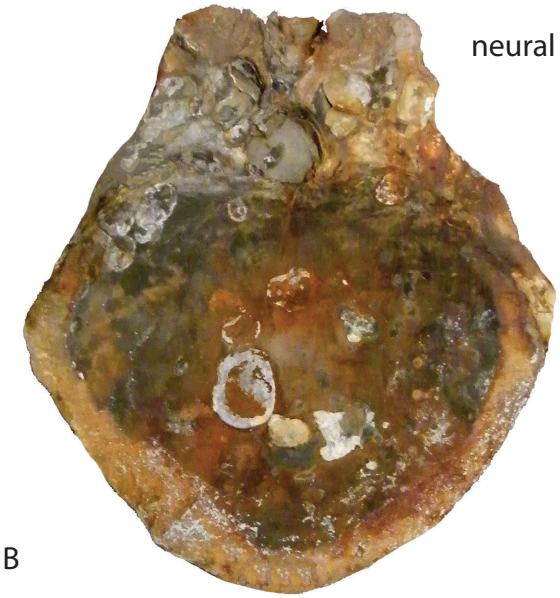
Figure 2(on next page)

Anterior caudal PETMG R272 (Photographs taken by FH).

In anterior (A), posterior (B), lateral (C), ventral (D), and dorsal (E) views. Scalebar is 10 cm.

A





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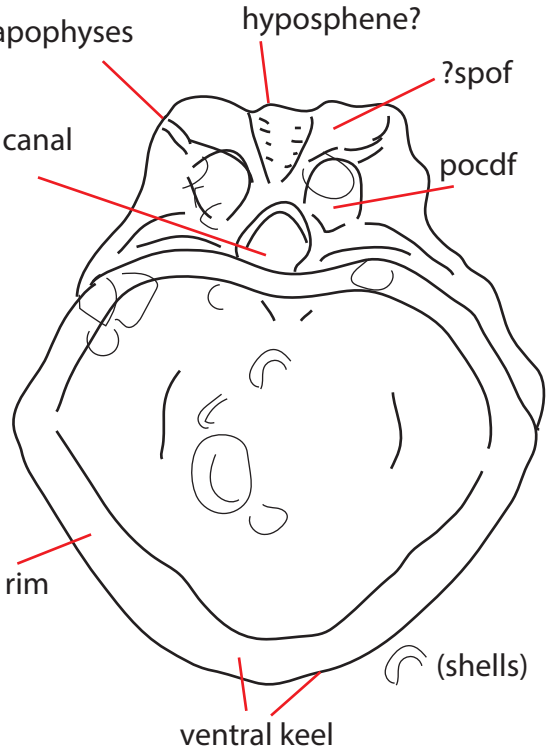
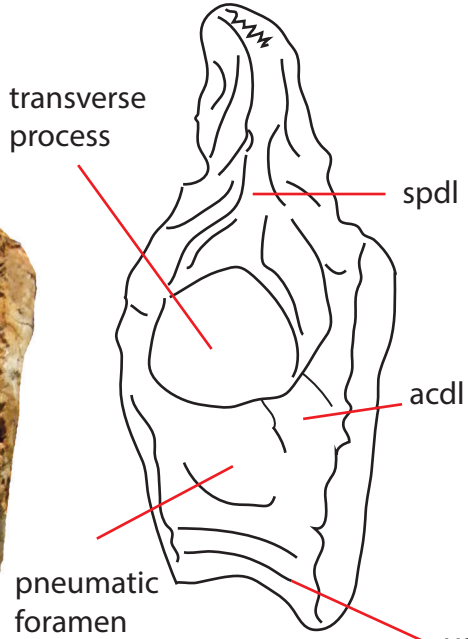
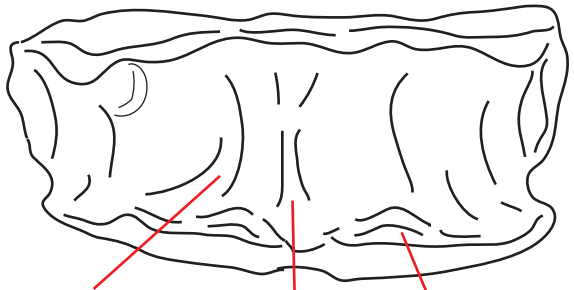


C



D



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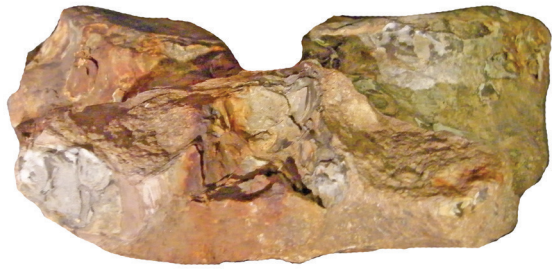
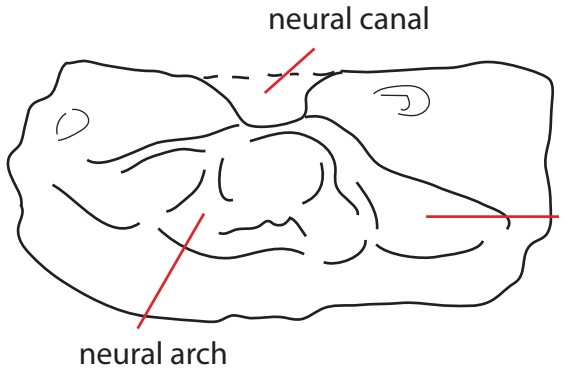




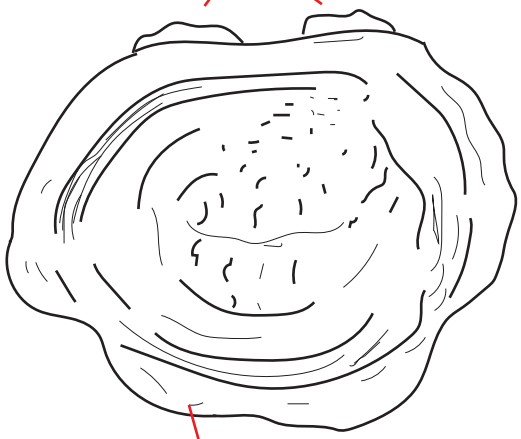
10 cm

Figure 3(on next page)

Middle caudal Leict G418.1956.21.0 (Photographs by FH).

In anterior (A) right lateral (B), posterior (C), left lateral (D), dorsal (E), ventral (F) views. Scalebar 10 cm.

A



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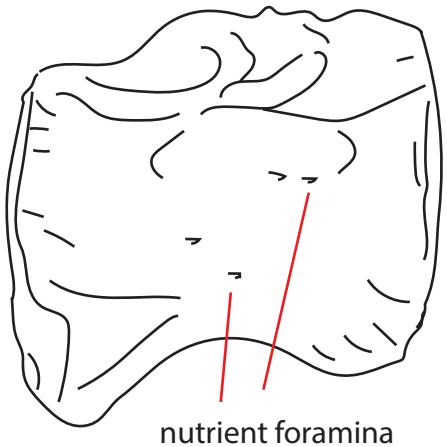

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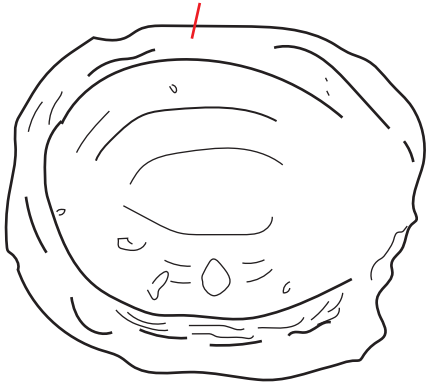
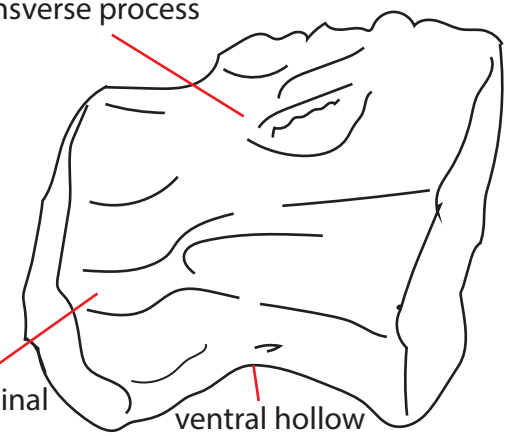


D



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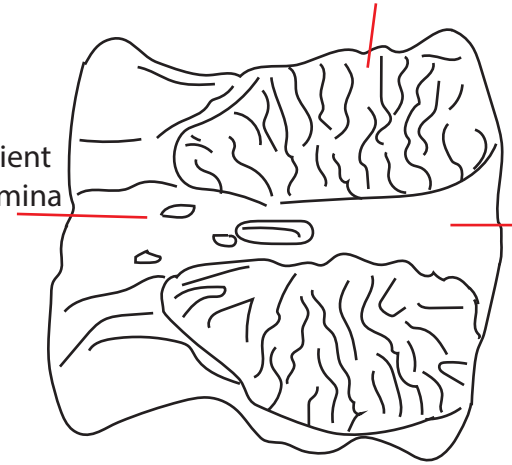


F

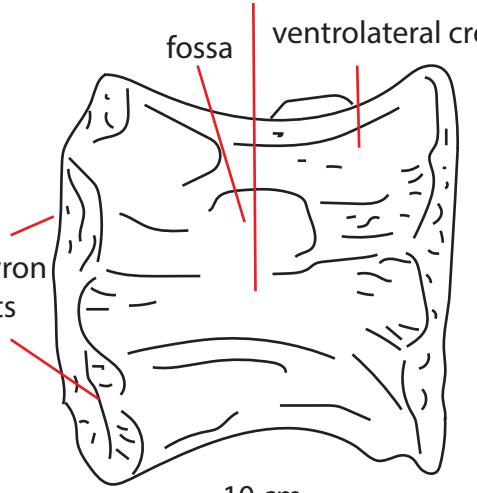
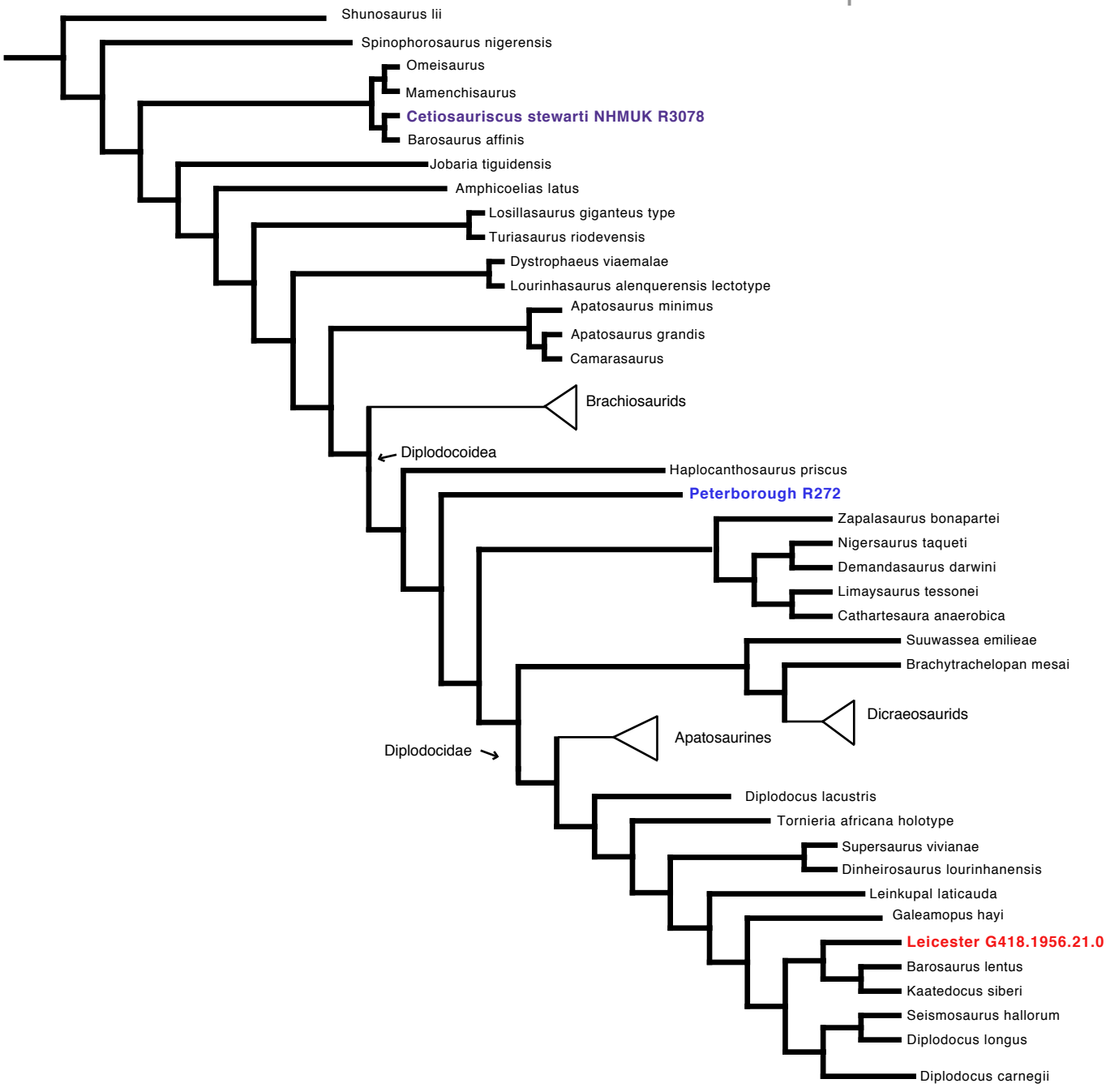


Figure 4(on next page)

50% majority rule consensus tree based on Tschopp et al., (2015).

With positions of *Cetiosauriscus* (purple), and additionally PETMG R272 (blue) and Leict G.418.1956.21.0 (red) as OTU's.


Shunosaurus lii
Spinophorosaurus nigerensis
Omeisaurus
Mamenchisaurus
Cetiosauriscus stewarti NHMUK R3078
Barosaurus affinis
Jobaria tiguidensis
Amphicoelias latus
Losillasaurus giganteus type
Turiasaurus riodevensis
Dystrophaeus viaemalae
Lourinhasaurus alenquerensis lectotype
Apatosaurus minimus
Apatosaurus grandis
Camarasaurus
Brachiosaurids
Diplodocoidea
Haplocanthosaurus priscus
Peterborough R272
Zapalasaurus bonapartei
Nigersaurus taqueti
Demandasaurus darwini
Limaysaurus tessonei
Cathartesaura anaerobica
Suuwassea emilieae
Brachytrachelopan mesai
Dicraeosaurids
Apatosaurines
Diplodocidae
Diplodocus lacustris
Tornieria africana holotype
Supersaurus vivianae
Dinheirosaurus lourinhanensis
Leinkupal laticauda
Galeamopus hayi
Leicester G418.1956.21.0
Barosaurus lentus
Kaatedocus siberi
Seismosaurus hallorum
Diplodocus longus
Diplodocus carnegii