The systematics of Late Jurassic tyrannosauroid theropods from Europe and North America

STEPHEN L. BRUSATTE and ROGER B.J. BENSON

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Recent discoveries of more than ten new species of tyrannosauroid theropods are helping to understand the origin and evolution of colossal body size and other characteristic features of *Tyrannosaurus rex* and its terminal Cretaceous relatives. Particularly important has been the discovery and reinterpretation of Late Jurassic tyrannosauroids from Europe and North America, which are intermediate in size and phylogenetic position between small basal tyrannosauroids and the largest Late Cretaceous species. The fragmentary nature of these Jurassic specimens, however, has frustrated attempts to understand their systematics and phylogeny. A new specimen from the Late Jurassic of England was recently named as a new species (*Stokesosaurus langhami*) of the genus *Stokesosaurus*, which is known from several fragmentary fossils from North America. We review the systematics and phylogeny of these European and North American specimens and show that there are no unequivocal synapomorphies uniting them. Furthermore, a revised phylogenetic analysis does not recover them as sister taxa. This necessitates a taxonomic revision of this material, and we name a new genus (*Juratyrant*) for the British specimen.

Key words: Dinosauria, Theropoda, Tyrannosauridae, *Tyrannosaurus*, anatomy, Jurassic, Europe, North America.

Stephen L. Brusatte [brusatte@gmail.com], Division of Paleontology, American Museum of Natural History, Central Park West at 79th St., New York, NY, 10024, USA and Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA; current address: School of GeoSciences, The University of Edinburgh, Grant Institute, The King's Buildings, West Mains Road, Edinburgh EH9 3JW, UK;
Roger B.J. Benson [rbb27@cam.ac.uk], Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ, UK and Department of Earth Sciences, University College London, Gower Street, London WC1E 6BT, UK; current address: Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK.

Introduction

Over the past decade, a wealth of new fossil discoveries, phylogenetic analyses, and explicit biomechanical studies have shed new light on the anatomy, evolution, and biology of tyrannosauroid theropod dinosaurs (see review in Brusatte et al. 2010). A major driver of this resurgence has been the discovery of more than 10 new tyrannosauroid species, many of which are small-bodied animals, not much larger than a human, that lived up to 100 million years before the iconic terminal Cretaceous *Tyrannosaurus rex* (e.g., Hutt et al. 2001; Rauhut 2003a; Xu et al. 2004, 2006; Carr et al. 2005, 2011; Benson 2008; Brusatte et al. 2009; Ji et al. 2009; Sereno et al. 2009; Averianov et al. 2010; Carr and Williamson 2010; Li et al. 2010). These new species have begun to unveil the sequence of character and body size changes during the transition from small-bodied basal tyrannosauroids to the colossal tyrannosaurids (*T. rex* and close relatives) that lived during the final 20 million years of the Cretaceous and exceeded 1 tonne in mass (Erickson et al. 2004).

Among this influx of new tyrannosauroid discoveries is a specimen from the Late Jurassic of England that was described by Benson (2008) as the holotype of a new species, *Stokesosaurus langhami* (OUMNH J.3311-1–J.3311-30). This specimen is particularly important because it is one of the most complete tyrannosauroid fossils from the Jurassic, a time that tyrannosauroids appear to have had a wide (and perhaps cosmopolitan) distribution, but during which they lived in the shadow of other giant predatory dinosaurs (basal tetanurans; Benson 2010; Benson et al. 2010; Carrano et al. 2012). In his initial description, Benson (2008) noted several similarities between the new specimen and the fragmentary remains of another species, *Stokesosaurus clevelandi* Madsen, 1974 (the type species of *Stokesosaurus*), from the Late Jurassic of North America. As a result, Benson (2008) referred the new species to the genus *Stokesosaurus*. Over the past few years, however, the discovery of several new tyrannosauroids suggests that many of the characters used by Benson (2008) to unite *S. clevelandi* and *S. langhami* may actually be more widely distributed among basal tyrannosauroids. This leaves

open the question of whether the two species are sister taxa, and therefore, whether *S. langhami* can be retained in the genus *Stokesosaurus* or requires a new generic name.

We here provide a systematic reassessment of the genus *Stokesosaurus* and its two constituent species. We show that the characters used by Benson (2008) to unite both species are problematic, either because they indeed are more widely distributed among basal tyrannosauroids, or because they cannot confidently be assessed in many other tyrannosauroids. Thus, strong evidence for a clade comprising *S. clevelandi* and "*S.*" *langhami* may be lacking. We then provide a new phylogenetic analysis, based on the recent comprehensive dataset of Brusatte et al. (2010), which does not find support for a sister grouping of *S. clevelandi* and *S. langhami*. This necessitates the removal of "*S.*" *langhami* from *Stokesosaurus*, and requires the erection of a new generic name for the British material.

Institutional abbreviations.—BMR, Burpee Museum of Natural History, Rockford, Illinois, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; FRDC, Fossil Research and Development Center, Gansu Bureau of Geology and Mineral Resources Exploration, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LH, Long Hao Institute of Geology and Paleontology, Hohhot, Nei Mongol Autonomous Region, China; MIWG, Museum of Isle of Wight Geology, Isle of Wight County Museum Service, Sandown, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; UMNH, Utah Museum of Natural History, Salt Lake City, Utah, USA.

Review of putative *Stokesosaurus* synapomorphies

Benson (2008) considered four characters to be unique synapomorphies shared only by *Stokesosaurus clevelandi* and "*Stokesosaurus*" *langhami* among tyrannosauroids. Where comparisons were possible, these characters were demonstrated to be absent in other tyrannosauroids, including non-tyrannosaurid taxa such as *Aviatyrannis*, *Dilong*, and *Guanlong*. They were regarded, therefore, as unequivocal autapomorphies of a monophyletic genus *Stokesosaurus*. Recent discoveries have revealed that all four of these characters are problematic because most are more widely distributed among tyrannosauroids, especially an array of basal taxa that have recently come to light (e.g., Xu et al. 2006; Ji et al. 2009; Li et al. 2010). We review each of these characters here.

Iliac blade with semi-oval outline in lateral view.—Benson (2008) did not specifically define this character, but we quantify it here as an iliac blade whose posterior margin is less than half as tall dorsoventrally as the region above the acetabulum, which results in a curved dorsal margin and overall "semi-oval" appearance. This condition contrasts with the more general theropod morphology in which the ilium is sub-rectangu-lar in shape and nearly as tall posteriorly as above the acetabulum (e.g., Madsen 1976; Colbert 1989; Norell and Makovicky 1999; Peyer 2006; Carrano 2007). This general morphology is present in most tyrannosauroids, including *Aviatyrannis* (Rauhut 2003a), *Guanlong* (Xu et al. 2006), and tyrannosaurids (e.g., Brochu 2003). The semi-oval morphology, on the other hand, is indeed present in both *S. clevelandi* and "*S.*" *langhami* (Fig. 1A, B). However, in the course of the present study it was also observed in the basal tyrannosauroids *Dilong* (IVPP V14243; Xu et al. 2004: fig. 1k), *Sinotyrannus* (Ji et al. 2009: fig. 3), and *Xiongguanlong* (Li et al. 2010: fig. 6a in supplementary material). Most notably, *Xiongguanlong* has an ilium whose proportions and overall shape are remarkably similar to those of both putative species of *Stokesosaurus*. Therefore, a semi-oval ilium is not a unique synapomorphy of *S. clevelandi* and "*S.*" *langhami*, but is rather a more widely distributed character among basal tyrannosauroids.

Narrow preacetabular notch.—The open space between the preacetabular process and pubic peduncle of the ilium is narrow in both *S. clevelandi* and "*S.*" *langhami*, and it remains narrow across its entire length when seen in lateral view (Fig. 1A, B). In contrast, the notch of other tyrannosauroids is wider, and expands in width as it continues anteriorly. This wide condition is present in *Guanlong* (Xu et al. 2006: fig. 2e), *Aviatyrannis* (Rauhut 2003a: fig. 1), *Raptorex* (Sereno et al. 2009: fig. 2e), and tyrannosaurids (e.g., *Gorgosaurus*, Lambe 1917: fig. 6; *Tyrannosaurus*, Brochu 2003: fig. 90), as well as close tyrannosauroid outgroups (e.g., Currie and Chen 2001; Ji et al. 2003; Peyer 2006). Therefore, the narrow morphology is shared only by *S. clevelandi* and "*S.*" *langhami* among tyrannosauroids. We hesitate to consider this a robust synapomorphy, however, as the preacetabular notch is broken in other basal tyrannosauroids sharing overall morphological similarity (e.g., a semi-oval iliac blade, above) with putative *Stokesosaurus* species: *Dilong* (IVPP V14243), *Eotyrannus* (MIWG 1997.550), *Sinotyrannus* (Ji et al. 2009), and *Xiongguanlong* (Li et al. 2010). Any of these taxa may have a narrow preacetabular notch, resulting in a wider distribution of this feature. However, the absence of data renders current phylogenetic optimizations preliminary.

Posterodorsally inclined ridge on lateral surface of ilium.—Tyrannosauroids are unusual among theropods in possessing a discrete, linear ridge extending dorsal to the acetabulum on the lateral surface of the iliac blade (e.g., Holtz 2004), which probably served to separate major hindlimb muscles (Carrano and Hutchinson 2002). The ridge projects straight dorsally, or nearly so, on most known tyrannosauroid specimens (e.g., tyrannosaurids, Lambe 1917; Brochu 2003; *Aviatyrannis*, Rauhut 2003a), but Benson (2008) noted that *S. clevelandi* and "*S.*" *langhami* shared an atypical condition in which the ridge is oriented posterodorsally at a strong angle from the vertical (Fig. 1A, B). Recent re-examination of the holotype specimen of the basal tyrannosauroid *Eotyrannus* by one of us (SLB) revealed the presence of a fragmentary left ilium that was not described in the initial publication naming

Fig. 1. Ilia of basal non-tyrannosaurid tyrannosauroids with a posterodorsally inclined ridge on the lateral surface of the ilium. **A**. Right ilium (reversed) of *Juratyrant langhami* Benson, 2008 (OUMNH J.3311-21), Kimmeridge Clay, Dorset England, Late Jurassic (early Tithonian). **B**. Left ilium of *Stokesosaurus clevelandi*, Madsen 1974 (UMNH VP 7473), Morrison Formation, Utah, USA, Late Jurassic (early Tithonian). **C**. Left ilium of *Eotyrannus lengi* Hutt, Naish, Martill, Barker, and Newberry, 2001 (MIWG 1997.550), Wessex Formation, Isle of Wight, England, Early Cretaceous (Barremian). All in lateral view. Arrows denote the lateral ridge.

this genus (Hutt et al. 2001) and has yet to be mentioned in the literature (MIWG 1997.550) (Fig. 1C). Although fragmentary, the specimen is identified as a left ilium because the base of one of the ventral peduncles is preserved, and it is mediolaterally narrow like the pubic peduncle of tyrannosauroids and other coelurosaurs but unlike the thicker and more conical ischial peduncle (e.g., Brochu 2003; Rauhut 2003b). A linear ridge is present, well preserved, and well developed on the lateral surface of the blade, and it extends strongly posterodorsally at approximately the same angle as seen in *Stokesosaurus clevelandi* and "*S.*" *langhami*. Therefore, a posterodorsally-inclined iliac ridge can no longer be considered as a unique synapomorphy of a monophyletic *Stokesosaurus*.

Even if our identification of the posterodorsal ridge is incorrect in *Eotyrannus* (we could be misidentifying the one partially preserved peduncle as the pubic peduncle; if it is the ischial peduncle then the ridge would be directed strongly anterodorsally), we argue that the orientation of the ridge may

not be a systematically robust character. Brusatte et al. (2009) identified an anterodorsally oriented ridge as an autapomorphy of *Alioramus altai*, but subsequent reexamination of specimens show that this feature is also seen in some, but not all, specimens of *Daspletosaurus* (CMN 8506), *Gorgosaurus* (CMN 2120), and *Tyrannosaurus* (BMR 2002.4.1) (Brusatte et al. 2012), genera which usually have a dorsally directed ridge. Therefore, there is wide variation in the orientation of the ridge in some tyrannosaurid taxa, which suggests that this feature may be too variable to confidently use in taxon diagnoses.

Corrugated structure on the medial surface of the iliac blade, opposite of the ridge on the lateral surface.— Benson (2008) noted that both *S. clevelandi* and "*S.*" *langhami* possess a furrow on the medial surface of the iliac blade, directly corresponding to the shape and position of the linear ridge on the lateral surface. This morphology is not seen in other tyrannosauroids represented by ilia whose medial surfaces are well preserved and visible (i.e, not articu-

lated with the sacrum), including the basal taxon *Aviatyrannis* (Rauhut 2003a: fig. 1c) and the derived tyrannosaurid *Tyrannosaurus* (Brochu 2003: fig. 92B). Unfortunately, the medial surface of the ilium cannot be observed, or is not well enough preserved to assess the presence of a corrugated furrow, in any known specimen of the basal tyrannosauroids *Dilong*, *Eotyrannus*, *Guanlong*, *Sinotyrannus*, and *Xiongguanlong*. Therefore, we hesitate to consider this a robust synapomorphy of a monophyletic *Stokesosaurus*.

Revised phylogenetic analysis of tyrannosauroid interrelationships

The above discussion makes clear that the four characters considered by Benson (2008) to be unique synapomorphies of a monophyletic *Stokesosaurus* are problematic, either because they are now known to be more widely distributed among basal tyrannosauroids or because they cannot confidently be scored in many of the closest relatives of *S. clevelandi* and "*S.*" *langhami*. The strongest arbiter of whether these two species form a monophyletic genus, however, is a numerical cladistic analysis that takes into account as many characters as possible. Recent phylogenetic analyses have included *Stokesosaurus* as a terminal, but it has usually been scored either as a composite or based solely on "*S.*" *langhami* (Benson 2008; Brusatte et al. 2010). *S. clevelandi* and "*S.*" *langhami* were included as separate terminals in the analysis of Choiniere et al. (2010), but this did not include a full array of basal tyrannosauroid taxa or characters relevant to tyrannosauroid ingroup relationships. Therefore, the monophyly of *Stokesosaurus* has yet to be comprehensively and explicitly tested.

Here, we analyze the phylogenetic relationships of tyrannosauroids and assess the monophyly of *Stokesosaurus* by including both *S. clevelandi* and "*S.*" *langhami* as terminals in a revised version of the cladistic dataset of Brusatte et al. (2010). This dataset includes every well known tyrannosauroid taxon and a thorough sample of over 300 characters specific to tyrannosauroid ingroup relationships. The original version of the analysis, which represented *Stokesosaurus* with the character scores of "*S.*" *langhami*, resulted in a single most parsimonious tree, with most clades well supported. Thus, it is the most appropriate dataset for testing the monophyly of *Stokesosaurus*.

We made several small modifications to the original dataset. In addition to separating *S. clevelandi* and "*S.*" *langhami* into distinct terminals, we also added *Aviatyrannis* as a new terminal, with all character scores based on the description of Rauhut (2003a). Although *Aviatyrannis* is a fragmentary taxon represented solely by an ilium (we do not score characters based on the isolated ischium referred to the taxon by Rauhut 2003a), it is critical to consider because it shares several characters with one or both putative species of *Stokesosaurus*, and may be a closely related (or perhaps congeneric) taxon. We also added seven new characters relating

to the ilium and dorsal vertebrae, including some of the characters considered by Benson (2008) to be synapomorphies of a monophyletic *Stokesosaurus*, and modified two character scores for *Dryptosaurus* based on the recent redescription of this taxon by Brusatte et al. (2011). Full details of the additions and changes to the dataset see Supplementary Online Material (SOM) available at http://app.pan.pl/SOM/app58-Brusatte_Benson_SOM.pdf. The end result is a 25-taxon, 314-character dataset.

The dataset was subjected to a parsimony analysis in TNT v. 1.1 (Goloboff et al. 2008), with the ingroup constrained as monophyletic. First, we analyzed the matrix under the "New Technology search" option, using sectorial search, ratchet, tree drift, and tree fuse options with default parameters. The minimum length tree was recovered in 10 replicates, a process that aimed to sample as many tree islands as possible. This resulted in eight most parsimonious trees (MPTs) of 573 steps (consistency index [CI] = 0.637, retention index [RI] = 0.833). These eight trees were then analyzed under traditional TBR branch swapping to more fully explore each tree island. This resulted in one additional most parsimonious tree. The strict consensus of the nine MPTs is moderately well resolved: the relationships of taxa more derived than *Xiongguanlong* are fully resolved, but many basal taxa fall into a polytomy at the base of Tyrannosauroidea. One of the clades falling into this polytomy is a trichotomy of *S. clevelandi*, "*S.*" *langhami*, and *Eotyrannus*.

Examination of the individual MPTs showed that the basal polytomy was due solely to the fragmentary taxon *Aviatyrannis*, which acts as a wildcard because it can equally parsimoniously occupy several positions among basal Tyrannosauroidea. Therefore, we ran a second analysis in which *Aviatyrannis* was deleted, using the same search strategy outlined above. This analysis resulted in a single most parsimonious tree (Fig. 2) of 570 steps, with a CI of 0.640 and RI of 0.835. "*S.*" *langhami* and *Eotyrannus* are recovered as sister taxa, with *S. clevelandi* as their closest outgroup. Therefore, a monophyletic *Stokesosaurus* was not recovered. The "*S.*" *langhami* and *Eotyrannus* clade, however, is poorly supported, with a Bremer support of 1 and a bootstrap percentage of less than 50%. This is almost certainly due to the fragmentary nature of *S. clevelandi*, which is only scored for characters relating to the holotype ilium (see Benson [2008] for an explanation of why other material previously referred to *S. clevelandi* cannot confidently be assigned to this taxon).

To test the robustness of our results, we also ran a modified analysis (excluding the wildcard *Aviatyrannis*) in which the orientation of the linear ridge on the lateral surface of the ilium is scored as uncertain for *Eotyrannus* (character 258). This is a conservative score that addresses the possibility that we have misidentified the ridge as extending posterodorsally, which is the score in the original Brusatte et al. (2010) analysis (see above). This modified analysis results in three most parsimonious trees (also of 570 steps, with a CI of 0.640 and RI of 0.835). The strict consensus topology is identical to of the original analysis (Fig. 2), except that
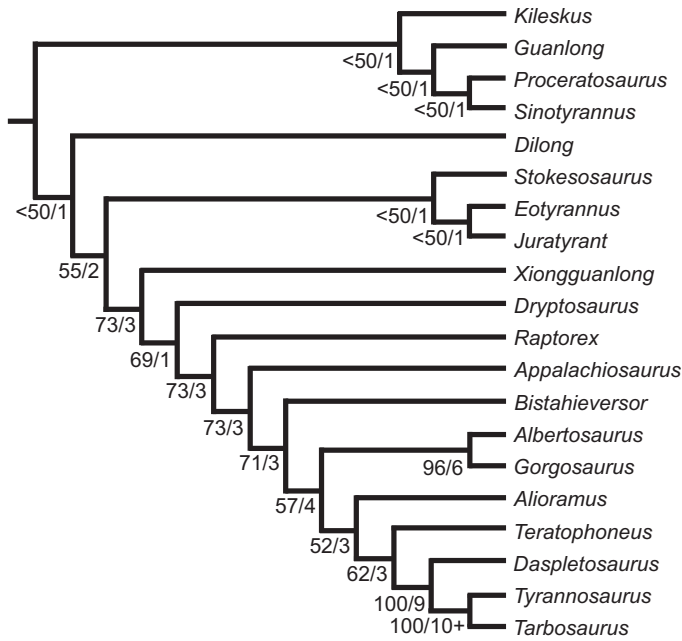
Fig. 2. The phylogenetic relationships of tyrannosauroids, based on a revised analysis of the Brusatte et al. (2010) dataset. Details of the analysis are described in the text and the dataset is presented in SOM. The cladogram shown here is the single most parsimonious tree recovered by the analysis, with the wildcard taxon *Aviatyrannis* excluded (570 steps, CI = 0.640, RI = 0.835). Numbers next to nodes denote bootstrap percentages (based on 1000 replicates) and Bremer support. Note that *Stokesosaurus clevelandi* and "*S.*" *langhami* (here referred to by its new genus name, *Juratyrant*) are not found as sister taxa, and therefore a monophyletic *Stokesosaurus* is not recovered. When *Aviatyrannis* is included in the analysis, the strict consensus of nine most parsimonious trees (not figured) shows identical and fully resolved relationships among *Xiongguanlong* and all more derived taxa. However, *Stokesosaurus clevelandi*, "*S.*" *langhami*, and *Eotyrannus*, form a polytomy. This clade, in turn, is part of a large basal polytomy that also includes the *Xiongguanlong* + more derived clade, *Dilong*, *Aviatyrannis*, *Guanlong*, *Kileskus*, *Proceratosaurus*, and *Sinotyrannus*. On the figured cladogram, the following unambiguous synapomorphies support major clades, with character numbering following that in the character list of Brusatte et al. (2010) and SOM: all tyrannosauroids more derived than *Dilong* (33, 41, 49, 80, 180, 181, 196, 198, 221, 239, 241, 244, 257, 274, 281, 289, 290); the clade of *S. clevelandi*, *Juratyrant*, and *Eotyrannus* (258, 310, 311, 313); the clade of *Juratyrant* and *Eotyrannus* (no unambiguous synapomorphies).

Eotyrannus, *S. clevelandi*, and "*S.*" *langhami* fall into a basal polytomy with the clade comprised of *Xionggualong* and more derived tyrannosauroids. Therefore, while this sensitivity analysis does not indicate a positive grouping of *Eotyrannus* and "*S.*" *langhami*, it does not provide clear evidence for a monophyletic *Stokesosaurus* either.

Systematic revisions

In summary, because (i) there are no autapomorphies or unique combination of characters that unite *Stokesosaurus clevelandi* and "*Stokesosaurus*" *langhami* relative to other basal tyrannosauroids (especially phylogenetically proximal taxa such as *Eotyrannus*, *Xiongguanlong*, and *Aviatyrannis*);

and (ii) a phylogenetic analysis does not recover *S. clevelandi* and "*S.*" *langhami* forming a clade exclusive of other taxa, then a new generic name must be erected for "*S.*" *langhami*. Here, we provide a systematic revision of *S. clevelandi* and "*S.*" *langhami*, present updated diagnoses, and name a new genus for "*S.*" *langhami*.

Systematic palaeontology

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Tyrannosauroidea Osborn, 1905 (sensu Sereno et al. 2005)

Genus *Stokesosaurus* Madsen, 1974

Type species: *Stokesosaurus clevelandi* Madsen, 1974; see below.

Diagnosis.—Same as for the type and only known species.

Stokesosaurus clevelandi Madsen, 1974

Figs. 1B, 3C.

Holotype: UMNH 2938 (formerly UUVP 2938), a left ilium.

Type horizon: Brushy Basin Member of the Morrison Formation, lower Tithonian, Upper Jurassic.

Type locality: Cleveland-Lloyd Dinosaur Quarry, Utah, USA.

Emended diagnosis.—Tyrannosauroid theropod with a single autapomorphy: a swollen rim around the articular surface of the pubic peduncle, which is especially prominent on the medial surface (Benson 2008). Furthermore, *S. clevelandi* can be differentiated from other phylogenetically proximal tyrannosauroids by a unique combination of characters: an anteroposteriorly thick ridge on the lateral surface of the ilium which projects posterodorsally and extends to the dorsal margin of the iliac blade.

Remarks.—The sole autapomorphy of *Stokesosaurus clevelandi* is absent in "*Stokesosaurus*" *langhami* (Benson 2008), *Aviatyrannis* (Rauhut 2003a), *Guanlong* (Xu et al. 2006; IVPP V14531), *Raptorex* (Sereno et al. 2009; LH PV18), and tyrannosaurids (e.g., *Gorgosaurus*, Lambe 1917; *Tyrannosaurus*, Brochu 2003). It appears to be absent in the type and only known specimen of *Xiongguanlong* (FRDC-GS JB16-2-1), but there is some breakage in this region. This character cannot be assessed in *Dilong* (IVPP V14243) and *Eotyrannus* (MIWG 1997.550) because the pubic peduncle is damaged in all known specimens.

The unique combination of characters differentiates *S. clevelandi* from "*S.*" *langhami* and all other tyrannosauroids. A thickened lateral ridge, defined here (and used in the phylogenetic analysis) as a ridge with an anteroposterior width greater than 20% of its dorsoventral height, is also present in *Guanlong* (Xu et al. 2006), *Sinotyrannus* (Ji et al. 2009), and tyrannosaurids (e.g., Brochu 2003). A thin ridge, however, is present in "*S.*" *langhami* (Benson 2008), *Dilong* (IVPP V14243), *Eotyrannus* (MIWG 1997.550), *Aviatyrannis* (Rauhut 2003a), and *Xiongguanlong* (Li et al. 2010). The lateral ridge extends
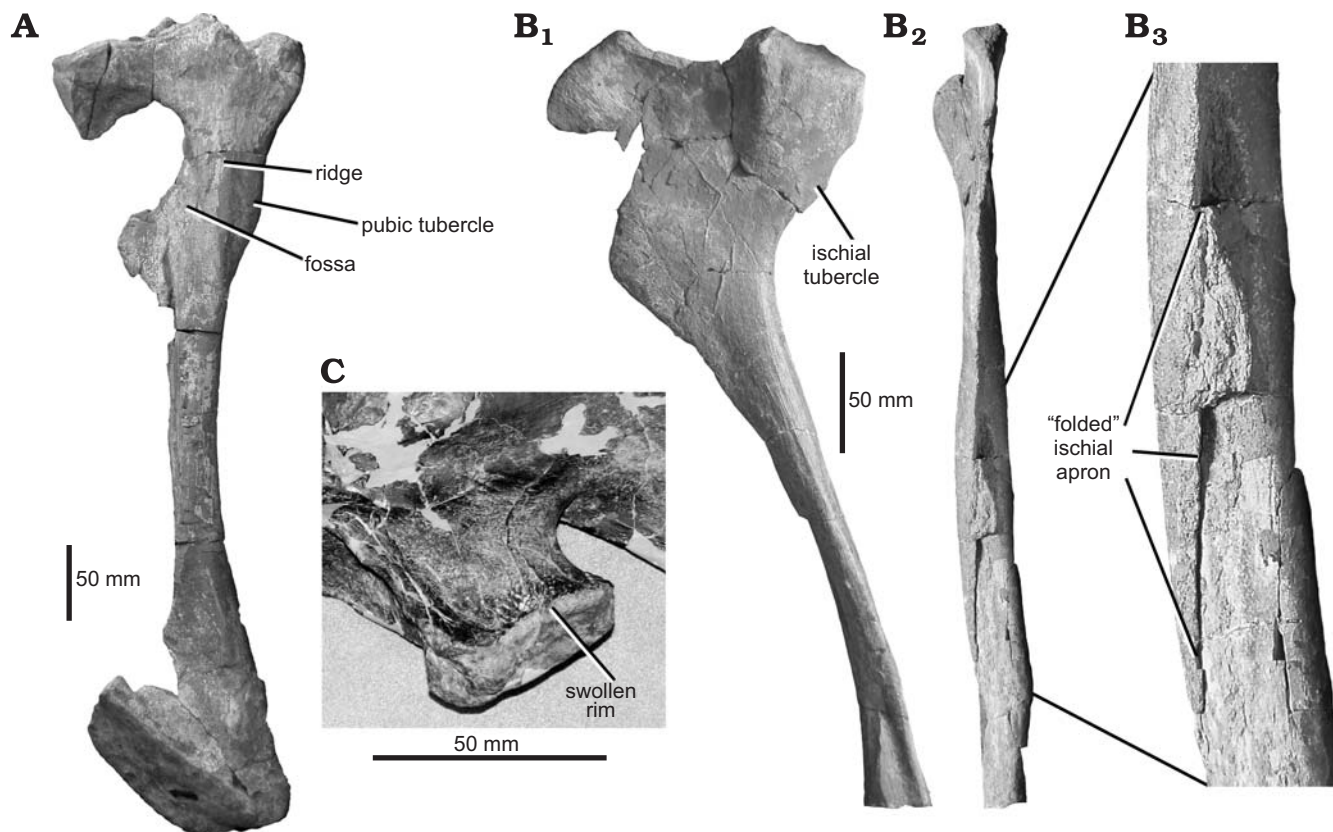
Fig. 3. Autapomorphies of tyrannosauroids *Juratyrant langhami* Benson, 2008, Kimmeridge Clay, Dorset England, Late Jurassic (early Tithonian) (A, B) and *Stokesosaurus clevelandi* Madsen, 1974, Morrison Formation, Utah, USA, Late Jurassic (early Tithonian) (C). **A**. Right pubis (OUMNH J.3311-22) in lateral view, with the autapomorphic lateral fossa denoted. **B**. Left ischium (OUMNH J.3311-25) in lateral (B₁) and anterior (B₂) views, with an inset close up (2.5× magnification) of the autapomorphic folded proximal region of the ischial apron (B₃). The autapomorphic convex ischial tubercle is also denoted. **C**. Pubic peduncle of the left ilium (UMNH 2938) in medial view, with the autapomorphic swollen rim indicated.

to the dorsal margin of the ilium in *Guanlong*, *Sinotyrannus*, and *Aviatyrannis*, whereas it stops short of the dorsal margin in "*S.*" *langhami*, *Eotyrannus*, *Xiongguanlong*, and tyranno-saurids. Finally, the posterodorsally oriented ridge is present in "*S.*" *langhami* and *Eotyrannus* (see above). *S. clevelandi*, therefore, is the only tyrannosauroid that possesses a combina-tion of a thick, posterodorsally-trending ridge that extends to the dorsal margin of the ilium.

Genus *Juratyrant* nov.

Type species: *Juratyrant langhami* Benson, 2008; see below.

Etymology: "Jura" refers to the Jurassic age of the taxon and "tyrant" is an Anglicized version of the Greek "tyrannos" and Latin "tyrannus," in ref-erence to the vernacular characterization of tyrannosauroids as "tyrant di-nosaurs" (based on the original etymology of *Tyrannosaurus rex*).

Diagnosis.—Same as for the type and only known species.

Juratyrant langhami Benson, 2008
Figs. 1A, 3A, B.

Holotype: OUMNH J.3311-1–J.3311-30, an associated partial skeleton from a mature individual (see Benson [2008] for details). Individual bones include: one cervical vertebra (OUMNH J.3311-1); five dorsal vertebrae (OUMNH J.3311-2–J.3311-5 and J.3311-30); a complete sa-crum (OUMNH J.3311-6–J.3311-9); five caudal vertebrae (OUMNH J.3311-10–J.3311-14); four isolated vertebral transverse processes (OUMNH J.3311-16–J.3311-19); the complete pelvic girdle (left ilium,

J.3311-20; right ilium, J.3311-21; right pubis, J.3311-22; left pubis, J.3311-23; right ischium, J.3311-24; left ischium, J.3311-25); both femora (left femur, J.3311-26; right femur, J.3311-27); both tibiae (right tibia, J.3311-28; left tibia, J.3311-29); and an unidentified bone fragment (OUMNH J.3311-15).

Type horizon: The *Pectinatites pectinatus* Ammonite Zone, *P. eatleco-ttensis* Subzone, Kimmeridge Clay, Upper Jurassic: lower Tithonian.

Type locality: Dorset, England, United Kingdom. The specimen was re-covered 6 miles west of Swanage between Rope Lake Head and Fresh-water Steps (marked as Kimmeridge Ledges on Ordnance Survey maps, Ordinance Survey, 1979).

Emended diagnosis.—Tyrannosauroid theropod with four autapomorphies: ischial apron with a "folded" appearance (Benson 2008); a fibular flange that continues as a distinct low ridge to the proximal end of the tibia (Benson 2008); ischial tubercle of the ischium expressed as a convex bulge (Brusatte et al. 2010); deep fossa on the lateral surface of the pubis ventral to the acetabulum (new character). Further-more, *Juratyrant langhami* possesses two probable autapo-morphies, which are difficult to assess in other taxa because of damage or non-preservation of the bone in question: a prominent hyposphene that extends posteriorly as a thin sheet on the fifth sacral vertebra (Benson 2008) and an extensor groove of the femur expressed as a broad, concave outline in distal view (Brusatte et al. 2010).

Remarks.—Benson (2008) considered a "folded" ischial apron (figured here in Fig. 3B) and a proximally extensive fibular flange as autapomorphies of *Juratyrant langhami*, and we confirm that these still remain unique to this taxon among all known tyrannosauroids. Benson (2008) further regarded a prominent hyposphene on the fifth sacral vertebra to be unusual to *J. langhami*, and we tentatively consider this an autapomorphy here but note that it is difficult to assess in most other tyrannosauroids, especially basal taxa phylogenetically proximal to *J. langhami* (e.g., *Dilong*, *Eotyrannus*, *Raptorex*, *Sinotyrannus*, *Xiongguanlong*). *Guanlong* also possesses a prominent hyposphene on the fifth sacral, and it projects even further posteriorly relative to the centrum face than in *J. langhami*, but it is not sheet-like as in *J. langhami* (IVPP V14531). Tyrannosaurids, on the other hand, do not possess a prominent hyposphene that projects far posterior to the centrum face (e.g., *Alioramus* IGM 100/1844, Brusatte et al. 2012; *Tyrannosaurus*, Brochu 2003).

We note three additional autapomorphies, two of which are definitive and one of which is probable. First, the ischial tubercle of *J. langhami* is present as a convex bulge on the posterior surface of the ischium. In *Guanlong* (IVPP V14531) and outgroup taxa it is expressed as a groove, whereas in more derived taxa such as *Dryptosaurus* (Brusatte et al. 2011), *Raptorex* (Sereno et al. 2009), *Appalachiosaurus* (Carr et al. 2005), and tyrannosaurids (e.g., Lambe 1917; Brochu 2003) it is present as a discrete, either ovoid or triangular, flange whose rugose lateral surface is depressed relative to the remainder of the ischium. *J. langhami* is the only taxon with a tubercle expressed as a bulge, which is not depressed or discretely offset from the posterior margin of the ischium. This unusual condition was noted by Brusatte et al. (2010) and treated as an intermediate morphology between the groove-like and flange-like states in an ordered character statement (character 278).

Second, we note that there is a deep fossa on the lateral surface of the pubis ventral to the acetabulum, which is bordered anteriorly by a stout ridge (Fig. 3A). This ridge separates the fossa from the rugose pubic tubercle on the anterior surface of the pubis. The fossa and corresponding ridge are absent in all other tyrannosauroids known from well preserved pubes, including *Guanlong*, *Raptorex*, and tyrannosaurids (e.g., Brochu 2003).

Third, *J. langhami* possesses a uniquely-shaped extensor groove on the anterior surface of the distal femur, in which the groove is present, but shallow, and expressed as a broad concave margin in distal view (Benson 2008: fig. 11F). In more basal taxa such as *Guanlong* (IVPP V14531) and *Dilong* (IVPP V14243) the extensor groove is absent and the anterior surface of the femur is flat, and in more derived taxa (*Xiongguanlong*, *Dryptosaurus*, *Raptorex*, tyrannosaurids) the groove is present and expressed as a deep, U-shaped cleft in distal view. *J. langhami*, therefore, is unique in possessing a shallow and broad extensor groove, and this was noted by Brusatte et al. (2010) who scored *J. langhami* for its own intermediate character in an ordered character statement related to the presence and depth of the groove (character 290). We ac-

knowledge, however, that the femora of OUMNH J.3311 (the holotype and only specimen of *J. langhami*) are deformed; the right femur is crushed mediolaterally and does not exhibit an extensor groove whereas the left is crushed anteroposteriorly and shows a broadly curved groove (Benson 2008). Thus, this feature is only proposed hesitantly as an autapomorphy.

Finally, Benson (2008) described *Juratyrant langhami* as possessing an autapomorphic condition of the posterior dorsal vertebrae, in which the postzygapophyses are reduced and raised dorsally relative to the prezygapophyses (Benson 2008: fig. 3). This condition is not present in the basal tyrannosauroid *Guanlong* (IVPP V14531), but is present in *Xiongguanlong* (Li et al. 2010; FRDC-GS JB16-2-1), *Raptorex* (Sereno et al. 2009; LH PV18), and tyrannosaurids (e.g., *Alioramus*, IGM 100/1844; *Tarbosaurus*, Maleev 1974; *Tyrannosaurus*, Brochu 2003). We include this character in our revised phylogenetic analysis and recover the derived state (dorsally elevated postzygapophyses) as a synapomorphy of the clade of all tyrannosauroids more derived than, and including, *J. langhami*.

Conclusions

Specimens such as OUMNH J.3311-1–J.3311-30 and the various fossils of *Stokesosaurus clevelandi* are important, as they represent Late Jurassic tyrannosauroids that are intermediate in phylogenetic position and body size between small basal tyrannosauroids (e.g., *Dilong* and *Guanlong*) and the largest and latest-surviving tyrannosaurids (e.g., *Albertosaurus* and *Tyrannosaurus*). Understanding the systematics of these specimens, however, is challenging because of their fragmentary nature. We here show that OUMNH J.3311-1–J.3311-30, which Benson (2008) described as the holotype of a new species of *Stokesosaurus* (*S. langhami*), does not share any unequivocal synapomorphies with the type species of *Stokesosaurus* (*S. clevelandi*). Furthermore, the two do not group together in a phylogenetic analysis. Therefore, we erect a new genus name for the British material, *Juratyrant*. Hopefully, as more complete specimens of *S. clevelandi* and other Jurassic tyrannosauroids are found, the systematics and phylogeny of these so-called "intermediate tyrannosauroids" will become better understood.

Acknowledgements

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