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A new large-bodied theropod dinosaur from the Middle Jurassic of Warwickshire, United Kingdom

ROGER B.J. BENSON and JONATHAN D. RADLEY



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Previously undocumented postcranial material from the Chipping Norton Limestone Formation (Middle Jurassic: Lower Bathonian) of Cross Hands Quarry, near Little Compton, Warwickshire represents a new large-bodied theropod dinosaur, distinct from the contemporaneous *Megalosaurus bucklandii*. *Cruxicheiros newmanorum* gen. et sp. nov. is diagnosed by a single autapomorphy, the presence of a proximomedially inclined ridge within the groove that marks the lateral extent of the posterior flange of the femoral caput (trochanteric fossa). *C. newmanorum* shows three tetanuran features: widely separated cervical zygapophyses, a swollen ridge on the lateral surface of the iliac blade and an anterior spur of the caudal neural spines. However, due to fragmentary preservation its affinities within Tetanurae remain uncertain: phylogenetic analysis places it as the most basal tetanuran, the most basal megalosauroid (= spinosauroid) or the most basal neotetanuran.

Key words: Dinosauria, Theropoda, Tetanurae, *Megalosaurus*, *Cruxicheiros*, Bathonian, Chipping Norton Limestone Formation, England.

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Introduction

The recognition of dinosaur fossils as the remains of gigantic fossil reptiles was based on theropod bones from the shallow- to marginal-marine Middle Jurassic Bathonian Stage of the United Kingdom (Parkinson 1822; Buckland 1824). Prior to this, theropod and other dinosaur material was recovered from these strata but remained unrecognised (Plot 1677: pl. 8: 4; Lluyd 1699: pl. 16: 1328; Woodward 1728; Brookes 1763: vol. 5, fig. 317; Delair and Sarjeant 1975, 2002). Throughout a long history of collection, most theropod remains of this provenance have been referred uncritically to either *Megalosaurus* (large-bodied individuals, represented by the majority of specimens) or *Iliosuchus* (small-bodied individuals) (Owen 1842; Phillips 1871; von Huene 1926; Steel 1970; Benton and Spencer 1995).

However, recent work (Benson 2009, 2010) has clarified the status of the core of this material, mostly collected from the Taynton Limestone Formation (Middle Bathonian) of Stonesfield, Oxfordshire, the type locality of *Megalosaurus* and *Iliosuchus*. This work established that only one large-bodied theropod taxon was present in the most productive UK Bathonian localities: Stonesfield (above) and New Park Quarry (Chipping Norton Limestone Formation, Lower Bathonian), Gloucestershire (Benson 2009). This led to the identification of unique diagnostic features (autapomorphies) of *Megalosaurus* and the recognition of additional *Megalosaurus* remains in the Chipping Norton Limestone Formation (Lower Bathonian) of Oakham Quarry, Sarsgrove and Workhouse quarries, Oxfordshire (Benson 2010). We also now recognise that no material outside of the Lower–Middle Bathonian formations of the United Kingdom can currently be referred to *Megalosaurus*.

The present contribution documents a collection of theropod remains from the Chipping Norton Limestone Formation (Lower Bathonian) of Cross Hands Quarry near Little Compton, Warwickshire, UK that can be referred to a new taxon of large-bodied theropod dinosaur. The stratigraphy and palaeontology of this site, part of which is preserved as a Site of Special Scientific Interest (protected status awarded by the UK government), was recently documented by Sumbler (2002). The theropod material was previously reported by Sumbler (2002) but until now had not been studied in any detail.

The Middle Jurassic saw the early history of Tetanurae, a taxonomically and ecologically diverse theropod clade (Holtz et al. 2004). Unfortunately however, Middle Jurassic dinosaur faunas are still poorly understood. Middle Jurassic theropod fossils are rare and determinate remains have only been reported from Europe, Argentina and China (Weishampel et al. 2004). Most Middle Jurassic European theropod taxa are megalosaurids (sensu Benson 2010), although *Pro-*

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ceratosaurus (a tyrannosauroid coelurosaur; Rauhut and Milner 2008; Rauhut et al. 2010) and *Poekilopleuron* (a possible allosauroid; Benson 2010) are exceptions. Benson (2010) reported geographically localised distributions for Middle Jurassic theropod clades and new specimens can add detail to this biogeographic hypothesis. As such, the Cross Hands Quarry theropod remains represent an important data point for studies of dinosaur biogeography, phylogeny and faunal composition. The remains are also significant as they cast doubt on uncritical referrals of indeterminate theropod remains from the Bathonian of the United Kingdom to *Megalosaurus*, primarily abundant isolated teeth and bones (Benton and Spencer 1995).

Based on correspondence held at the Birmingham Museum and Art Gallery (BIRMG) and recollections of one of the present landowners (Mr. Stephen Newman) the new remains were collected from Cross Hands Quarry in the early 1960s. They were brought to the BIRMG for preparation and some formed part of a temporary display that was installed in the early 1990s. The material was recently (2008) transferred to the Warwickshire Museum Service (WARMS), prompting its study.

Institutional abbreviations.—BIRMG, Birmingham Museum and Art Gallery, Birmingham, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; UC OBA, Department of Organismal Biology, University of Chicago, Chicago, USA; WARMS, Warwickshire Museum Service, Warwick, UK.

Systematic palaeontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Tetanurae incertae sedis

Genus *Cruxicheiros* nov.

Type species: *Cruxicheiros newmanorum* gen. et sp. nov.

Etymology: From Latin *crux*, cross; and Greek *cheiros*, hand; intended as "cross hand", a version of the locality name.

Diagnosis.—As for the type and only species.

Cruxicheiros newmanorum sp. nov.

Figs. 1–3.

Etymology: After the Newman family, owners of Cross Hands Quarry, Warwickshire, United Kingdom.

Type material: Holotype: WARMS G15770, a partial right femur. Paratypes: WARMS G15771, additional theropod material from the type locality that probably represents the same individual as the holotype: an anterior dorsal or posterior cervical vertebra; a dorsal neural arch; a partial dorsal vertebra; the anterior half of a middle-distal caudal vertebra; a partial right scapulocoracoid; a partial left ilium; the proximal end of a left pubis; numerous rib and bone fragments.

Type locality: Chipping Norton Limestone Formation (Lower Bathonian *Zigzagiceras zigzag* Biozone; Torrens 1980) of Cross Hands Quarry (National Grid Reference [NGR] SP 269 291) near Little Compton, Warwickshire.

Type horizon: The Chipping Norton Limestone Formation of the Little Compton area is characterised by sandy ooidal and bioclastic limestones, yielding a marine bivalve fauna (Sellwood and McKerrow 1974; Sumbler 2002). Abundant terrestrial plant material (Sumbler 2002) indicates significant terrigenous input into a shallow marine environment and a potentially appropriate mechanism for derivation of the dinosaur remains.

Diagnosis.—Tetanuran theropod with autapomorphic proximomedially inclined ridge within the trochanteric fossa of the femur. Differs from the contemporaneous *Megalosaurus bucklandii* in posessing low proportions of the dorsal neural spines, transversely broader dorsal neural spines, a prominent posterior flange of the femoral caput and a lower ratio of anteroposterior length to mediolateral width of the pubic peduncle (1.60 in *Megalosaurus* and estimated between 1.00 and 1.10 in *C. newmanorum*). Few informative comparisons can be made between *C. newmanorum* and *Dubreuillosaurus* or *Poekilopleuron* from the lower Bathonian of France because of limited overlap between known material. However, *Dubreuillosaurus* shows two large internal chambers separated by a midline septum in pneumatic vertebrae and an unfused scapula and coracoid (perhaps due to immaturity of the holotype) (Allain 2005) whereas *C. newmanorum* vertebrae have more numerous internal pneumatic chambers and the scapulocoracoid suture is fused and swollen. *Poekilopleuron* also differs from *C. newmanorum* as it lacks prominent anterior spur on the caudal neural spines.

Remarks.—Collections records for the specimens are scant and there is no formal record of their association such as a quarry map. However, the relative sizes and the absence of repeated elements are consistent with the hypothesis that they represent a single individual. Additionally, the remains were collected over a short time period of one or maybe two field seasons (BIRMG, unpublished collections records), and all preserve an identical matrix of sandy bioclastic ooidal limestone as well as residual patches of re-deposited stalagmitic calcite. They therefore probably correspond to a point locality. Finally, diagnostic remains of large-bodied theropods other than *Megalosaurus* are rarely preserved in British Bathonian deposits (Benson 2010), but most of the Cross Hands Quarry specimens are demonstrably different from *Megalosaurus*. If the material does represent multiple individuals then it is very unlikely that it represents more than one of these rare non-*Megalosaurus* taxa.

The following specimens from Cross Hands Quarry are listed in the accessions register at BIRMG: metacarpal; coracoid; 3 ribs; fibula; vertebra; 2 vertebrae; left ilium, left femur fragment; lower femur fragment; and pubic bone fragment (BIRMG, unpublished collection records). The listed metacarpal and fibula are unaccounted for and may be lost or have originally been misidentified. Additionally, four vertebrae are present whereas only three were listed. This leaves the possibility that one of the vertebrae described here was not recovered from Cross Hands Quarry but as there is no way to identify which this is, they are all described.

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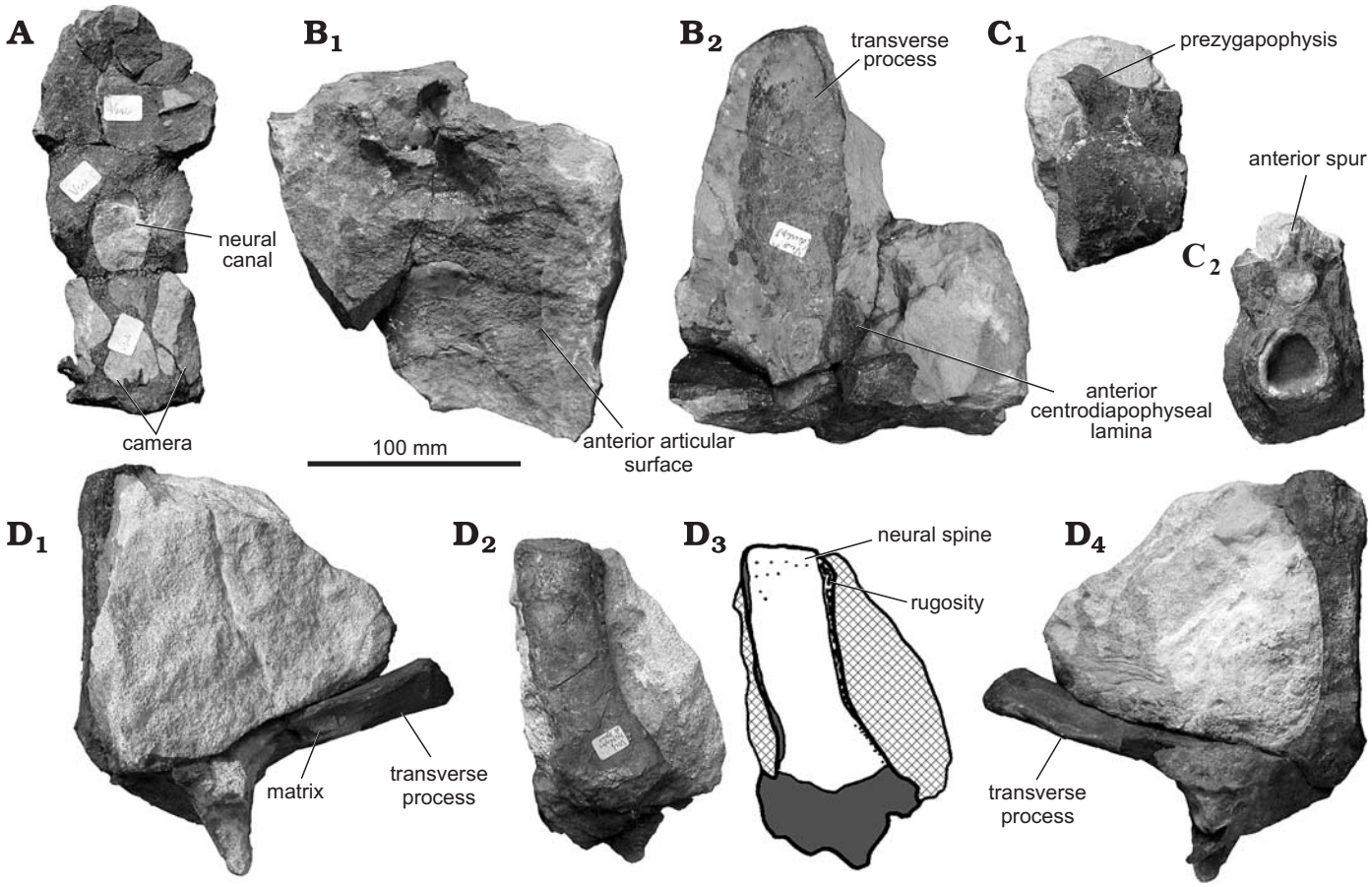


Fig. 1. Tetanuran theropod *Cruxicheiros newmanorum* gen. et sp. nov. axial vertebrae (WARMS 15771) from the Chipping Norton Limestone Formation, Bathonian of the United Kingdom. **A**. Posterior cervical or anterior dorsal vertebra in posterior view. **B**. Partial middle-posterior dorsal vertebra in right lateral view showing a sagittal cross-section (B_1) and in dorsal view (B_2). **C**. Middle-distal caudal vertebra in left lateral (C_1) and posterior (C_2) views. **D**. Middle-posterior dorsal neural arch in anterior (D_1), right lateral (D_2, D_3), and posterior (D_4) views. Photographs (A, B_1, B_2, C_1, C_2, D_1, D_2, D_4) and line drawing (D_3). Crossed-hatching indicates matrix and grey tone indicates broken bone.

An additional specimen, a fragmentary right tibia (OUMNH J.29831), was collected from Cross Hands Quarry by Mr. P. Stewart and donated to the OUMNH in 1980. This specimen is very poorly preserved and its affinities within Theropoda cannot be determined. It is not referred to *Cruxicheiros newmanorum* herein as the details of its collection, from where and which horizon in the quarry it was collected, cannot be established at present. The specimen should be considered as Theropoda indet.

Stratigraphic and geographic range.—Only known from a single locality in the Lower Bathonian of Warwickshire, United Kingdom.

Description

Vertebrae.—A fragmentary posterior cervical or anterior dorsal vertebra is preserved as a transverse slice from close to the posterior end of the bone (Fig. 1A). This reveals the neural canal and several large internal chambers (camerae) in the centrum. These camerae are probably pneumatic in origin, arising from invasion of the bone by pneumatic diverticulae via large pneumatic foramina ("pleurocoels") in the lateral surfaces of the centrum, as is common in theropods (Britt 1993). They are similar to the confirmed pneumatic camerae of *Sinraptor* (Britt 1993: fig. 21.1–3, 22.11) but are smaller and more numerous than those of megalosauroids (= spinosauroids) such as *Marshosaurus* (Britt 1993: fig 19.3–4) and *Torvosaurus* (Britt 1991, 1993), in which two large, main chambers are usually divided by a midline septum. Vertebrae with thin external walls and very large numbers of small internal chambers are termed "camellate". These are known in neoceratosaurs and carcharodontosaurian allosauroids among basal theropods (Britt 1993), which therefore differ markedly from *C. newmanorum*.

A dorsal centrum and transverse process (Fig. 1B) is mostly concealed by attached matrix. The centrum lacks internal pneumatic cavities, indicating that pneumatic foramina (= pleurocoels) were absent. A prominent anterior centrodiapophyseal lamina is visible. A dorsal neural spine and left transverse process (Fig. 1D) also have a large block of attached matrix in the space between them. The transverse process is oriented dorsolaterally, and the combined anterior and posterior centrodiapophyseal laminae form a stout longitudinal ridge along its ventral surface. Some matrix is still attached to the bone surface adjacent to this ridge anteriorly

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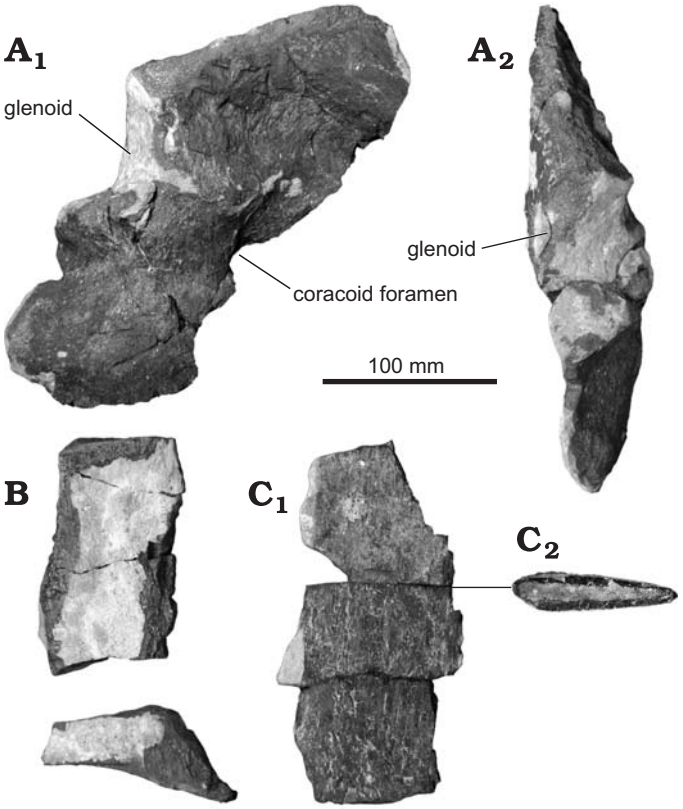


Fig. 2. Tetanuran theropod *Cruxicheiros newmanorum* gen. et sp. nov. right scapulocoracoid (WARMS 15771) from the Chipping Norton Limestone Formation, Bathonian of the United Kingdom. **A**. Scapulocoracoid in lateral (A_1) and ventral (A_2) views. **B**, **C**. Scapular fragments in medial or lateral views (B, C_1) and in cross-section (C_2).

and posteriorly, giving the impression (Fig. $1D_1$) that large foramina are present. However, they are absent. The neural spine is abraded posteriorly, but a thick, rugose, ligament ossification is present on the anterior surface, as in various basal tetanurans, including *Marshosaurus* (DMNH 3718) and the allosauroids *Aerosteon* (Sereno et al. 2008), *Allosaurus* (Madsen 1976), *Neovenator* (Brusatte et al. 2008) and *Tyrannosaurus* (Brochu 2002). Less prominent ligament ossifications are present in other large theropods such as *Torvosaurus* (Britt 1991). The distal end of the dorsal neural spine of WARMS G15771 is abraded but expands transversely (Fig. $1D_4$), indicating that the distal end is almost complete. In the British Jurassic theropods *Megalosaurus* (Benson 2010) and *Metriacanthosaurus* (OUMNH J.12144), and in *Ceratosaurus* (Madsen and Welles 2000) and *Sinraptor* (Currie and Zhao 1994), the neural spine is over 1.5 times the height of the centrum and substantially longer than the transverse processes. However, in *Cruxicheiros* the neural spine is approximately the same length as the transverse process, indicating relatively low proportions as in various other theropods including *Allosaurus* (Madsen 1976), *Marshosaurus* (DMNH 3718), *Torvosaurus* (Britt 1991) and *Piatnitzkysaurus* (Bonaparte 1986).

The anterior half of a middle-distal caudal vertebra (WARMS G15771) has a shallowly concave anterior articular surface and short prezygapophyses. A lump of limestone matrix adheres to the dorsal surface of the neural arch anteriorly. On the posterior surface of this lump, a section through the low anterior portion of the neural spine is preserved which indicates that an anterior spur of the neural spine was present. This feature is a tetanuran synapomorphy (Rauhut 2003).

Pectoral girdle.—A right scapulocoracoid fragment (Fig. 2A) preserves portions of the fused scapula and coracoid. The area of fusion is swollen and heavily ossified, as in *Megalosaurus* (Benson 2010), and the glenoid faces posterolaterally. The ventral margin of the coracoid foramen is preserved, forming a suboval opening on both the medial and lateral surfaces of the bone, as it does in most other theropods. The specimen is highly abraded and it is not possible to determine the morphology of the coracoid tubercle or posteroventral process, although this process is clearly present. Fragments of the scapula are also preserved (Fig. 2B). These are not adequate to assess the proportions of the blade. However, they do indicate that it was mediolaterally narrow with a cross-section that tapers dorsally and ventrally (Fig. $2C_2$) as in other theropods.

Pelvic girdle.—The left ilium is 477 mm long as preserved, missing the anterior blade, posterior and medial blades, supracetabular crest, and ischial peduncle (Fig. 3A). The pubic peduncle and periphery of the iliac blade were damaged during preparation, so the bone surface is stripped away around the margins of the bone. A low, swollen median ridge is present on the lateral surface of the blade. This ridge is a tetanuran synapomorphy that is widely-distributed among basal members of the clade (Bonaparte 1986; Benson 2009; Zhao et al. 2010). Bone surface preservation is not sufficient to determine whether associated nutrient foramina were present in *C. newmanorum*. The supracetabular crest is damaged but seems to project ventrolaterally as a shelf, as in tetanurans other than *Chuandongocoelurus* and *Monolophosaurus* (Zhao et al. 2010). As preserved, the pubic peduncle is slightly longer anteroposteriorly (95 mm) than its maximum mediolateral width (90 mm). However, medial and posterior portions are broken off and it may have been as wide as long, or only slightly longer than wide. In *Megalosaurus* and most other tetanurans the pubic peduncle is at least 1.3 times as long anteroposteriorly as it is wide mediolaterally, but in the megalosaurid *Eustreptospondylus* (OUMNH J.13558, J.29774; Sadleir et al. 2008) and the allosauroid *Fukuiraptor* (Azuma and Currie 2000) it is approximately as broad as long, resembling the condition in non-tetanurans. This may also have been the case in *C. newmanorum*.

The proximal end of the left pubis is abraded. The smooth anterior margin of the obturator "foramen" is preserved, but preservation is not good enough to determine if it was open as a notch or closed posteriorly to form a foramen.

Hindlimb.—A right femur is preserved in three pieces. One piece comprises the head and proximal part of the shaft (Fig. 3C), another comprises a portion of the shaft including the fourth trochanter (Fig. 3D), and the third comprises the abraded distal end (Fig. 3E). The proximal and posterior sur-

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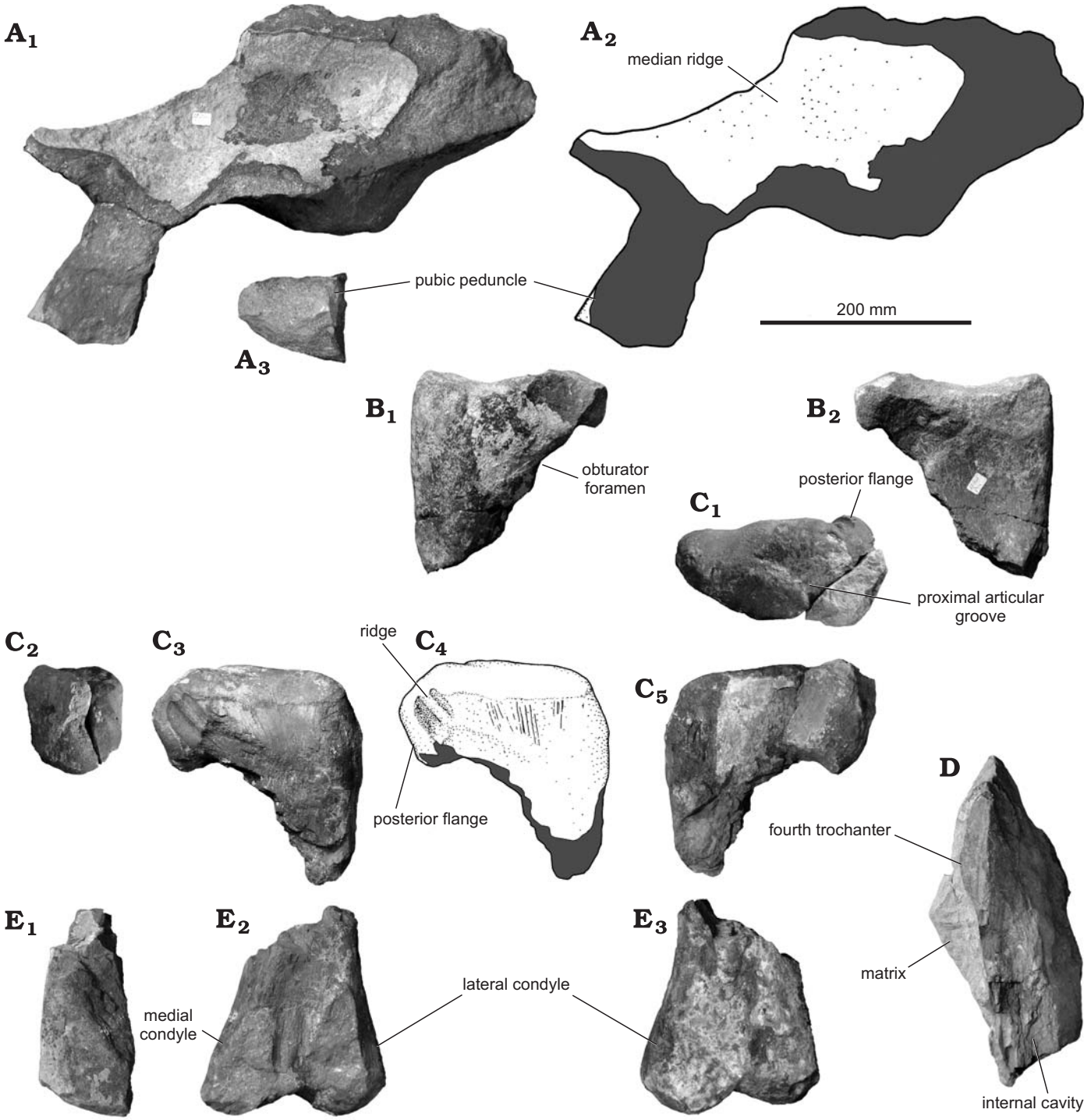


Fig. 3. Tetanuran theropod *Cruxicheiros newmanorum* gen. et sp. nov. pelvic bones (WARMS 15771) and right femur (WARMS 15770) from the Chipping Norton Limestone Formation, Bathonian of the United Kingdom. **A**. Left ilium in lateral view (A_1, A_2) and pubic peduncle in ventral view (A_3). **B**. Left pubis in lateral (B_1) and medial (B_2) views. **C**. Proximal portion of right femur in proximal (C_1), medial (C_2), posterior (C_3, C_4) and anterior (C_5) views. **D**. Shaft fragment of right femur in lateral view. **E**. Distal portion of right femur in medial (E_1), posterior (E_2) and anterior (E_3) views.

faces of the head and posterior surface of the caput are well-preserved. The head measures 185 mm mediolaterally and 95 mm anteroposteriorly at the caput. The greater trochanter is narrower than the caput, so the outline of the head in proximal view narrows from medial to lateral as in non-coelurosaurian theropods (Hutchinson 2001). The proximal surface of the head bears a shallow, anteromedially oriented groove, the proximal articular groove, which is present in non-neotetanuran theropods and many non-theropods (Hutchinson 2001). The posterior flange of the caput is prominent and extends further posteriorly than the posterior surface of the head (Fig. $3C_4$), as in most basal theropods. However, this is unlike the

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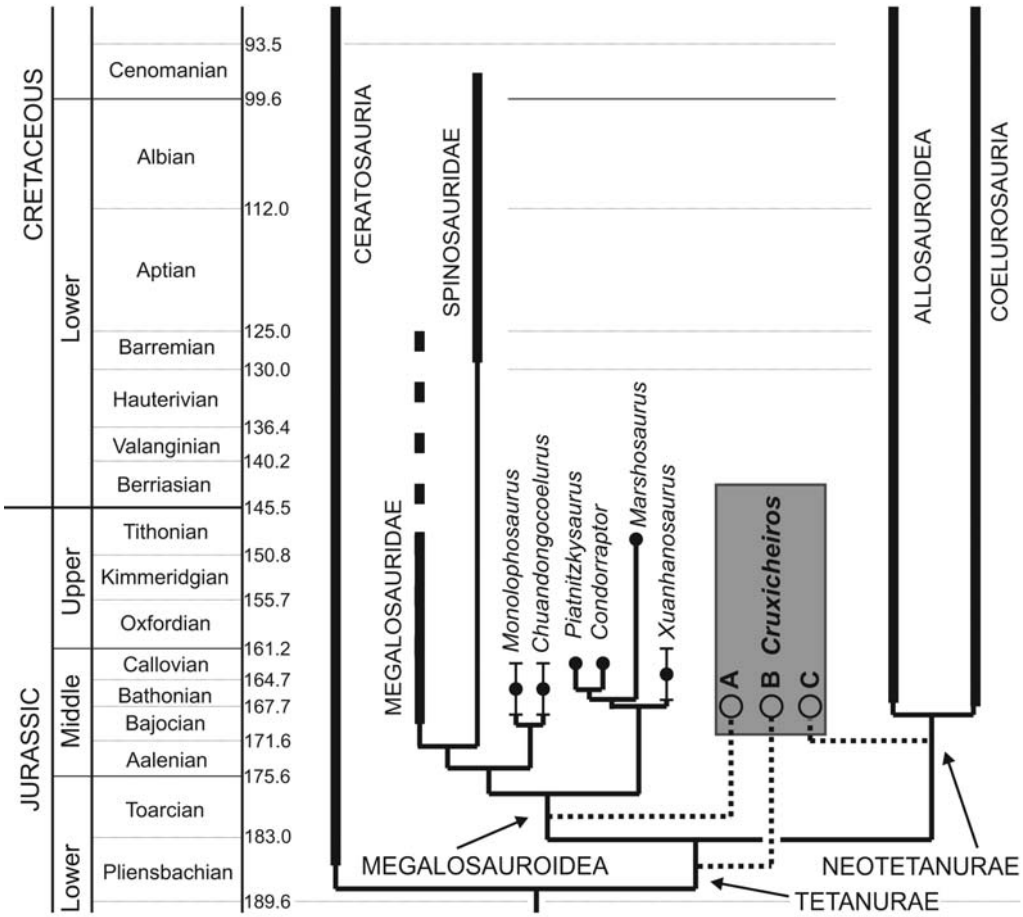


Fig. 4. Simplified cladogram showing the alternative possible phylogenetic placements of *Cruxicheros newmanorum* based on analysis of the modified data set of Benson (2010). *Fukuiraptor* was not included in this scheme as it was recently demonstrated to be a derived allosauroid and not a basal neotetanuran (Benson et al. 2010). *C. newmanorum* was recovered as either a basal megalosauroid (**A**), a basal tetanuran (**B**) or a basal neotetanuran (**C**).

low posterior flange of most megalosaurids, including *Afrovenator* (UC OBA 1) and *Megalosaurus* (Benson 2010). The trochanteric fossa, the groove bounding the posterior flange laterally on the posterior surface of the femur, is anteroposteriorly broad. Within this fossa, nearly parallel to the posterior flange, is a prominent ridge. This ridge is not present in any other basal theropod femur (e.g., Madsen 1976; Bonaparte 1986; Holtz et al. 2004; Sadleir et al. 2008) including the Bathonian taxa *Dubreuillosaurus* (MNHN 1998-13) and *Megalosaurus* (Benson 2010), and is considered here as an autapomorphy of *C. newmanorum*. The base of the lesser trochanter is preserved along with the lateral part of the anterior surface of the greater trochanter region. However, as it is very incomplete it is not possible to determine the morphology of the lesser trochanter.

Discussion

Affinities of *Cruxicheiros*.—Although preserved materials of *Cruxicheiros* are limited, various features support determination of its systematic affinities. The swollen ridge on the lateral surface of the iliac blade, anterior spur of the caudal neural spine and widely-separated cervical prezygapophyses are unique tetanuran synapomorphies (Rauhut 2003, Benson 2010). The posterior flange of the femoral caput is prominent, extending past the posterior surface of the femoral head. In megalosaurids more derived than *Eustreptospondylus*, such as *Afrovenator* (UC OBA 1) and *Megalosaurus*, the posterior flange is low and does not extend past the posterior surface of the head, so it is unlikely that *Cruxicheiros* is a derived megalosaurid. The dorsal neural spines of *Cruxicheiros* are unlike the tall, transversely narrow spines of *Megalosaurus* (Benson 2010), but resemble those of *Marshosaurus* (DMNH 3718), *Piatnitzkysaurus* (Bonaparte 1986) and some allosauroids, including *Aerosteon* (Sereno et al. 2008), *Allosaurus* (Madsen 1976), and *Neovenator* (Brusatte et al. 2008). This resemblance results from their relatively low dorsoventral height, combined with prominent, rugose ridges occupying the anterior and posterior surfaces and the transversely expanded dorsal ends. Contrastingly, in most basal tetanurans with similar spine proportions, such as *Monolophosaurus* (Zhao and Currie 1994) and some megalosaurids (Britt 1991; Sadleir et al. 2008), rugose ridges on the anterior and posterior

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surfaces of the dorsal neural spines are generally less prominent and the dorsal end of the spine is less expanded.

The pubic peduncle of the ilium is reconstructed as being approximately as long anteroposteriorly as it is broad mediolaterally. This is shared with non-tetanuran theropods but is also present as a local autapomorphy in the basal megalosaurid *Eustreptospondylus* (Sadleir et al. 2008: pl. 20: 4) and the allosauroid *Fukuiraptor* (Azuma and Currie 2000). This feature in *Cruxicheiros* suggests a possible basal position within Tetanurae. The proximal end of the femoral head bears an oblique "articular" groove. This feature is widespread among basal theropods but is lost in neotetanurans including allosauroids (Hutchinson 2001; Benson 2010).

Cruxicheiros was scored for the phylogenetic data matrix of Benson (2010). The matrix was slightly corrected based on recent descriptive work on *Monolophosaurus*, which is now scored as possessing a straight pubis (ch. 171.0) (Zhao et al. 2010) and narrow paradental groove (ch. 81.0) (Brusatte et al. in press). After a priori exclusion of "wildcard" taxa identified by Benson (2010) we recovered 24 most parsimonious cladograms (MPTs) of length 585 steps, an ensemble consistency index (CI) of 0.444, a retention index (RI) of 0.618, and a rescaled consistency index (RC) of 0.275. Relationships among taxa included in the original analysis were unaltered and *Cruxicheiros* was recovered in three positions, each represented by eight of the MPTs: the most basal megalosauroid, branching off outside of all megalosauroid clades recovered by Benson (2010); the most basal neotetanuran, branching off outside of the split between *Fukuiraptor*, Allosauroidea, and Coelurosauria; or the most basal tetanuran, branching off outside of the split between Megalosauroidea and Neotetanurae. These results suggest that *Cruxicheiros* represents a very basal tetanuran but that current materials are insufficient to determine its precise phylogenetic affinities. When *Cruxicheiros* was constrained to fall within a monophyletic Megalosauridae, analysis resulted in 8 trees of 586 steps. In all these trees *Cruxicheiros* was the sister taxon of *Eustreptospondylus*, the most basal megalosaurid. When *Cruxicheiros* was constrained to be the sister taxon of *Megalosaurus bucklandii*, analysis recovered 8 trees of 588 steps. This confirms that *Cruxicheiros* does not belong within the genus *Megalosaurus*. With only one additional step, *Cruxicheiros* falls within Megalosauridae, but the small size of this length increase may arise from incomplete knowledge of the taxon (93.9% missing data) rather than the possibility of megalosaurid affinities.

UK Bathonian theropods.—The presence of *Cruxicheiros* yields new data on the diversity of large-bodied theropods represented by abundant, but often fragmentary, specimens from the Lower–Middle Bathonian of the United Kingdom. This assemblage has often been interpreted as a monospecific fauna of *Megalosaurus bucklandii*, essentially for taxonomic convenience (e.g., Benton and Spencer 1995; Weishampel et al. 2004), and recent suggestions that two such taxa were present in key localities at Stonesfield, Oxfordshire and New Park Quarry, Gloucestershire (Allain and Chure 2002; Day and Barrett 2004; Naish and Martill 2007) are unfounded (Benson 2009). Consequently, material of *Cruxicheiros* is the first unequivocal report of an additional large-bodied theropod taxon from British Bathonian strata. A third taxon represented by more fragmentary remains from the Lower Bathonian of Oakham Quarry, Oxfordshire will be the subject of a later publication (RBJB, unpublished data).

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Appendix 1

Scores for *Cruxicheiros newmanorum* for the data set of Benson (2010).

Cruxicheiros newmanorum

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