








A HIGHLY PNEUMATIC MIDDLE CRETACEOUS THEROPOD FROM THE BRITISH LOWER GREENSAND

by CHRIS T. BARKER^{1,2*} , DARREN NAISH³ , CLAIRE E. CLARKIN^{1,3} , PAUL FARRELL⁴, GABRIEL HULLMANN⁵, JAMES LOCKYER⁶, PHILIPP SCHNEIDER² , ROBIN K. C. WARD⁷ and NEIL J. GOSTLING^{1,3*} 

¹Institute for Life Sciences, University of Southampton, University Road, Southampton, SO17 1BJ, UK; ctb1g14@soton.ac.uk

²Faculty of Engineering & Physical Sciences, University of Southampton, University Road, Southampton, SO17 1BJ, UK;

³School of Biological Sciences, Faculty of Environment & Life Sciences, University of Southampton, University Road, Southampton, SO17 1BJ, UK; n.j.gostling@soton.ac.uk

⁴Binstead, Isle of Wight, PO33 3TE, UK

⁵Dinosaur Isle Museum, Culver Parade, Sandown, Isle of Wight, PO36 8QA, UK

⁶Whaplode, Lincolnshire, PE12 6SY, UK

⁷Broom, Warwickshire, B50 4HL, UK

*Corresponding authors

Typescript received 18 March 2020; accepted in revised form 16 July 2020

Abstract: A series of axial elements from the Aptian Ferruginous Sands Formation of the Lower Greensand Group, discovered on the foreshore near Knock Cliff on the Isle of Wight, UK are (bar some isolated teeth and fragmentary post-cranial material from the Cenomanian Cambridge Greensand) the youngest non-avian theropod remains reported from the British Mesozoic. These specimens have the potential to shed light on a poorly known section of the European dinosaur record. Consistency in size, appearance and adhering matrix indicates that the vertebrae belong to the same individual. This was a mid-sized tetanuran, the presence of several diagnostic characters indicating that it should be recognized as a new taxon, herein named *Vectaerovenator inopinatus*. The cervical

and dorsal vertebrae are camerate and highly pneumatic. Tetanuran features include opisthocoealous cervicals and pneumatic foramina located within fossae; however, assigning this specimen to a specific clade is problematic. Within Tetanurae, *Vectaerovenator* possesses axial structures and homoplastic features seen in megalosauroids, carcharodontosaurians and certain coelurosaurs. Not only is *Vectaerovenator* one of the UK's youngest non-bird dinosaurs, and one of few valid British Greensand taxa, it is also the first diagnosable theropod taxon to be named from Aptian deposits of Europe.

Key words: Aptian, Cretaceous, pneumaticity, theropod, vertebra.

WESTERN Europe has a rich Early Cretaceous dinosaur record. The majority of British Early Cretaceous dinosaurs are from the Wealden Supergroup (Berriasian to lower Aptian) (Martill & Naish 2001; Naish & Martill 2007; Naish & Martill 2008; Sweetman & Insole 2010), exposures of which crop out on the southern coasts of the Isle of Wight and East Sussex. Wealden dinosaur fossils mostly come from floodplain and flood channel deposits, and only those in the Vectis Formation (Barremian to lower Aptian) come from strata with an obvious marine contribution. The Early Cretaceous dinosaurs represented by these fossils include tetanuran theropods of several lineages, rebbachisaurid and titanosauriform sauropods, ankylosaurs and ornithopods (Martill & Naish 2001; Naish & Martill 2007; Lomax & Tamura 2014).

Among theropods, baryonychines are known from isolated teeth and the holotype of *Baryonyx walkeri* (Charig & Milner 1997); *Neovenator salerii* represents carcharodontosaurian allosauroids (Brusatte *et al.* 2008); and there are fragments that may belong to noasaurids (Naish 2011) and early diverging tetanurans (Benson *et al.* 2009); coelurosaurs include the probable compsognathid *Aristosuchus pusillus*, the tyrannosauroid *Eotyrannus lengi* and fragmentary remains belonging to dromaeosaurids and perhaps other maniraptoran groups (Hutt *et al.* 2001; Naish *et al.* 2001; Sweetman 2004; Naish & Martill 2007; Naish 2011; Naish & Sweetman 2011).

Of those British Cretaceous units overlying the Wealden, the lower Aptian to lower Albian Lower Greensand and middle-late Albian to lower Cenomanian Upper

Greensand formations have yielded dinosaurs, while the chalk (a wholly marine deposit) preserves fragmentary and dubious ornithischian remains (Naish & Martill 2008; Lomax & Tamura 2014). In contrast to the Wealden, the Greensand has yielded few dinosaur specimens and low taxonomic diversity. Fragmentary remains and isolated teeth referred to *Iguanodon*, *Polacanthus* and a putative brachiosaurid sauropod have been recovered from the Lower Greensand of the Isle of Wight (Blows 1998), as has the famous ‘Mantel-piece’ iguanodontian, today referred to *Mantellisaurus*, from Kent (Naish & Martill 2008). Teeth assigned to indeterminate theropods are also known from the Lower Greensand of Dorset (Barrett *et al.* 2010). Meanwhile, the Upper Greensand has yielded indeterminate sauropod remains from the Isle of Wight (Wilson & Upchurch 2003), nodosaurid remains from Folkestone (Naish & Martill 2007), and indeterminate theropod teeth from Charmouth (Barrett *et al.* 2010).

These units represent generally shallow marine depositional environments, and the paucity of dinosaur material known from them probably reflects the overall lack of terrestrial strata deposited around this time (Buffetaut & Nori 2012; Krumenacker *et al.* 2017). Diagnostic Aptian dinosaur material is rare in the European fossil record as a whole, probably due to a return to marine conditions following the early Aptian transgression (Hopson 2011). Non-bird dinosaur remains are considered uncommon in marine sediments (Pasch & May 1997), and are often fragmentary (Farke & Phillips 2017), although their rarity may reflect a collection bias in some localities (Horner 1979). Several mechanisms have been suggested for the allochthonous or parautochthonous presence of dinosaurs in marine sediments (Benton *et al.* 1995), including the passive drifting of carcasses out to sea from river systems, the exploitation of marine environments as a source of food, or predation by marine vertebrates using hunting strategies akin to modern crocodylians or orcas.

Despite rarity overall, members of all major dinosaurian groups are known from marine rocks (Horner 1979; Bartholomai & Molnar 1981; Pasch & May 1997; Martill *et al.* 2000; Pereda-Suberbiola *et al.* 2015; Brown *et al.* 2017; Longrich *et al.* 2017; although marginocephalians are notably scarce: Farke & Phillips 2017) and some marine sediments, such as those of the Middle and Upper Jurassic of England (Benton *et al.* 1995; Martill *et al.* 2006), are well known sources of dinosaur material. Members of some non-bird dinosaur groups (in particular nodosaurids and hadrosaurids) show a significant association with marine palaeoenvironments, and their representation in these deposits is perhaps linked to a preference for fluvial and/or coastal habitats (Butler & Barrett 2008).

Nevertheless, no theropod type specimens are known from the Aptian of Europe, although fragmentary body fossils of spinosaurids, allosauroids, maniraptoriforms and other indeterminate theropods have been reported (Pereda-Suberbiola *et al.* 2012). Here, we report the fragmentary remains of a new Aptian tetanuran from the Lower Greensand of Knock Cliff on the Isle of Wight, which we diagnose and name. This species possesses a mix of features seen elsewhere within Tetanurae, notably in members of Allosauroidae, Megalosauroidae and Megaraptora (a controversial group regarded by some workers as part of Allosauroidae, and by others as part of Coelurosauria and perhaps Tyrannosauroidae). However, the presence of probable homoplastic character states renders its position within Tetanurae uncertain, pending the discovery of further material.

The Knock Cliff theropod is therefore significant in being the first diagnosable non-avian theropod from the Greensand, while also being the youngest named non-avian theropod yet reported from the British fossil record and the first diagnosable Aptian theropod taxon from Europe. As described below, it possesses a complex degree of pneumatization, some detailed aspects of which are unlike those reported elsewhere within Theropoda. Our aim in this work is to describe and diagnose the remains of this new taxon, to identify its vertebrae to specific anatomical location, and to evaluate the new taxon’s phylogenetic position.

Institutional abbreviation. IWCMS, Dinosaur Isle Museum (Isle of Wight County Museum Service), Sandown, Isle of Wight, UK.

GEOLOGICAL SETTING

The specimens described here were recovered on the foreshore at Knock Cliff (Fig. 1A), between Shanklin and Luccombe, Isle of Wight, as three independent sets of remains over a period of several months: the more anterior dorsal and caudal vertebrae were collected in tandem, while the cervical and more posterior dorsal were recovered as singular elements (Fig. 2). All were surface finds, discovered with adhering glauconitic sandstone matrix.

The succession at Knock Cliff is formed of the three strata of the Lower Greensand Group: the uppermost members of the Ferruginous Sands Formation (late Aptian in age; Ruffell *et al.* 2002), the Sandrock Formation (age undetermined), and the Monk’s Bay Sandstone Formation (Albian in age; Ruffell *et al.* 2002; Gale 2019). The last of these can be discounted as a source for the fossils because sediment from this formation is gritty and dark brown; furthermore, vertebrate fossils

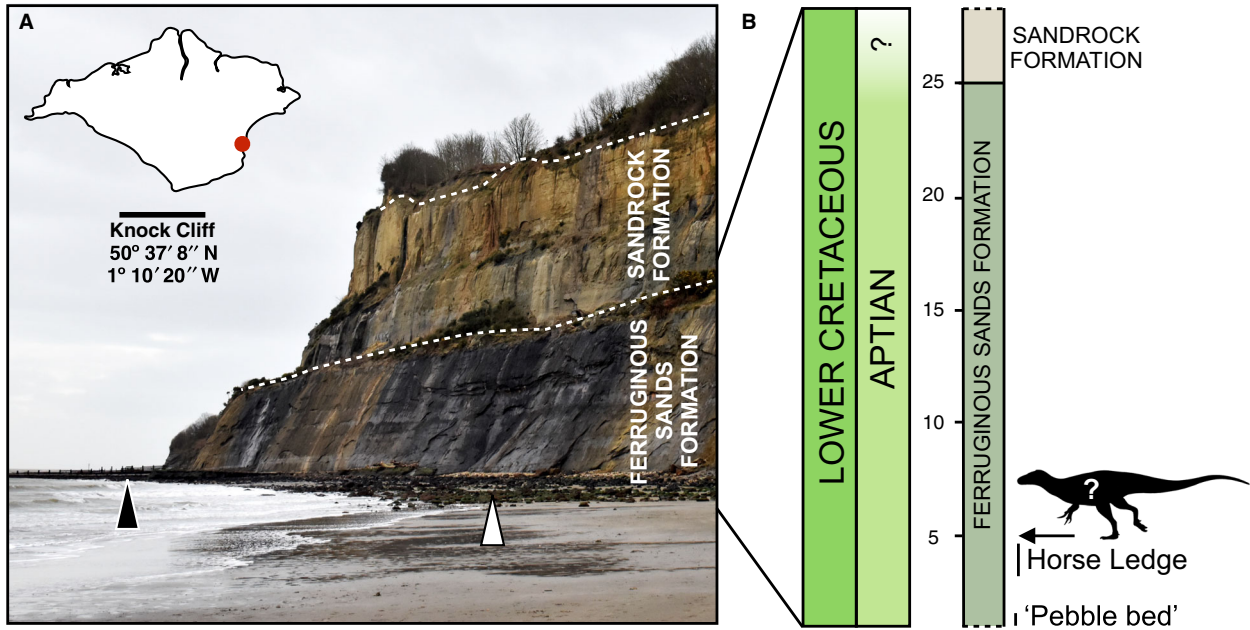


FIG. 1. Locality map of the new theropod taxon and stratigraphy of the Ferruginous Sands formation at Knock Cliff, Isle of Wight (UK). A, map of the Isle of Wight (inset) and photograph of Knock Cliff at Shanklin (credit: Trudie Wilson), where the specimens were collected. B, stratigraphy of Knock Cliff, focusing on the Ferruginous Sands Formation; black triangle indicates Horse Ledge; white triangle indicates the location of the 'pebble bed'. Based on Ruffell *et al.* (2002), Young *et al.* (2014) and Gale (2019). Scale bar represents 10 km.

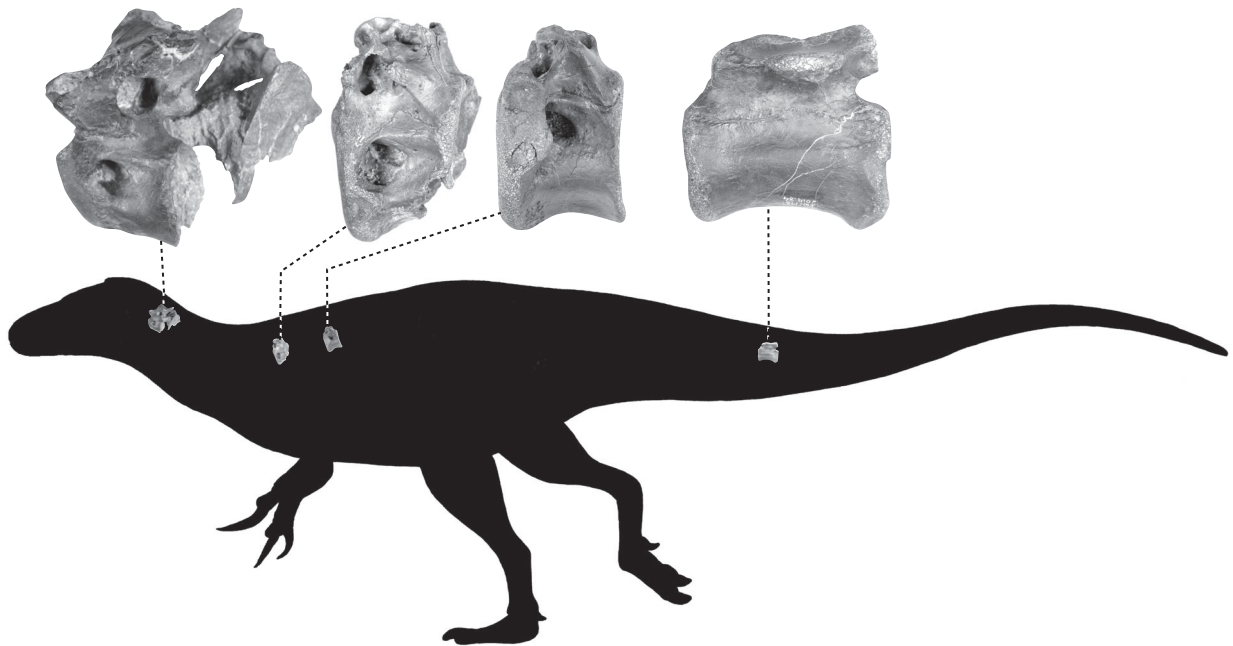


FIG. 2. Silhouette of *Vectaerovenator* showing the approximate position of the vertebral elements (see description for further discussion). Elements not to scale.

remain unreported (Young *et al.* 2014). The Sandrock formation can also be discounted based on the fine-grained, yellow and white sands that form its strata

(Gale 2019). This renders the relatively fossiliferous Ferruginous Sands Formation as the most plausible provenance. This is supported by the sedimentology of the

matrix surrounding the specimens, as discussed further below.

Eleven informal (=‘local’; Rawson 2006) ‘members’ (units) have been identified within the Ferruginous Sands Formation (Insole *et al.* 1998; Hopson *et al.* 2008). Those exposed at Shanklin form its uppermost members, and include the Old Walpen Chine (XII) Member, the New Walpen Chine (XIII) Member and the unnamed Member XIV (Ruffell *et al.* 2002; Young *et al.* 2014). All are late Aptian in age. The glauconitic, fine to medium-grained sandstone matrix adhering to the vertebrae matches that of the New Walpen (XIII) Member (Insole *et al.* 1998; Fig. 1B). Specifically, the material may originate from the ‘Urchin bed’, located on top of Horse Ledge (Ruffell *et al.* 2002), of the *sub-articum* subzone within this member (M. I. Simpson, pers. comm.) Moreover, it is unlike the dark, pebbly clays that mark the base of Member XIII, or the more argillaceous and pyritic greensands of Member XIV above (White 1921; Ruffell *et al.* 2002; Gale 2019). In addition, longshore drift trends from south-west to north-east at Sandown Bay, making transport of the fossils from the nearest Wealden beds at Yaverland unlikely, and there are no indications that they might represent reworked or transported material from the underlying Wessex or Vectis Formations.

The Lower Greensand Group was deposited in shallow marine and possibly estuarine environments following the major Aptian marine transgression (Insole *et al.* 1998; Rawson 2006). Specifically, the majority of the Ferruginous Sands Formation, and thus the New Walpen (XIII) Member, is regarded as consisting of shallow marine shelf deposits (Insole *et al.* 1998). Dinosaur remains are very rare in these deposits, the material reported here all shares the same matrix, and the substantial pneumaticity and thus fragile nature of the material make it unlikely that the remains of several individuals have been rolling around on the beach for any length of time prior to recovery. We therefore consider it likely that the remains described here belong to the same individual.

METHOD AND TERMINOLOGY

Measurements were recorded in millimetres using digital callipers and the results rounded to one decimal place (Tables 1, 2). Nomenclature of vertebral fossae and laminae follows Wilson *et al.* (2011). Positioning within the axial series follows the suggestions of Evers *et al.* (2015), who identified potentially useful anatomical traits to help position isolated material.

SYSTEMATIC PALAEOLOGY

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
TETANURAE Gauthier, 1986
INCERTAE SEDIS

Genus *VECTAEROVENATOR* nov.

LSID. urn:lsid:zoobank.org:act:316560EA-1314-4413-8C55-2D4E0BD6A204

Derivation of name. *Vectis* (Latin): referring to the discovery of this new taxon on the Isle of Wight; *aero* (Greek): ‘air’, referring to its high degree of skeletal pneumaticity; *-venator* (Latin): meaning hunter. We imagine the name to be pronounced ‘vect-air-oh-ven-ah-tor’.

Type species. *Vectaerovenator inopinatus* sp. nov.

Diagnosis. As for type and only species.

Vectaerovenator inopinatus sp. nov.

Figures 2–7

LSID. urn:lsid:zoobank.org:act:E88CFD45-34CF-4C47-BC31-FADC7AE483E9

Derivation of name. *inopinatus* (Latin): ‘unexpected’, referring to its surprise discovery in the notably dinosaur-poor Lower Greensand strata of the Isle of Wight. The name thus translates as ‘unexpected Isle of Wight air-filled hunter’.

Holotype. IWCMS 2020.407, 2019.84, 2020.400.

Diagnosis. Tetanuran theropod diagnosed by: conspicuous lateral furrow between the lateral margin of the postzygapophysis and prezygoepiphyseal lamina in cervical vertebrae; convex spinoprezygapophyseal laminae in anterior cervical vertebra; curved lamina bisecting the postzygocentrodiaepiphyseal fossa; external extension of the air sac ventral to the parapophysis of anterior dorsal vertebra; complex partitioning of the anterior-most dorsal pneumatic foramen into several internal pneumatic features; anterior articular facet of anterior dorsal vertebrae wider than centrum such that vertebra is T-shaped in dorsal or ventral view; shallow fossae lateral to the base of the postzygapophyses in mid caudal vertebrae.

Type locality and horizon. Knock Cliff, Isle of White, UK. Upper Aptian, Lower Greensand, Ferruginous Sands Formation, Member XIII, *Parahoplites nutfieldensis* Zone (possibly *Tropaeum sub-articum* subzone; Fig. 1A).

TABLE 1. Measurements (in mm) of IWCMS 2020.407, 2019.84 and 2020.400.

	Cervical (IWCMS 2020.407)	Dorsal (IWCMS 2019.84)	Dorsal (IWCMS 2020.400)	Caudal (IWCMS 2019.84)
AP length of centrum (from laterodorsal extremities of anterior and posterior articular surfaces)	54.7	52	52.3	77.7
DV height of anterior articular surface	36.4	60.1	59.5	47.4
ML width of anterior articular surface	51.4	64.1	66.2	41.5
ML width across parapophyses	59.8	69.3	77.9	-
DV height of posterior articular surface	44.9	41.4 (incomplete)	61.6	48 (inc. chevron facet)
ML width of posterior articular surface	54.7	59.2	57.4 (incomplete)	40.8
DV height of anterior neural canal	15.7	23	21.9	13.9
ML width of anterior neural canal	17.7	22.7	19.8	13.1
DV height of posterior neural canal	12.5	20.8	20.5	13.3
ML width of posterior neural canal	19.2	18.4	18.3	13.5
ML width across prezygapophyses	72.2 (incomplete)	n/a	n/a	n/a
ML width across postzygapophyses	74.1	n/a	n/a	n/a
Length of neural arch from anterior end of prezygapophyses to posterior end of postzygapophyses	80.7	n/a	n/a	n/a

AP, anteroposterior; DV, dorsoventral; ML, mediolateral.

Description

Cervical vertebrae and rib. Three components of the cervical series are known for *Vectaeovenator*: a well preserved cervical vertebra lacking some or most of the neural spine; left prezygapophysis, diapophysis and epipophysis (the right epipophysis and lateral margin of the posterior articular surface are also damaged), an associated cervical rib, and a portion of a second cervical vertebra represented only by a prezygapophysis (IWCMS 2020.407, Fig. 3A, B). We here describe each of these elements in turn but the second prezygapophyseal fragment, which offers little additional insight.

The more complete cervical vertebra is mid-sized for a non-avian theropod, with a total centrum length of 54.7 mm. The neurocentral sutures are still visible externally. The centrum is opisthocelous: its posterior articular facet is markedly concave yet the anterior articular facet is only incipiently convex. The anterior facet is anteroposteriorly thickest dorsally, such that the anterior facet margin trends posteroventrally in lateral view. The anterior facet is dorsoventrally shorter than the posterior

articular facet, but their dorsal margins are at the same horizontal level. Both surfaces are wider than tall, and punctate, unlike the smooth cortical bone covering most of the specimen. The anterior articular surface is generally ellipsoidal, but the neural canal marginally excavates its dorsal margin (Fig. 3C). The posterior articular surface has a straight dorsal margin and is wider than the anterior articular surface (Fig. 3D). The ventral surface of the centrum is convex and lacks a keel, and minor mediolateral constriction of the centrum can be clearly noted (Fig. 3E). Anteriorly, this surface possesses irregular radial grooves between the parapophyses, the median of which extend posteriorly to the ventral midpoint of the centrum.

The parapophyses are small and located just ventral to the centrum's midline; they project laterally only slightly. They possess a flat, punctate lateral surface. An elongate, anterodorsal–posteroventral trending pneumatic fossa excavates the centrum posterodorsal to each parapophysis, the left posterodorsal margin of which is marked by a poorly developed lamina. A rounded pneumatic foramen is present anteriorly within each fossa, and penetrates the anterior and medial regions of the centrum. The entrance of the left foramen, the largest of the two, measures 15.7 mm dorsoventrally and 15.1 mm mediolaterally. Together, the fossa and foramen form a pneumatic feature that spans much of the centrum's length. Internally, the foramen is incompletely divided by a low, anteriorly tapering septum, such that a shallow ventral portion lateral to the septum excavates the medial surface of the parapophysis while a larger, mediolateral portion opens into a substantial chamber within the centrum (Figs 3A, 4A).

The incomplete neural arch is tall and highly pneumatic. The broken left prezygapophysis reveals a matrix-filled hollow. The complete right prezygapophysis projects anteriorly from the base of the neural arch, and only just extends past the anterior articular surface of the centrum. Its inclined facet is flat and ovate, and faces dorsomedially. Its long axis is almost perpendicular to

TABLE 2. Measurements (in mm) of IWCMS 2020.407 rib

	IWCMS 2020.407 rib
DV height of anterior rib surface	33.3
ML width of anterior rib surface	23.5
AP length of cervical rib	87.4 (incomplete)
ML width of capitulum	12.9
AP length of capitulum	18.7
ML width of tuberculum	12
AP length of tuberculum	16.9

AP, anteroposterior; DV, dorsoventral; ML, mediolateral.

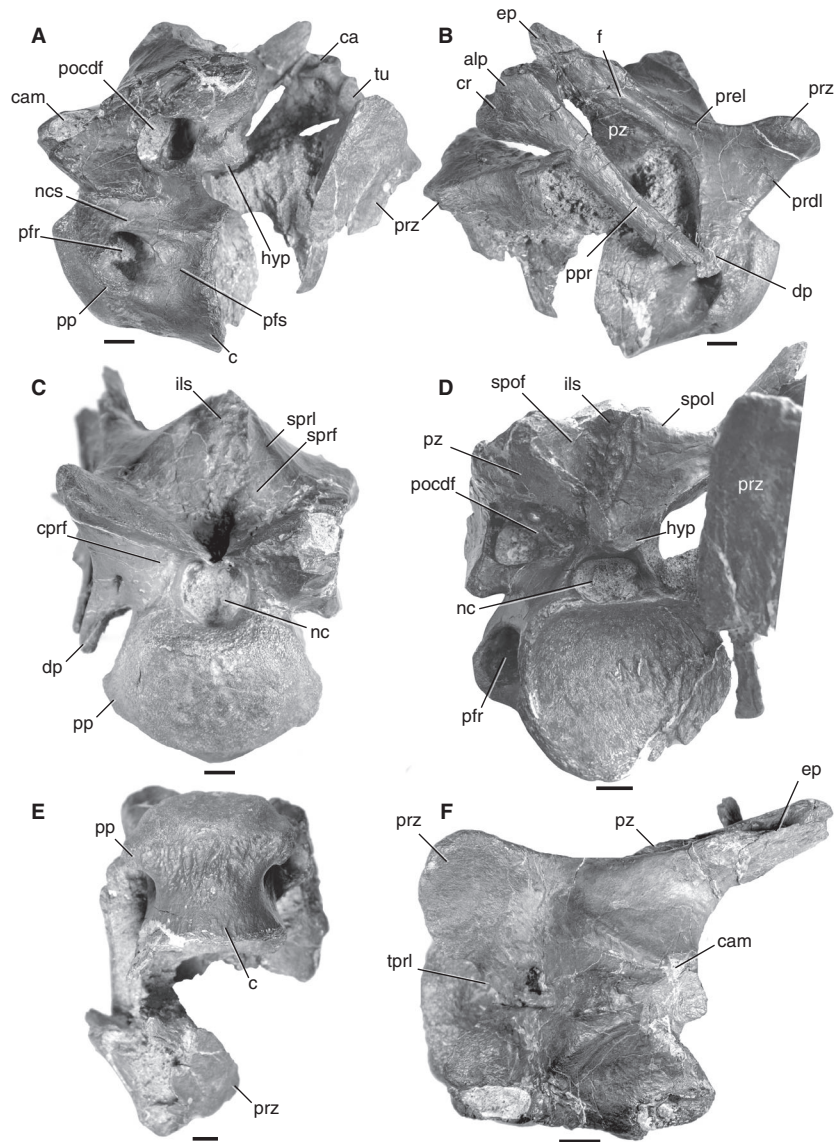


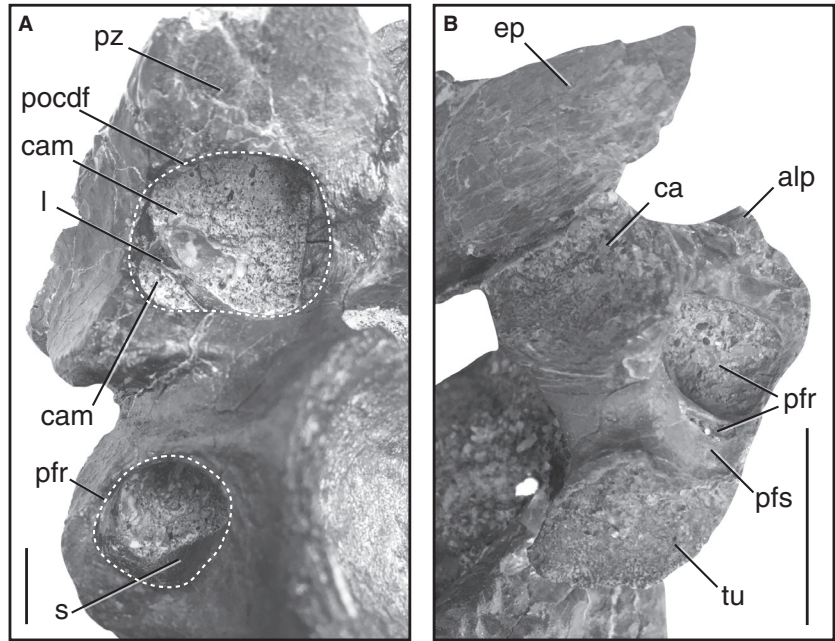
FIG. 3. Cervical vertebrae (IWCMS 2020.407), in: A, left lateral; B, right lateral; C, anterior; D, posterolateral; E, ventral; F, dorsal view. *Abbreviations:* alp, anterolateral process of cervical rib; c, centrum; ca, capitulum; cam, camera; cprf, centroprezygapophyseal fossa; cr, cervical rib; dp, diapophysis; ep, epiphysis; f, furrow; hyp, hyposphene-like lamina; ils, interspinous ligament scar; nc, neural canal; ncs, neurocentral suture; pfr, pneumatic foramen; pfs, pneumatic fossa; pocdf, postzygocentrodiaepophyseal fossa; pp, parapophysis; ppr, posterior process of cervical rib; prdl, prezygodiaepophyseal lamina; prel, prezygoepiphysal lamina; prz, prezygapophysis; pz, postzygapophysis; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinopostzygapophyseal lamina; tb, tuberculum; tprl, intraprezygapophyseal lamina. Scale bars represent 1 cm.

the long axis of the neural arch. A small medial projection of the prezygapophyseal facet is visible in dorsal view (Fig. 3F). In lateral view, the pedicle of the right prezygapophysis has a crenulated cortical bone texture. The anterior surface of this pedicle is perforate by a small, presumably vascular foramen just above the diapophysis.

Anteriorly, the neural canal is vaguely heart-shaped, with a subtly concave dorsal margin (Fig. 3C). A poorly developed centroprezygapophyseal fossa is present laterodorsal to the neural canal, and is best preserved ventral to the complete right

prezygapophysis. The intraprezygapophyseal laminae are short due to the close proximity of the prezygapophysis, and have incurred slight damage at their midpoint. The margins of the spinoprezygapophyseal laminae are rounded (i.e. not sharp ridges) and do not contact the prezygapophyseal facets anteriorly. They are prominently convex in lateral view. These laminae delineate an anteriorly diamond-shaped spinoprezygapophyseal fossa. A narrow, rugose prespinal ligamentous attachment site medially bisects this fossa. The right ventral margin of the ligamentous attachment site contacts a small pneumatic foramen

FIG. 4. A, details of the pneumatic features of IWCMS 2020.407, in posterolateral view. B, details of the articular facets and pneumaticity of the associated cervical rib, in anterior view. Dotted lines delineate entrances to pneumatic features. *Abbreviations:* alp, anterolateral process of cervical rib; ca, capitulum; cam: camera; ep, epiphysis; l, lamina; pfr, pneumatic foramen; pfs, pneumatic fossa; pocdf, postzygocentrodiaepiphyseal fossa; pz, postzygapophysis; s, septum; tb, tuberculum. Scale bars represent 1 cm.



that is not mirrored on the left-hand side. The right prezygapophysis is connected to the right epiphysis by a pronounced prezygoepiphyseal lamina. This is slightly concave in lateral and dorsal view and possesses a sharp margin. The elongate right epiphysis is abraded, projecting posterodorsally and tapering dorsally.

The complete right diapophysis projects posteroventrally and is located ventral to the neurocentral suture. It is mediolaterally compressed and slightly abraded at its ventral end (Fig. 3B). In lateral view, the prezygodiaepiphyseal lamina projects anterodorsally from the diapophysis while the postzygodiaepiphyseal lamina is subvertical. Consequently, the generally ventrally projecting diapophysis has a triangular outline. In anterior view, the prezygodiaepiphyseal lamina is slightly concave laterally. The anterior and posterior centrodiaepiphyseal laminae are very weakly developed. The exposed left postzygocentrodiaepiphyseal fossa is deep and contains three internal pneumatic features: two visible camerae and a pneumatic foramen (Fig. 4A). The medial camera is the largest and excavates the neural arch medially. It is separated from the smaller lateral camera by a thin, anteriorly curved lamina. The lateral camera probably excavates the left pedicle of the prezygapophysis, and may connect to the aforementioned hollow made visible by the loss of the left prezygapophyseal facet. The posterior foramen excavates the thin left ventral wall of the spinopostzygapophyseal fossa, such that the latter communicates with the postzygocentrodiaepiphyseal fossa. This latter condition is not mirrored on the right side.

Posteriorly, the complete right postzygapophyseal facet is flat and somewhat inclined (Fig. 3D). It possesses a subtriangular outline that tapers medially. A strongly projecting, convex lateral margin, running almost parallel to the prezygoepiphyseal lamina, demarcates the ventral border of a lateral furrow leading to the long, thin epiphysis (Fig. 3B). We are not aware of such a

prominently demarcated furrow elsewhere within Theropoda and hence regard this as an autapomorphy. The postzygapophyses border a deep, roughly rhomboidal spinopostzygapophyseal fossa. This fossa is bisected medially by a rugose triangle of bone, the postspinal ligamentous attachment site. The spinopostzygapophyseal laminae are thick, with rounded margins. The thinner intrapostzygapophyseal laminae curve ventrally and meet medially as a broad, U-shaped hyposphene-like structure. This latter structure overhangs the neural canal, which is horizontally oval in shape. The exposed cross-section of the anteroposteriorly short, posteriorly placed and posterodorsally projecting neural spine is triangular. Two small pneumatic chambers suggest that the spine was also pneumatic, perhaps communicating with one of the aforementioned pneumatic foramina excavating the postzygocentrodiaepiphyseal fossa.

The cervical vertebrae are associated with a well-preserved right cervical rib (Fig. 4B). Its medial surface is obscured by matrix, and whether it belonged to the more complete vertebra is uncertain. However, the distances between the articular surfaces of the rib are roughly equivalent to the distance between the right diapophysis and parapophysis. The anterolateral process of the cervical rib is poorly developed. The posterior process is anteriorly convex, flattens posteriorly, and barely tapers along its preserved length. A sharp ridge extends posteriorly to form the ventral margin of the rib, separating the lateral and ventral surfaces. A large pneumatic fossa is present on the rib's anterior surface, which measures 9.9 mm dorsoventrally and 11.6 mm mediolaterally (Fig. 4H). The pneumatic fossa houses two pneumatic foramina, the larger and more ventrally placed of which is separated by a thin lamina from its substantially smaller dorsal neighbour. The larger foramen is further bisected internally, with a deeply inset lamina separating it into medial and lateral portions. In medial view the tuberculum facet is subtriangular in shape, whereas the capitulum is ovate. Both lie in the same

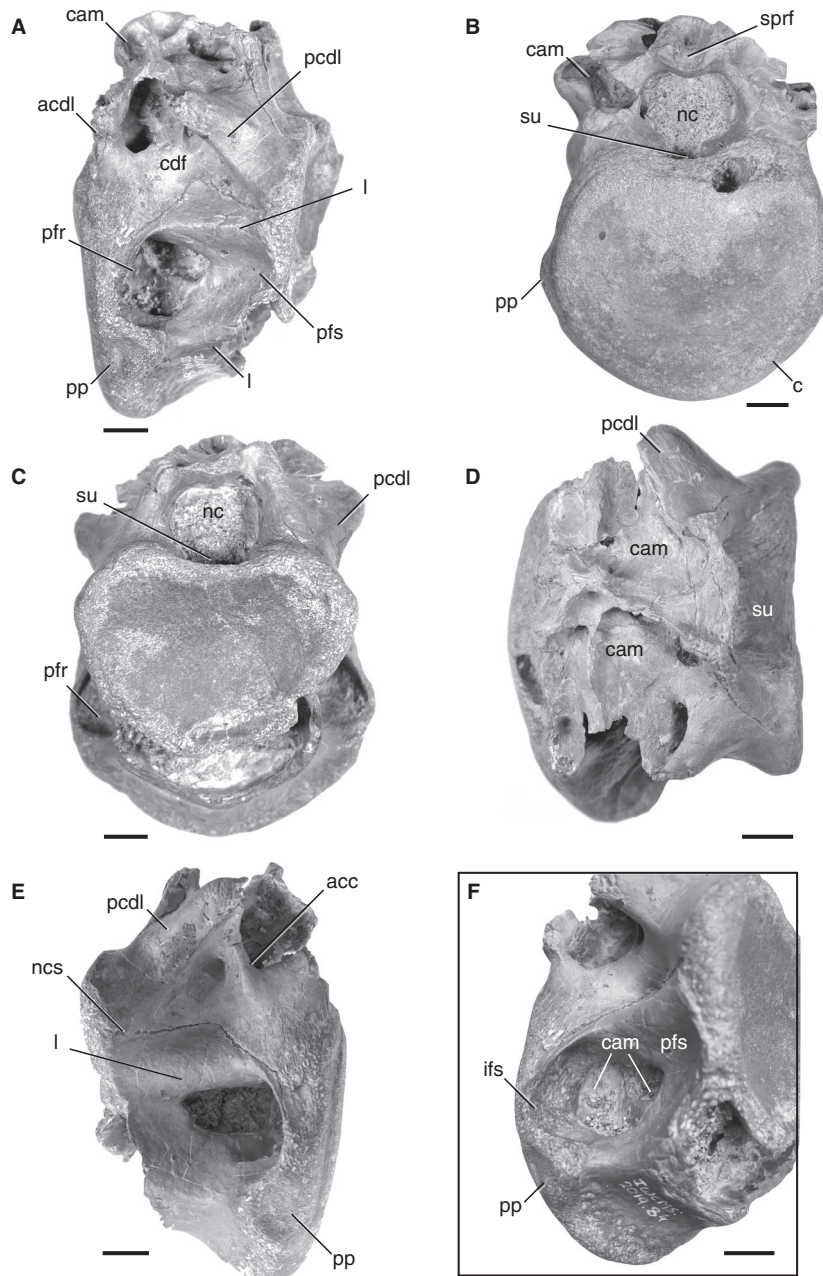


FIG. 5. Anterior dorsal vertebra (IWCMS 2019.84) in: A, left lateral; B, anterior; C, posterior; D, dorsal; and E, right lateral view. F, detail of the pneumatic features of the centrum in left posterolateroventral view. *Abbreviations:* acdl, anterior centrodiapophyseal lamina; acc, accessory centrodiapophyseal lamina; c, centrum; cam, camera; cdf, centrodiapophyseal fossa; ifs: internal pneumatic fossa; l, lamina; nc, neural canal; ncs, neurocentral suture; pcdl, posterior centrodiapophyseal lamina; pfr, pneumatic foramen; pfs, pneumatic fossa; pp, parapophysis; sprf, spinoprezygapophyseal fossa; su, sulcus. Scale bars represent 1 cm.

plane relative to one another and are separated by 6.7 mm of bone.

Dorsal vertebrae. Dorsal vertebra IWCMS 2019.84 lacks the posteroventral portion of the centrum and most components of the neural arch (Fig. 5A–C, E). The centrum is anteroposteriorly short; its anterior articular facet is complete, and taller than the

centrum's length (Fig. 5A, B). The margins of the articular facets are eroded and have a punctate bone texture. At the dorsal midline, the margin of the anterior articular facet is concave, but rounded elsewhere (Fig. 5B). The mediadorsal section of the anterior articular facet possesses a cambered portion that flattens out ventrally and laterally. A portion of bone on the left side is missing, revealing a matrix-infilled hole that penetrates the

centrum and communicates with a pneumatic chamber posteriorly. The incomplete posterior articular facet is concave and reniform in outline (Fig. 5C). It is narrower than its anterior counterpart, rendering both pneumatic foramina visible in posterior view. Both facets are parallel and their dorsal margins are in line with one another. The neural canal excavates the dorsal surface of the centrum, forming a recessed area delimited laterally by the base of the neural arch. The anterior recess is medio-laterally narrow relative to the posterior excavation.

Laterally, the centrum contacts the neural arch via a medially constricted, inverted V-shaped neurocentral suture. The most prominent features of the centrum's lateral surfaces are the extensive, elongate pneumatic fossae, which occupy much of the centrum's length and are demarcated dorsally and ventrally by thick, subparallel laminae, the latter of which extends posteriorly from the parapophysis. Both of these laminae are gently concave in coronal view. Single, bilateral pneumatic foramina excavate the centrum dorsal to the flat parapophyses: the latter are situated anteroventrolaterally, roughly midway between the anteriormost end of the neurocentral suture and the ventral margin of the anterior articular facet. The pneumatic foramina are large and somewhat ovate, the left-hand one of which measures 19 mm dorsoventrally and 24.3 mm mediolaterally, and both are divided into three, sequentially organized internal pneumatic features (Fig. 5F). These internal features present as two medially positioned camerae that are bordered laterally by a shallow internal fossa. The medial-most camera is anteroposteriorly elongate and penetrates the medial centrum body. It is separated from its more dorsoventrally oriented lateral neighbour by a thin lamina. The shallow fossa that borders both camerae is variably indented depending on the side examined: the left internal fossa possesses several indentations relative to the smoother right-hand equivalent, which probably represent small outpocketings of the air sac system. Both excavate the mediodorsal surface of the parapophysis and the anterodorsal and anterior portion of the centrum (behind the rim of the anterior articular surface).

As noted above, the posteroventral portion of the centrum is absent, leaving behind a large, matrix-infilled hollow. The ventral surface of the centrum is pinched but fails to produce a substantial keel or ridge.

The extensively pneumatic neural arch is very eroded and is missing its zygapophyses, both transverse processes and the neural spine (Fig. 5E). Camerae and internal septa are visible throughout. In anterior view, the neural canal is slightly wider than it is tall, and the mediodorsal margin of the canal becomes concave. Immediately dorsal to this, a shallow, medially placed recess is present and is interpreted here as the remains of a spinoprezygapophyseal fossa. Posteriorly, the neural canal is taller than wide, and has a straight dorsal margin.

Laterally, and ventral to the incomplete left diapophysis, a triangular centrodiaepophyseal fossa is demarcated anteriorly by the vertically oriented anterior centrodiaepophyseal lamina and an anterodorsally inclined posterior centrodiaepophyseal lamina. In its ventral part, the left fossa contains two pneumatic foramina, a configuration that is not mirrored on the element's right side. Instead, the right posterior centrodiaepophyseal lamina possesses an accessory lamina that projects anteroventrally to delimit a small fossa (Fig. 5E). This fossa is perforated by a pinhole-like

foramen that communicates with a large internal hollow, made visible by the loss of the right diapophysis. Internally, a lamina bisects the hollow into anteroventral and posterior camerae.

A second dorsal vertebra (IWCMS 2020.400) has a complete and well-preserved centrum missing only the right margin of the posterior articular surface (Fig. 6). Only the base of the neural arch is present; all of the more dorsal structures are absent.

The centrum is anteroposteriorly short, possessing articular surfaces that are taller relative to centrum length (Fig. 6A–C). In coronal view, the mediolaterally broad anterior surface, combined with the weakly constricted midsection and mediolaterally narrower posterior articular surface, gives the element a roughly T-shaped appearance (Fig. 6D, E). Thanks to this configuration, the pneumatic fossae and lateral margins of the anterior articular surface are visible in posterior view (Fig. 6B).

The anterior articular facet is subcircular but for a straight section present along the dorsal midline (Fig. 6A). The articular face is flat, bar a subtle mediodorsal convexity. The shallowly concave posterior articular facet is taller than wide, again with a straight edge along its dorsal margin (Fig. 6B). The preserved left lateral margin is convex before descending steeply to the ventral midpoint. The neural canal excavates the dorsal surface of the centrum. However, in contrast to the other dorsal vertebra, the canal barely excavates the dorsal margin of the posterior articular facet.

The parapophyses project weakly laterally from the margins of the anterior articular surface, and are bisected by the neurocentral sutures. The better-preserved left parapophysis shows that these structures were dorsoventrally tall (Fig. 6C). The centrum-bound portion of the left parapophysis extends posteriorly to form the anterolateral wall of the pneumatic foramen. It has a concave lateral margin in anterior view, compared with the flatter right-hand element. The left parapophysis narrows dorsally, and the section that extends onto the neural arch has a shallowly concave lateral surface. The ventral margin of the centrum is concave in lateral view and pinched in transverse section, forming a small, ventrally rounded median ridge (Fig. 6E, F). Anteroposteriorly short radial grooves ornament the median anteroventral surface of the centrum.

The bilateral, elongate pneumatic fossae excavate much of the posterodorsal lateral surface and their single anterior foramina deeply penetrate the anterior centrum body. These fossae are demarcated dorsally by a small lamina just ventral to the neurocentral suture. The left foramen opens medially and ventrally into the centrum where it splits into four further pneumatic features: three camerae and an internal pneumatic fossa (Fig. 6G). The three camerae are separated from one another by two thin laminae; two camerae excavate the medial centrum body, while a third excavates the centrum ventrally. The shallow, laterally placed internal fossa borders the camerae and excavates the medial wall of the parapophysis and anterodorsal corner of the centrum. Ventral to the parapophyses, shallow, anteroventral–posterodorsal trending sulci communicate with the large pneumatic fossae that excavate the laterodorsal centrum surface. These sulci suggest an external lateroventral expansion of the pneumatic features. The neural arch is incomplete and eroded, revealing a camerate internal structure. The camerae are broadly symmetrical in dorsal view; an anterior pair excavates the prezygapophyseal pedicles and dorsal part of the parapophysis, the

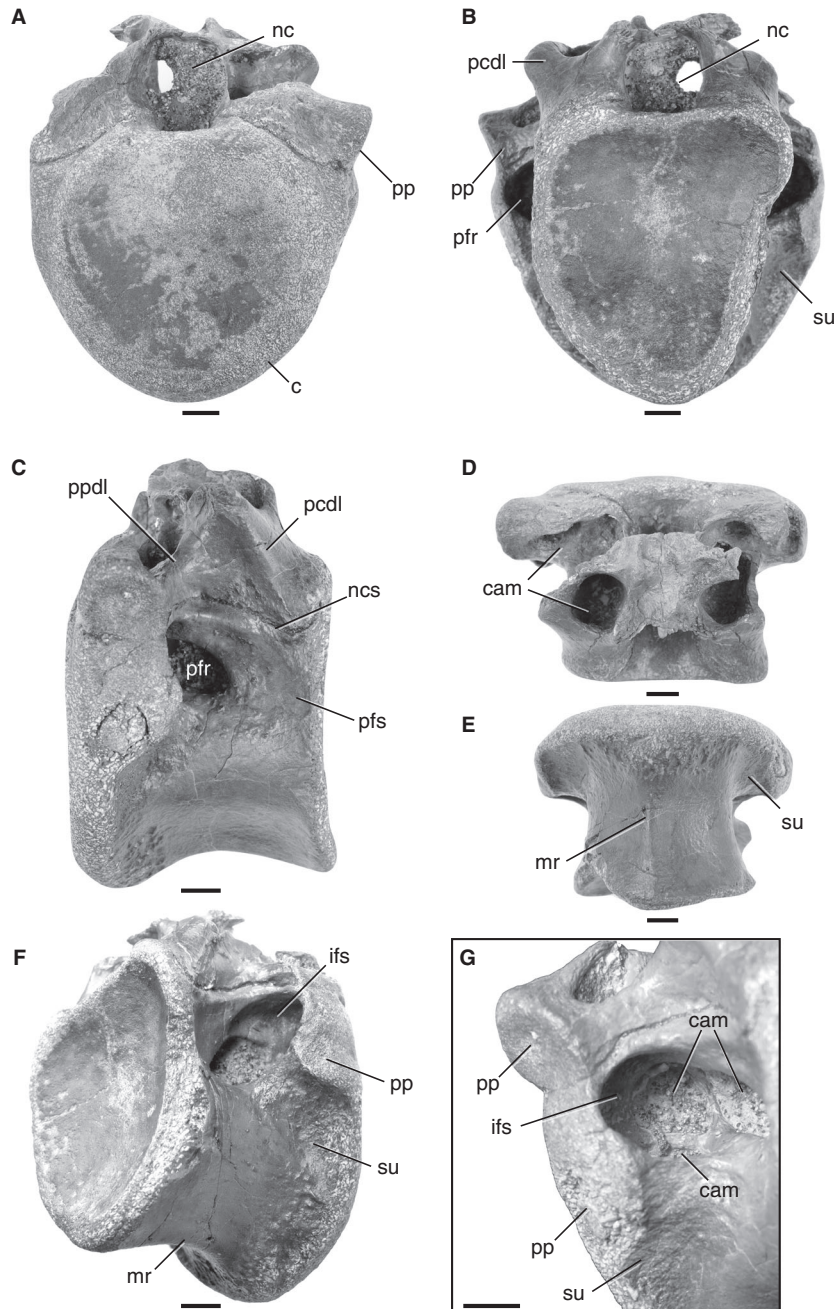


FIG. 6. Anterior dorsal vertebra (IWCMS 2020.400) in: A, anterior; B, posterior; C, left lateral; D, dorsal; E, ventral view. F, details of the pneumatic fossa in right posterolateroventral view. G, detail of the pneumatic features of the centrum in left posterolateral view (credit: Alex Peaker). *Abbreviations:* c, centrum; cam, camera; ifs, internal pneumatic fossa; nc, neural canal; ncs, neurocentral suture; pcdl, posterior centrodiapophyseal lamina; mr, median ridge; pfr, pneumatic foramen; pfs, pneumatic fossa; pp, parapophysis; ppdl, paradiapophyseal lamina; su, sulcus. Scale bars represent 1 cm.

left side of which is bisected by an internal lamina; while two dorsoventrally deep camerae excavate the neural arch medially to the centrodiapophyseal fossae (Fig. 6D). The mid-section of the neural arch is constricted, such that the neurocentral suture is V-shaped in coronal view. A shallow, subtriangular centrodiapophyseal fossa is present, dorsal to the neurocentral suture. The neural canal

is tall and relatively broad, and as previously stated excavates the dorsal margin of the centrum.

Caudal vertebra. A single caudal vertebra (IWCMS 2019.84) is a heavier, more robust element than the others described above (Fig. 7). Its centrum is complete and well-preserved; the neural

arch is missing its zygapophyses, neural spine, and lateral ends of the transverse processes. Erosion of the rims of the articular surfaces, and loss of the aforementioned neural arch structures has exposed the interior trabeculae. The neurocentral suture is visible and has a somewhat irregular, sinusoidal shape.

The centrum is anteroposteriorly elongate and almost 1.7 times its height (Fig. 7A); its articular surfaces are shallowly concave and taller than wide (Fig. 7B, C). The dorsal margins of the articular surfaces are straight. The anterior articular surface shows slight transverse expansion across its midpoint. The posterior articular surface is more rounded and a chevron facet is present. Some damage, however, has occurred to the left side of the articular surface just dorsal to the facet. Minor mediolateral constriction is present along the middle portion of the centrum, such that the articular facets are wider. In lateral view, the dorsal portion of the centrum bears a shallow pleurocentral depression that occupies nearly the entire dorsal width of the centrum. Ventrally, the centrum has a somewhat pinched, featureless underside.

The neural arch roofs a generally subcircular neural canal whose ventral margins also excavate the dorsal surface of the centrum. The left spinoprezygodiapophyseal lamina is present, delimiting a small yet deep spinoprezygapophyseal fossa that extends posteriorly beneath the anterior portion of the neural arch (Fig. 7B, D). A low, thin prespinal lamina roofs the fossa and extends posteriorly to the abraded base of the neural spine. The diapophyses are dorsoventrally flat and hemispherical in dorsal view due to the erosion of their lateral tips.

Ventral to the diapophyses, the remnants of the anterior and posterior centrodiaepophyseal laminae are perceptible as subtle ridges, whose ventral ends do not reach the centrum (Fig. 7A). These delineate a poorly developed centrodiaepophyseal fossa. The postzygapophyses are missing except for their bases, the lateral surfaces of which are concave. These depressions are bounded dorsally by the postzygodiapophyseal laminae and anteroventrally by accessory laminae (Fig. 7C). These resemble centropostzygapophyseal fossae, but they are not bound laterally by centropostzygapophyseal lamina, and are thus unnamed for

the sake of brevity. The postzygapophyseal bases, along with the abraded spinopostzygapophyseal laminae, delimit a narrow, oval spinopostzygapophyseal fossa.

Remarks

The anteroventral position of the parapophysis and presence of epipophyses indicate that the more complete vertebra of IWCMS 2020.407 belongs to the cervical series. The ventrolaterally projecting diapophyses and anteroventral inclination of the anterior articular facet are present in the anterior cervicals of several other theropods. The absence of a ventral keel (typically present in more posterior cervical vertebrae) supports its position in the anterior to middle part of the cervical series. Typically, cervical vertebrae VI–IX are longest in Neotheropoda (Holtz 2000), although comparisons are difficult owing to the lack of additional cervical elements. The capitulum and tuberculum are closely spaced, their articular facets lying in the same plane. In contrast, the articular facets of posterior cervical ribs are widely separated, although they do also lie in the same plane (Dai *et al.* 2020). The proximity of the rib to the more complete cervical vertebra indicates that it pertains to this bone or an adjacent vertebra, and indeed its detailed anatomy appears inconsistent with a more posterior position. Based on comparisons with *Allosaurus* (Madsen 1976), this vertebra is most similar to cervical III in the relative distance between the diapophysis and parapophysis (which increases posteriorly), and in the anterior projection of the prezygapophysis (which projects further anteriorly in the mid-series and sits atop taller pedicles in the posterior elements; Chokchaloemwong *et al.* 2019). All neurocentral sutures in this specimen are open, consistent with putative measures of relative morphological immaturity (Brochu 1996; a trait that can be extended to the other recovered axial elements).

Presacral vertebra IWCMS 2019.84 could either be a posterior cervical or anterior dorsal. The parapophyses are restricted to

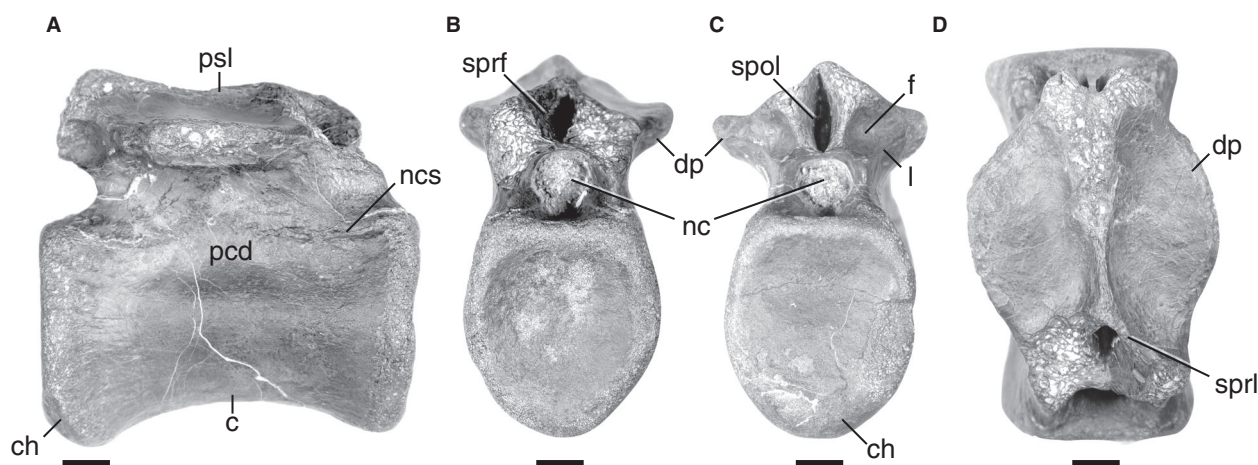


FIG. 7. Mid-caudal vertebra (IWCMS 2019.84) in: A, right lateral; B, anterior; C, posterior; D, dorsal view. *Abbreviations:* c, centrum; ch, chevron facet; dp, diapophysis; f, fossa; l, lamina; nc, neural canal; ncs, neurocentral suture; pcd, pleurocentral depression; psl, prespinal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinopostzygapophyseal lamina. Scale bars represent 1 cm.

the ventral portion of the anterior centrum; in most non-bird theropods, these are located anteroventrally up to the 10th cervical vertebra (Evers *et al.* 2015). They are usually more dorsally situated in the anterior dorsal series and migrate to the neural arch in the posterior rib-bearing vertebrae (Currie & Dong 2001). However, this transition is less marked in the anterior dorsals of certain taxa (Evers *et al.* 2015). The first dorsal vertebra figured for *Aerosteon* possesses an anteroventrally situated parapophysis, for example (Serenio *et al.* 2008). Similarly, Madsen (1976) figured the first to third dorsal vertebrae of *Allosaurus* as having anteroventrally situated parapophyses. Regardless, the cervical–dorsal transition is difficult to ascertain in the absence of associated ribs (Harris 1998). Horizontal or dorsolaterally projecting diapophyses may also help identify a position in the dorsal series (Evers *et al.* 2015), but again these are lacking in this specimen. The orientations of the anterior and posterior centrodiaepophyseal laminae suggest, however, that the diapophyses of IWCMS 2019.84 were laterally projecting. In summary, we provisionally identify the specimen as the first or second dorsal vertebra.

In IWCMS 2020.400, the presence of parapophyses that span the neurocentral suture and the orientation of the posterior centrodiaepophyseal laminae clearly support an anterior position among the dorsal vertebrae. Such vertebrae have been termed ‘cervicodorsals’ (Coria & Currie 2006) or ‘pectorals’ (Currie & Zhao 1993), and typically represent the 11th to 13th/14th presacral vertebrae, although this nomenclature has not been widely adopted. The position of the parapophysis in IWCMS 2020.400 resembles the condition in the fourth and fifth dorsal vertebrae of *Allosaurus* (Madsen 1976). The specimen also resembles the fourth dorsal vertebra of *Aerosteon* (Serenio *et al.* 2008) further suggesting a position at or near this point in the dorsal series.

The identification of IWCMS 2019.84 as a caudal vertebra is supported by its lack of parapophyses, sacral rib attachments and pneumatic fossae (Charig & Milner 1997; Brougham *et al.* 2019). The presence of transverse processes indicates that it is a proximal caudal, belonging to the part of the tail anterior to the transition point that separates the proximal and distal parts of the tail skeleton (Russell 1972). Its exact position in the proximal caudal series cannot be determined, but an approximate position can be deduced based on several traits. The lack of a hyposphene (which is variably present in theropod caudals), elongate centrum body, poorly developed centrodiaepophyseal laminae (Rauhut *et al.* 2018), rounded ventral margin and presence of a chevron facet suggest it was part of the posterior proximal series, located closer to the transition point than the sacrum. This corresponds to the ‘mid’ caudals of some authors.

DISCUSSION

Theropod affinity of the material

The overall appearance of the cervical (IWCMS 2020.407) and combination of epipophyses, anteroventrally situated parapophyses, a neural arch with lateral depressions,

distinct pre- and postzygapophyses as well as pneumatization of the vertebra (a trait that can be extended to dorsal elements IWCMS 2019.84 and 2020.400) and associated rib clearly identify IWCMS 2020.407 as belonging to a saurischian dinosaur (Gauthier 1986; Rauhut 2003). Moreover, it shares several synapomorphies with Theropoda: closely placed diapophyses and parapophyses in anterior (and mid) cervicals, as well as pleurocoels in anterior presacral vertebrae (Gauthier 1986; Cau 2018). Further, the camerate internal chambers within the cervicals have been tentatively suggested as an additional theropodan apomorphy in some analyses (Rauhut 2003).

A sauropod identification can also be discredited, despite the presence within this group of opisthocoelous cervical vertebrae and pneumatization in the vertebral column, as well as the discovery of a putative brachiosaurid from the nearby Lower Greensand locality of Luccombe Chine (Blows 1995). In contrast to sauropods (Rauhut 2003; Nicholl *et al.* 2018), the cervical postzygapophyses of *Vectaeovenator* are in line relative to the prezygapophyses, a keel is absent on the anterior cervical vertebra, and the anterior articular facet of the anterior cervical vertebra is horizontally ovate rather than rounded or high-oval in shape. In addition, the cervical is not strongly opisthocoelous as in most sauropods (Upchurch 1995), the cervical pneumatic foramina are undivided, unlike most neosauropods (Upchurch 1995; Whitlock 2011), and the cervical rib is elongate and most probably overlapped the posterior centrum in life, unlike the short non-overlapping ribs of diplodocoid neosauropods (Whitlock 2011).

Theropod traits are also evident in the caudal vertebra of *Vectaeovenator*: it has dorsoventrally compressed transverse processes elevated above the dorsal margin of the centrum and weakly developed laminae (Brougham *et al.* 2019). Furthermore, while synapomorphic ornithopodan characters are typically restricted to cranial and appendicular elements, the caudal vertebra retains its transverse processes and lacks the hexagonal or octagonal cross-section present in iguanodontians (Norman 2004; Verdú *et al.* 2019), further supporting the element’s theropodan affinities.

Comparative anatomy

Within Theropoda, *Vectaeovenator* possesses traits indicative of averostran and tetanuran affinities: the opisthocoely (albeit subtle) of its cervical centrum is consistent with this, as are its bilateral cervical pneumatic foramina located within fossae (Rauhut 2003; Benson *et al.* 2012; Cau 2018). Dorsoventral compression of the anterior cervicals has also been recovered as a tetanuran synapomorphy (Cau 2018), and the non-fusion of the

cervical rib to its vertebra and lack of an elongate anterolateral process also support this placement (Poropat *et al.* 2019). However, *Vectaerovenator* is unusual with respect to two proposed tetanuran synapomorphies: the width between the prezygapophyses is subequal to that of the neural canal (i.e. the median margins of the prezygapophyses are not strongly laterally displaced relative to the neural canal), and the ventral narrowing of the anterior dorsals is not quite as pronounced and fails to produce a sharp keel (Rauhut 2003; Carrano *et al.* 2012).

Nevertheless, in certain analyses, cervical opisthocoely is characteristic of Neotetanurae in particular (Cau 2018), and is notably pronounced in megalosauroids and allosauroids (Evers *et al.* 2015); although the one sufficiently complete cervical of *Vectaerovenator* is opisthocoelous, the condition is weak and about comparable to that present in such tetanurans as *Monolophosaurus* (Zhao *et al.* 2009), *Sinraptor* (Currie & Zhao 1993), *Piatnitzkysaurus*, such tyrannosauroids as *Dilong* (Rauhut 2003) and basal carcharodontosaurians such as *Siamraptor* (Chokchaloemwong *et al.* 2019) and *Concavenator* (the latter reflecting the basal condition within allosauroids; Cuesta *et al.* 2019). *Vectaerovenator* lacks a conspicuous rim around the anterior articular facet (a probable synapomorphy of Megalosauroidea; Dai *et al.* 2020; Evers *et al.* 2015) but does possess enlarged pneumatic foramina in the anteriormost dorsals, a character considered synapomorphic of the megalosauroid clade Megalosauria (*sensu* Carrano *et al.* 2012).

The cervical prezygapophyses of *Vectaerovenator* are not flexed, as in most coelurosaurians (Gauthier 1986). However, the cervical does possess a synapomorphy of coelurosaurian clade Tyrannoraptora: the centrum does not extend beyond the neural arch (Cau 2018). The presence of a prezygoepipophyseal lamina in the cervical vertebra (effectively separating the lateral and dorsal surfaces of the neural arch) has been recovered as an allosauroid synapomorphy in some analyses (Chokchaloemwong *et al.* 2019), although it is also present (and developed more prominently) in abelisauroids and megaraptorans (Calvo *et al.* 2004; Carrano & Sampson 2008) as well as in some megalosauroids (Rauhut *et al.* 2012). In addition, the offset between the articular surfaces in *Vectaerovenator* is minimal and similar to that present in the mid cervicals of carcharodontosaurids (Calvo *et al.* 2004; Chokchaloemwong *et al.* 2019). However, the cervical parapophyses are not located at the midlength of the centrum, as they are in carcharodontosaurids and *Megaraptor* (Calvo *et al.* 2004).

The postzygodiapophyseal lamina of *Vectaerovenator* is subvertically oriented as it is in carcharodontosaurians (Chokchaloemwong *et al.* 2019) and megaraptorans (Calvo *et al.* 2004). Posteriorly, the cervical possesses a hypophyse-like structure: the presence of this structure

anterior to the dorsal vertebrae is rare in saurischians but is present, however, in carcharodontosaurians (Chokchaloemwong *et al.* 2019), megaraptorans (Smith *et al.* 2008) and tyrannosaurids (Novas *et al.* 2013). In addition, the cervical epipophyses of *Vectaerovenator* appear to point posterodorsally, as they do in carcharodontosaurids (Novas 2009). Long epipophyses have been proposed as a carcharodontosaurid synapomorphy, although in some analyses they are also present in ceratosaurs and metriacanthosaurids (Cuesta *et al.* 2019).

Postaxial cervical (and anterior dorsal, see below) pneumaticity is typical for non-avian theropods (Benson *et al.* 2012), and most tetanurans present with single bilateral pneumatic foramina in the centrum; carcharodontosaurids (Sereno 1991; Chokchaloemwong *et al.* 2019; Cuesta *et al.* 2019) and megaraptorids (Novas *et al.* 2013; Porfiri *et al.* 2018; Aranciaga Rolando *et al.* 2019) are unusual in that these pneumatic foramina are bisected by lamina. Cervical rib pneumaticity is present in a range of non-avian theropods, including *Majungasaurus* (O'Connor 2006; where it is extensive), *Tyrannosaurus* (Brochu 2003) and *Aerosteon* (Sereno *et al.* 2008). It is thus not indicative of affinity with any particular clade. Nevertheless, the development and organization of pneumaticity in theropod vertebrae may vary within an individual or element, potentially reducing their use as indicators of phylogenetic position (O'Connor 2006; Brougham *et al.* 2019). The known cervical and dorsal vertebrae of *Vectaerovenator* are camerate, as they are in *Piatnitzkysaurus*, *Allosaurus*, *Torvosaurus*, sinraptorids, dromaeosaurids (Rauhut 2003) and the carcharodontosaurian *Siamraptor* (Chokchaloemwong *et al.* 2019). This is unlike the camellate condition of most carcharodontosaurians (Benson *et al.* 2010) and megaraptorans (Benson *et al.* 2012), although the camerate/camellate internal structure can vary within a single vertebra of members of the latter clade, as it does in *Megaraptor* (Porfiri *et al.* 2014).

The dorsal vertebrae of *Vectaerovenator* recall those of *Lajasvenator* in that the incipiently convex dorsal part of the anterior articular surface is just visible in lateral view (Coria *et al.* 2019). As mentioned above, the large foramina are similar to the condition present in various megalosaurians such as *Eustreptospondylus* (Sadleir *et al.* 2008; Carrano *et al.* 2012), although they are more centrally placed in the latter than they are in *Vectaerovenator*. However, the parapophyses on the more posterior dorsal of *Vectaerovenator* are large, as is the case in allosauroids and *Aerosteon* (Carrano *et al.* 2012). Further, the parapophyses project only slightly laterally, as they do in allosauroids (Carrano & Sampson 2008). The conspicuous fossa ventral to the parapophyses is of note, and a similarly placed fossa is present in the megalosauroid *Yunyan-gosaurus* (Dai *et al.* 2020).

The pair of conspicuous, laterally placed fossae on the pedicels of the postzygapophyses are also noteworthy in the caudal element, and similar structures have been noted in the anterior caudals of some megalosauroids (Rauhut *et al.* 2018). Similarly placed small depressions are also noted in the holotype mid caudal vertebra of the carcharodontosaurid *Veterupristisaurus* (Rauhut 2011); however, their relatively larger size and associated laminae in *Vectaeorvenator* may be diagnostic.

PHYLOGENETIC ANALYSIS

Vectaeorvenator was added to a comprehensive dataset of pan-avian taxa (Cau 2018). The final matrix included 1781 characters and 133 operational taxonomic units (OTUs; Barker *et al.* 2020). All characters were treated as unordered. The analysis was performed in TNT 1.5 (Goloboff & Catalano 2016). A driven search using the New Technology Search function was undertaken, with default settings for ratchet, sectorial and tree fusion, which stabilized consensus twice with a factor of 25. This retained 98 trees, with a tree length of 6797 steps, a consistency index (CI) of 0.244, and a retention index (RI) of 0.563. These trees were then subjected to tree bisection and reconnection (TBR) branch swapping using the Traditional Search function in order to explore the tree islands recovered in the former search, recovering 10 920 trees. Strict consensus recovered *Vectaeorvenator* as the sister taxon to Megaraptora + *Gualicho*, nested within Tyrannosauroidae. As a measure of absolute tree support, Bremer (decay indices) were calculated using the Bremer Supports function, using the ‘TBR from existing trees’ option and retaining trees suboptimal by 10 steps. While *Vectaeorvenator*’s phylogenetic position appears relatively well-resolved, the Bremer support values of 1 across most nodes indicated low support for this result (Fig. 8). Several constrained analyses were undertaken to assess the number of steps required to place *Vectaeorvenator* in alternative positions within basal tetanurans. Using the command ‘force = (taxon a taxon b ... taxon n)’, only two extra steps were required to place *Vectaeorvenator* as a megalosauroid, and three additional steps were required to recover it as an allosauroid.

Comments on the phylogenetic position of Vectaeorvenator

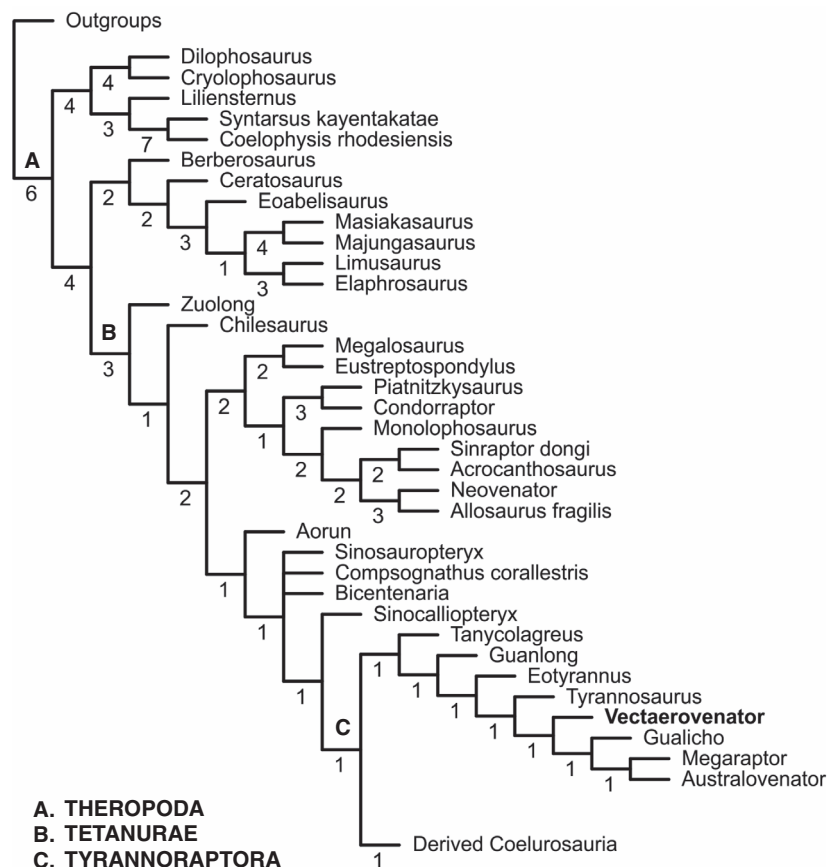
The recovery of *Vectaeorvenator* as a tyrannoraptoran (*sensu* Cau 2018), and more specifically as a tyrannosauroid, is perhaps unexpected given that the axial elements resemble those of allosauroids and megalosauroids in some respects. Nevertheless, as previously stated, *Vectaeorvenator* does possess a tyrannoraptoran axial synapomorphy (*sensu* Cau 2018; the centrum does not extend

beyond the neural arch), and its similarities with more basal tetanurans could be the result of homoplasy. Placement of *Vectaeorvenator* on a tyrannosauroid branch leading to Megaraptora is potentially significant given that the latter clade has yet to be recovered in Europe despite their wide temporal and geographical distribution (Aranciaga Rolando *et al.* 2019; White *et al.* 2020). Porfiri *et al.* (2014) found *Eotyrannus* from the Isle of Wight to be a megaraptoran, but examination of the character codings that support this phylogenetic position shows them to be erroneous (DN & A. Cau, unpub. data). Megaraptorans are known to exhibit homoplasy with allosauroids, and their position within Coelurosauria has been supported and refined in recent phylogenetic analyses. Originally described as unusual allosauroids (Benson *et al.* 2010), Megaraptora has since been recovered as an early diverging lineage within Coelurosauria, lacking close ties to any other recognized coelurosaurian lineage (Novas *et al.* 2013; Porfiri *et al.* 2014), or as nested within Tyrannosauroidae (Aranciaga Rolando *et al.* 2019), occasionally positioned as the sister group to tyrannosaurids (Novas *et al.* 2013; Porfiri *et al.* 2014). Our tree topography closely follows that recovered by Cau’s (2018) original analysis, in that Megaraptora is nested within Tyrannosauroidae.

However, the three synapomorphies supporting *Vectaeorvenator*’s association with the clade Megaraptora + *Gualicho* possess a broad distribution throughout Theropoda. These include the presence of a prezygoepipophyseal lamina (character (char.) 209), which as previously stated is present in several tetanuran and ceratosaur clades; the possession of a ‘peduncular fossa’ lateral to the neural canal in presacral vertebrae (char. 668), which is also found in abelisaurids such as *Majungasaurus* (O’Connor 2007) and tetanurans such as *Monolophosaurus* (Zhao *et al.* 2009); and a subvertical cervical postzygodiapophyseal lamina (char. 1591), which, as discussed above, is also noted in carcharodontosaurians. Further, *Vectaeorvenator* cannot be allocated to Megaraptora. This is due to the incomplete nature of the *Vectaeorvenator* holotype, the few axial synapomorphies recovered for megaraptorans (Aranciaga Rolando *et al.* 2019 reported no axial synapomorphies for this clade, for instance), and the fact that the relevant characters are present not only in megaraptorans but also in carcharodontosaurids and non-megaraptoran tyrannosauroids (Novas *et al.* 2013). Furthermore, our phylogenetic analysis locates *Vectaeorvenator* in an earlier branching position than *Gualicho* (the latter occupying the same position as in Cau’s 2018 original phylogeny), a taxon often considered a basal coelurosaur (Apesteguía *et al.* 2016; Aranciaga Rolando *et al.* 2019).

In summary, the low Bremer supports, combined with the low CI (and thus high number of homoplastic

FIG. 8. Strict consensus tree based on the data matrix of Cau (2018). Numbers below the nodes indicate Bremer support values; letters above nodes indicate clade names. See text regarding the context of this result, which reflects the fragmentary nature of the material, the low Bremer support and the low consistency index.



characters within the dataset) and few additional steps required to recover *Vectaerovenator* among other basal tetanuran clades suggest that this taxon's position within Tetanurae remains highly uncertain, and as such we find it is more parsimonious to currently identify it as *Tetanurae incertae sedis*. Our understanding of this dinosaur would thus benefit greatly from the recovery of further material.

CONCLUSIONS

Vectaerovenator inopinatus gen. et sp. nov. is a highly pneumatic, mid-sized theropod, its autapomorphies mostly concerning the distribution of pneumatic features on the centra and neural arches of the cervical and dorsal vertebrae. *Vectaerovenator* recalls several basal tetanuran clades in overall anatomy, but our inclusion of this new taxon in a phylogenetic analysis supports a position within Tyrannosauroida. Nevertheless, as detailed above, we find it more parsimonious to diagnose this theropod as an indeterminate tetanuran given the fragmentary nature of the holotype, the low support for the phylogenetic result, the numerous homoplastic traits and the few extra steps required to recover

Vectaerovenator among megalosauroids or allosauroids, respectively.

The recognition of a new tetanuran theropod from the English middle Cretaceous (specifically, a late Aptian upper 'member' of the Ferruginous Sands Formation of the Lower Greensand Group of the Isle of Wight) is significant in enhancing our knowledge of the diversity of European dinosaurs of this age. As a Lower Greensand dinosaur, *Vectaerovenator* is locally important in being the youngest diagnosable non-avian theropod yet reported from the British fossil record (some indeterminate theropod teeth are of similar age, while fragmentary postcranial material from the Cenomanian Cambridge Greensand, reported by Galton & Martin 2002 as perhaps belonging to a small non-avian theropod, is younger). Furthermore, *Vectaerovenator* is the first European theropod from the Aptian to be considered diagnostic and worthy of a taxonomic name.

Acknowledgements. We thank Martin Munt and Alex Peaker (both Dinosaur Isle Museum, Sandown, Isle of Wight) for access to the material and for help and guidance regarding the geology of the Lower Greensand; Gary Blackwell (Dinosaur Isle Museum) for his excellent preparatory work on these delicate specimens; Martin Simpson for his help identifying the geological provenance of the

material; Mark Chapman, Steve Vidovic (both University of Southampton) and Tom Smith (University of Bristol) for their advice with the phylogenetic analyses; and Dom Barker and Luis Coy (both University of Southampton) for their help with specimen photography. We would also like to thank Phillip Mannion and Sally Thomas, and reviewers Andrea Cau and Fernando Novas for their input and detailed insights during the review process that substantially improved the manuscript. The program TNT is made available thanks to the Willi Hennig Society. This study was supported by the Engineering and Physical Sciences Research Council (EPSRC), UK and the Institute for Life Sciences, University of Southampton, UK.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: <http://zoobank.org/References/7C7C4F6C-BC1D-42B5-8EBA-5D59C726EC1D>.

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8cz8w9gmj>.

Editor. Philip Mannion

REFERENCES

- APESTEGUÍA, S., SMITH, N. D., VALIERI, R. J. and MAKOVICKY, P. J. 2016. An unusual new theropod with a didactyl manus from the Upper Cretaceous of Patagonia, Argentina. *PLoS One*, **11**, e0157793.
- ARANCIAGA ROLANDO, A. M., NOVAS, F. E. and AGNOLÍN, F. L. 2019. A reanalysis of *Murusraptor barrosaensis* Coria & Currie (2016) affords new evidence about the phylogenetical relationships of Megaraptora. *Cretaceous Research*, **99**, 104–127.
- BARKER, C. T., NAISH, D., CLARKIN, C. E., FARRELL, P., HULLMANN, G., LOCKYER, J., SCHNEIDER, P., WARD, R. K. C. and GOSTLING, N. J. 2020. Data from: A highly pneumatic middle Cretaceous theropod from the British Lower Greensand. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.8cz8w9gmj>
- BARRETT, P., BENSON, R. and UPCHURCH, P. 2010. Dinosaurs of Dorset: Part II, the sauropod dinosaurs (Sauropsida, Sauropoda) with additional comments on the theropods. *Proceedings of the Dorset Natural History & Archaeological Society*, **131**, 113–126.
- BARTHOLOMAI, A. and MOLNAR, R. E. 1981. *Muttaborasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum*, **20**, 319–349.
- BENSON, R. B., BRUSATTE, S. L., HUTT, S. and NAISH, D. 2009. A new large basal tetanuran (Dinosauria: Theropoda) from the Wessex Formation (Barremian) of the Isle of Wight, England. *Journal of Vertebrate Paleontology*, **29**, 612–615.
- CARRANO, M. T. and BRUSATTE, S. L. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften*, **97**, 71.
- BENSON, R. B. J., RICH, T. H., VICKERS-RICH, P. and HALL, M. 2012. Theropod fauna from Southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS One*, **7**, e37122.
- BENTON, M., MARTILL, D. and TAYLOR, M. 1995. The first Lower Jurassic dinosaur from Scotland: limb bone of a ceratosaur theropod from Skye. *Scottish Journal of Geology*, **31**, 177–182.
- BLOWS, W. T. 1995. The Early Cretaceous brachiosaurid dinosaurs *Ornithopsis* and *Eucamerotus* from the Isle of Wight, England. *Palaeontology*, **38**, 187–198.
- 1998. A review of Lower and Middle Cretaceous dinosaurs of England. *New Mexico Museum of Natural History & Science Bulletin*, **14**, 29–38.
- BROCHU, C. A. 1996. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, **16**, 49–62.
- 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, **22**, 1–138.
- BROUGHAM, T., SMITH, E. T. and BELL, P. R. 2019. New theropod (Tetanurae: Avetheropoda) material from the ‘mid’-Cretaceous Griman Greek Formation at Lightning Ridge, New South Wales, Australia. *Royal Society Open Science*, **6**, 180826.
- BROWN, C. M., HENDERSON, D. M., VINTHER, J., FLETCHER, I., SISTIAGA, A., HERRERA, J. and SUMMONS, R. E. 2017. An exceptionally preserved three-dimensional armored dinosaur reveals insights into coloration and Cretaceous predator-prey dynamics. *Current Biology*, **27**, 2514–2521.e3.
- BRUSATTE, S. L., BENSON, R. B. J. and HUTT, S. 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Monograph of the Palaeontographical Society*, **162**, 1–166.
- BUFFETAUT, E. and NORI, L. 2012. Dinosaur remains from the “Sables Verts” (Early Cretaceous, Albien) of the eastern Paris Basin. 363–378. In GODEFROIT, P. (ed.) *Bernisart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press.
- BUTLER, R. J. and BARRETT, P. M. 2008. Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. *Naturwissenschaften*, **95**, 1027–1032.
- CALVO, J. O., PORFIRI, J. D., VERALLI, C., NOVAS, F. and POBLETE, F. 2004. Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana*, **41**, 565–575.
- CARRANO, M. T. and SAMPSON, S. D. 2008. The phylogeny of ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **6**, 183–236.
- BENSON, R. B. J. and SAMPSON, S. D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **10**, 211–300.

- CAU, A. 2018. The assembly of the avian body plan: a 160-million-year long process. *Bollettino Della Società Paleontologica Italiana*, **57**, 2.
- CHARIG, A. J. and MILNER, A. C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin Natural History Museum Geology Series*, **53**, 11–70.
- CHOKCHALOEMWONG, D., HATTORI, S., CUESTA, E., JINTASAKUL, P., SHIBATA, M. and AZUMA, Y. 2019. A new carcharodontosaurian theropod (Dinosauria: Saurischia) from the Lower Cretaceous of Thailand. *PLoS One*, **14**, e0222489.
- CORIA, R. A. and CURRIE, P. J. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, **28**, 71–118.
- ORTEGA, F. and BAIANO, M. A. 2019. An Early Cretaceous, medium-sized carcharodontosaurid theropod (Dinosauria, Saurischia) from the Mulichinco Formation (upper Valanginian), Neuquén Province, Patagonia, Argentina. *Cretaceous Research*, **111**, 104319.
- CUESTA, E., ORTEGA, F. and SANZ, J. L. 2019. Axial osteology of *Concavenator corcovatus* (Theropoda; Carcharodontosauria) from the Lower Cretaceous of Spain. *Cretaceous Research*, **95**, 106–120.
- CURRIE, P. J. and DONG, Z. 2001. New information on *Shanshanosaurus huoyanshanensis*, a juvenile tyrannosaurid (Theropoda, Dinosauria) from the Late Cretaceous of China. *Canadian Journal of Earth Sciences*, **38**, 1729–1737.
- and ZHAO, X.-J. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**, 2037–2081.
- DAI, H., BENSON, R., HU, X., MA, Q., TAN, C., LI, N., XIAO, M., HU, H., ZHOU, Y. and WEI, Z. 2020. A new possible megalosauroid theropod from the Middle Jurassic Xintiangou Formation of Chongqing, People's Republic of China and its implication for early tetanuran evolution. *Scientific Reports*, **10**, 1–16.
- EVERS, S. W., RAUHUT, O. W., MILNER, A. C., McFeters, B. and ALLAIN, R. 2015. A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the “middle” Cretaceous of Morocco. *PeerJ*, **3**, e1323.
- FARKE, A. A. and PHILLIPS, G. E. 2017. The first reported ceratopsid dinosaur from eastern North America (Owl Creek Formation, Upper Cretaceous, Mississippi, USA). *PeerJ*, **5**, e3342.
- GALE, A. 2019. *The Isle of Wight*. New edn. Geologists' Association, **60**.
- GALTON, P. M. and MARTIN, L. D. 2002. Postcranial anatomy and systematics of *Enaliornis* Seeley, 1876, a foot-propelled diving bird (Aves: Ornithurae: Hesperornithiformes) from the Early Cretaceous of England. *Revue de Paléobiologie*, **21**, 489–538.
- GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, **8**, 1–55.
- GOLOBOFF, P. A. and CATALANO, S. A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**, 221–238.
- HARRIS, J. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History & Science Bulletin*, **13**, 1–75.
- HOLTZ, T. R. Jr 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia*, **15**, 5–61.
- HOPSON, P. 2011. The geological history of the Isle of Wight: an overview of the ‘diamond in Britain’s geological crown’. *Proceedings of the Geologists’ Association*, **122**, 745–763.
- WILKINSON, I. and WOODS, M. 2008. *A stratigraphical framework for the Lower Cretaceous of England*. British Geological Survey.
- HORNER, J. R. 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-central Montana with a checklist of Upper Cretaceous dinosaur remains from marine sediments in North America. *Journal of Paleontology*, 566–577.
- HUTT, S., NAISH, D., MARTILL, D. M., BARKER, M. J. and NEWBERRY, P. 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research*, **22**, 227–242.
- INSOLE, A., DALEY, B. and GALE, A. 1998. *The Isle of Wight*. Geologists’ Association Guide, **60**.
- KRUMENACKER, L., SIMON, D. J., SCOFIELD, G. and VARRICCHIO, D. J. 2017. Theropod dinosaurs from the Albian–Cenomanian Wayan Formation of eastern Idaho. *Historical Biology*, **29**, 170–186.
- LOMAX, D. R. and TAMURA, N. 2014. *Dinosaurs of the British Isles*. Siri Scientific Press, Manchester.
- LONGRICH, N. R., PEREDA-SUBERBIOLA, X., JALIL, N.-E., KHALDOUNE, F. and JOURANI, E. 2017. An abelisaurid from the latest Cretaceous (late Maastrichtian) of Morocco, North Africa. *Cretaceous Research*, **76**, 40–52.
- MADSEN, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin*, **109**, 1–161.
- MARSH, O. C. 1881. Principal characters of American Jurassic dinosaurs, part V. *American Journal of Science*, 417–423.
- MARTILL, D. M. and NAISH, D. 2001. *Dinosaurs of the Isle of Wight*. Field Guides to Fossils, **10**. The Palaeontological Association.
- BATTEN, D. J. and LOYDELL, D. K. 2000. A new specimen of the thyreophoran dinosaur cf. *Scelidosaurus* with soft tissue preservation. *Palaeontology*, **43**, 549–559.
- NAISH, D. and EARLAND, S. 2006. Dinosaurs in marine strata: evidence from the British Jurassic, including a review of the allochthonous vertebrate assemblage from the marine Kimmeridge Clay Formation (Upper Jurassic) of Great Britain. *Actas de las III Jornadas Sobre Dinosaurios y su Entorno. Salas de los Infantes, Burgos*, **47**, 83.
- NAISH, D. 2011. Theropod dinosaurs. 526–559. In BATTEN, D. J. (ed.) *English Wealden fossils*. Field Guides to Fossils, **14**. The Palaeontological Association.
- and MARTILL, D. M. 2007. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: basal Dinosauria and Saurischia. *Journal of the Geological Society*, **164**, 493–510.
- — 2008. Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: Ornithischia. *Journal of the Geological Society*, **165**, 613–623.

- and SWEETMAN, S. C. 2011. A tiny maniraptoran dinosaur in the Lower Cretaceous Hastings Group: evidence from a new vertebrate-bearing locality in south-east England. *Cretaceous Research*, **32**, 464–471.
- HUTT, S. and MARTILL, D. M. 2001. Saurischian dinosaurs 2: Theropods. 242–309. In MARTILL, D. M. and NAISH, D. (eds) *Dinosaurs of the Isle of Wight*. Field Guides to Fossils, **10**. The Palaeontological Association.
- NICHOLL, C. S. C., MANNION, P. D. and BARRETT, P. M. 2018. Sauropod dinosaur remains from a new Early Jurassic locality in the Central High Atlas of Morocco. *Acta Palaeontologica Polonica*, **63**, 147–157.
- NORMAN, D. B. 2004. Basal iguanodontia. 413–437. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds) *The Dinosauria*. University of California Press.
- NOVAS, F. E. 2009. *The age of dinosaurs in South America*. Indiana University Press.
- AGNOLÍN, F. L., EZCURRA, M. D., PORFIRI, J. and CANALE, J. I. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. *Cretaceous Research*, **45**, 174–215.
- O'CONNOR, P. M. 2006. Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *Journal of Morphology*, **267**, 1199–1226.
- 2007. The postcranial axial skeleton of *Majungasaurus creatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, **27**, 127–163.
- OWEN, R. 1842. *Report on British fossil reptiles. Part II*. R. & J. E. Taylor, London.
- PASCH, A. D. and MAY, K. C. 1997. First occurrence of a hadrosaur (Dinosauria) from the Matanuska Formation (Turonian) in the Talkeetna Mountains of south-central Alaska. *Short Notes on Alaska Geology*, **1997**, 99–109.
- PEREDA-SUBERBIOLA, X., RUIZ-OMENACA, J. I., CANUDO, J. I., TORCIDA, F. and SANZ, J. L. 2012. Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. 379–408. In GODEFROIT, P. (ed.) *Bernisart dinosaurs and Early Cretaceous terrestrial ecosystems*. Indiana University Press.
- PÉREZ-GARCÍA, A., CORRAL, J. C., MURELAGA, X., MARTIN, G., LARRANAGA, J., BARDET, N., and BERRETEAGA, A. 2015. First dinosaur and turtle remains from the latest Cretaceous shallow marine deposits of Albaina (Lano quarry, Iberian Peninsula). *Comptes Rendus Palevol*, **14**, 471–482.
- PORFIRI, J. D., NOVAS, F. E., CALVO, J. O., AGNOLÍN, F. L., EZCURRA, M. D. and CERDA, I. A. 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Research*, **51**, 35–55.
- VALIERI, R. D. J., SANTOS, D. D. and LAMANNA, M. C. 2018. A new megaraptoran theropod dinosaur from the Upper Cretaceous Bajo de la Carpa Formation of northwestern Patagonia. *Cretaceous Research*, **89**, 302–319.
- POROPAT, S. F., WHITE, M. A., VICKERS-RICH, P. and RICH, T. H. 2019. New megaraptorid (Dinosauria: Theropoda) remains from the Lower Cretaceous Eumeralla Formation of Cape Otway, Victoria, Australia. *Journal of Vertebrate Paleontology*, **39**, e1666273.
- RAUHUT, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, **69**, 1–213.
- 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology*, **86**, 195–239.
- FOTH, C., TISCHLINGER, H. and NORELL, M. A. 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences*, **109**, 11746–11751.
- PIÑUELA, L., CASTANERA, D., GARCÍA-RAMOS, J.-C. and SÁNCHEZ CELA, I. 2018. The largest European theropod dinosaurs: remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain. *PeerJ*, **6**, e4963.
- RAWSON, P. F. 2006. Cretaceous: sea levels peak as the North Atlantic opens. 365–393. In BRENCHLEY, P. J. and RAWSON, P. F. (eds) *The geology of England and Wales*. 2nd edn. The Geological Society, London.
- RUFFELL, A. H., HESSELBO, S. P., WACH, G. D., SIMPSON, M. I. and WRAY, D. S. 2002. Fuller's earth (bentonite) in the Lower Cretaceous (Upper Aptian) of Shanklin (Isle of Wight, southern England). *Proceedings of the Geologists Association*, **113**, 281–290.
- RUSSELL, D. A. 1972. Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences*, **9**, 375–402.
- SADLER, R. W., BARRETT, P. and POWELL, H. P. 2008. *The anatomy and systematics of Eustreptospondylus oxoniensis, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England*. Monograph of the Palaeontographical Society, **160** (627).
- SERENO, P. C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology*, **11**, 1–53.
- MARTINEZ, R. N., WILSON, J. A., VARRICCHIO, D. J., ALCOBER, O. A. and LARSSON, H. C. E. 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS One*, **3**, e3303.
- SMITH, N. D., MAKOVICKY, P. J., AGNOLIN, F. L., EZCURRA, M. D., PAIS, D. F. and SALISBURY, S. W. 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society B*, **275**, 2085–2093.
- SWEETMAN, S. C. 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. *Cretaceous Research*, **25**, 353–364.
- and INSOLE, A. N. 2010. The plant debris beds of the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England: their genesis and palaeontological significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **292**, 409–424.
- UPCHURCH, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society B*, **349**, 365–390.

- VERDÚ, F. J., COBOS, A., ROYO-TORRES, R. and ALCALÁ, L. 2019. Diversity of large ornithomimid dinosaurs in the upper Hauterivian-lower Barremian (Lower Cretaceous) of Teruel (Spain): a morphometric approach. *Spanish Journal of Palaeontology*, **34**, 269–288.
- WHITE, O. 1921. A short account of the geology of the Isle of Wight. *Memoirs of the Geological Survey of Great Britain*.
- WHITE, M. A., BELL, P. R., POROPAT, S. F., PENTLAND, A. H., RIGBY, S. L., COOK, A. G., SLOAN, T. and ELLIOTT, D. A. 2020. New theropod remains and implications for megaraptorid diversity in the Winton Formation (lower Upper Cretaceous), Queensland, Australia. *Royal Society Open Science*, **7**, 191462.
- WHITLOCK, J. A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society*, **161**, 872–915.
- WILSON, J. A. and UPCHURCH, P. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria-Sauropoda), the first dinosaur genus with a ‘Gondwanan’ distribution. *Journal of Systematic Palaeontology*, **1**, 125–160.
- MICHAEL, D., IKEJIRI, T., MOACDIEH, E. M. and WHITLOCK, J. A. 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS One*, **6**, e17114.
- YOUNG, M. T., STEEL, L., FOFFA, D., PRICE, T., NAISH, D. and TENNANT, J. P. 2014. Marine tethysuchian crocodyliform from the ?Aptian-Albian (Lower Cretaceous) of the Isle of Wight, UK. *Biological Journal of the Linnean Society*, **113**, 854–871.
- ZHAO, X.-J., BENSON, R. B., BRUSATTE, S. L. and CURRIE, P. J. 2009. The postcranial skeleton of *Monolophosaurus jiangi* (Dinosauria: Theropoda) from the Middle Jurassic of Xinjiang, China, and a review of Middle Jurassic Chinese theropods. *Geological Magazine*, **147**, 13–27.