

A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England



*Stephen Hutt, †Darren Naish, †David M. Martill, †Michael J. Barker and
*Penny Newbery

*Museum of Isle of Wight Geology, Sandown, Isle of Wight PO36 8AF, UK

†School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth PO1 3QL, UK

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A new genus and species of coelurosaurian theropod dinosaur from the Wessex Formation (Early Cretaceous, Barremian) of the Isle of Wight, England, is described and named. Distinctive characters of the premaxilla, its dentition, maxilla and nasals allow it to be diagnosed. The teeth in the premaxilla are D-shaped in cross-section and the nasals are fused. The hands are elongate and slender and the hindlimbs are gracile. Lack of element fusion elsewhere in the skeleton suggests that it is a subadult. Numerous character states are shared with tyrannosaurids but the new taxon appears to be excluded from the group that comprises aublysodontine and tyrannosaurine tyrannosaurids. We conclude that the taxon is a basal tyrannosauroid and as such it is one of the earliest and (with the exception of some teeth and an isolated ilium from Portugal) the first from Europe. Implications for tyrannosauroid biogeography and evolution are discussed. The animal was part of an unusual taphonomic assemblage in which some elements were partially articulated while others were scattered or broken.

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1. Introduction

The Isle of Wight off the south coast of southern England has become famous for its fossil dinosaurs (Swinton, 1936; Blows, 1978; Benton & Spencer, 1995). Dinosaurs have been recovered from the cliffs and foreshore exposures of the island for well over 150 years (Fox, 1866) and the cliffs continue to be a source of valuable new material. The last 20 years have been particularly productive, with the discovery of several new specimens of iguanodontids, hypsilophodontids, a polacanthid ankylosaur and the new allosauroid theropod *Neovenator salerii* (Hutt *et al.*, 1996). Several isolated bones and at least one associated partial skeleton of a pterosaur have also been discovered (Martill *et al.*, 1996). There have also been recent reassessments of material collected during the 19th century (Howse & Milner, 1993; Blows, 1995; Naish, 1999a, b).

Here we report a new discovery in which an assemblage of bones comprises the associated remains of three individual dinosaurs. Among this material is a new coelurosaurian theropod and an ornithopod probably referable to *Valdosaurus*. All of this material

is currently accessioned to the Museum of Isle of Wight Geology (MIWG), Sandown, on the Isle of Wight. This material will be transferred to new premises in 2001, but the accession numbers will remain the same.

2. Locality

For reasons of security we do not reveal the exact location of the site of the new discovery, as it is likely that more material remains to be collected. As the cliff recedes due to natural erosion during the next few years, members of the MIWG staff will monitor the site for new material.

The new specimen described here was obtained from cliffs of Lower Cretaceous strata on the southwestern coast of the Isle of Wight between Atherfield Point and Hanover Point (Figure 1). The coast here is subject to constant erosion and land slippage. This ensures continuous fresh exposure of vertebrate-rich strata representing a range of ancient fluvial and floodplain environments (Stewart, 1981a, b). The area is heavily collected with the result that many

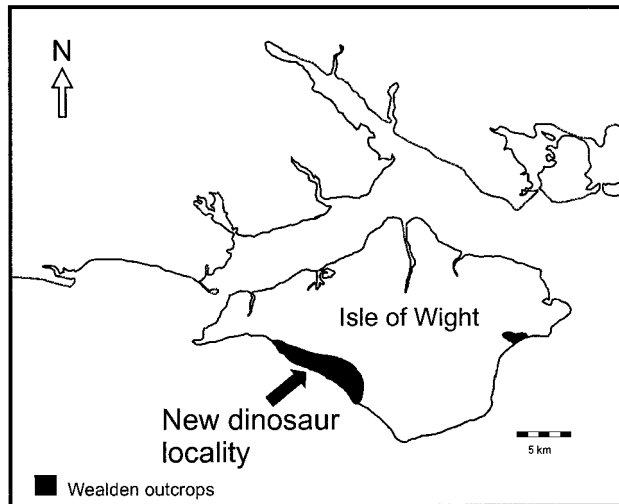


Figure 1. Sketch map of the Isle of Wight showing the approximate site of the new specimen and the distribution of dinosaur-bearing Lower Cretaceous strata on the island.

discoveries of dinosaurs (predominantly of isolated skeletal elements) are made each year. However, because those articulated and associated skeletons that are present tend to be uncovered over a period of several years, it is unfortunate that these important specimens tend to become dispersed through several collections. With the support of the local amateur fossil collectors and volunteers, the MIWG is attempting to monitor the whereabouts of Isle of Wight dinosaur material that exists in private collections.

3. Stratigraphy

The new specimen was obtained from a plant debris bed (Stewart, 1981a) in the Wessex Formation of the Wealden Group. The Wessex Formation is a largely argillaceous non-marine unit in which the most conspicuous lithologies are red or variegated clays with subordinate sandstones (Figure 2). Based on palynomorphs, much of the Wessex Formation is considered to be Hauterivian–Barremian in age, although the lower part may be Valanginian (Allen & Wimbledon, 1991). Plant debris beds form distinctive dark grey units 1–2 m thick within the Wessex Formation. Well known as a source of vertebrate remains, particularly dinosaur bones, they comprise flood-dominated accumulations of poorly sorted wood fragments (lignite and fusain) within a clay matrix. In some places there are irregular siderite concretions within the plant debris beds, often associated with bones. The beds are heavily pyritised in places, as are the bones.

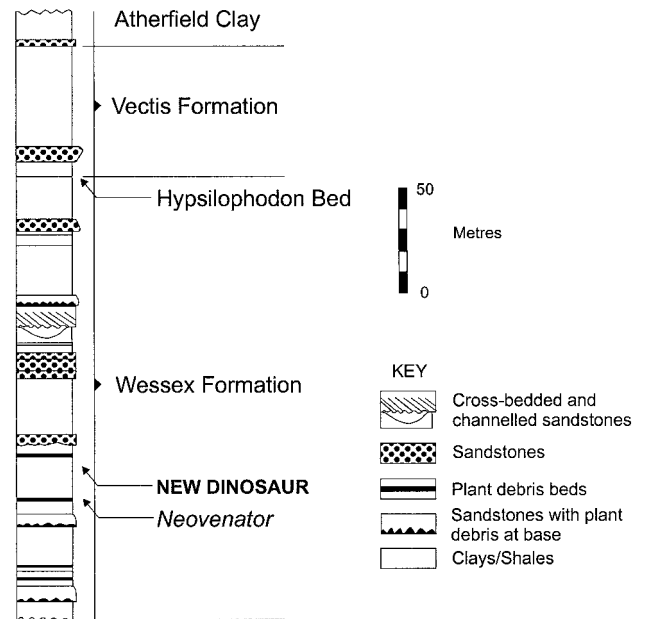


Figure 2. Simplified stratigraphic log for the Lower Cretaceous Wealden Group of the Isle of Wight indicating the stratigraphic horizon of the new dinosaur.

4. Material

Several bones, including a dentary, radius, ulna, several metatarsals and pedal phalanges, as well as numerous isolated teeth from the site represent a dryosaurid ornithomimid (MIWG 1997.885). The teeth show denticulations running over the tip of the crown indicating affinities with *Valdosaurus*: this material is here regarded as cf. *Valdosaurus* and is not discussed further.

There are many preserved elements pertaining to the new coelurosaur specimen including:

Skull. Right premaxilla; rostral portion of left maxilla; right lacrimal; fused nasals; left quadrate; both dentaries; isolated teeth.

Axial skeleton. Neural arch of axis; cervical, dorsal, sacral and probably caudal vertebrae.

Shoulder girdle and forelimbs. Both scapulae; left coracoid; both humeri; possible radius; portion of right ulna; one carpal; metacarpals; phalanges including unguals.

Pelvic girdle and hindlimbs. Fragments of ilium; proximal two-thirds of left tibia; left fibula; metatarsals; phalanges including one ungual.

This specimen represents a new genus and species and is here diagnosed and described.

5. Systematic palaeontology

Dinosauria Owen, 1842
 Saurischia Seeley, 1887
 Theropoda Marsh, 1881
 Tetanurae Gauthier, 1986
 Avetheropoda Paul, 1988
 Coelurosauria Huene, 1914
 Maniraptoriformes Holtz, 1996
 Tyrannosauroida Osborn, 1905
 Genus *Eotyrannus* gen. nov.

Type species. *Eotyrannus lengi* sp. nov., by monotypy.

Etymology. Generic name from Greek *eo*, early, and *tyrannus*, tyrant, in allusion to tyrannosauroids as 'tyrant dinosaurs'.

Diagnosis. As for the type and only species.

Eotyrannus lengi sp. nov.

Figures 3–7

Etymology. After Mr Gavin Leng, the discoverer.

Holotype. MIWG 1997.550. Partial skeleton including skull and postcranial elements.

Stratotype. Wessex Formation, Wealden Group, probably Barremian, Early Cretaceous.

Type locality. Southwest coast of the Isle of Wight, England.

Diagnosis. Tyrannosauroid coelurosaurian theropod with serrated carinae on D-shaped premaxillary teeth. Maxillary and dentary teeth with apically complete denticulation; rostral carinae bear denticles for less than half the length of the denticle-bearing part of the caudal carinae. Denticle size difference index of *c.* 1.5. Rostral portion of maxilla laterally flattened with rostral border to the antorbital fossa sharply defined, ventral edge of maxilla straight. Coracoid with prominent mediolaterally-wide, subcircular glenoid directed caudally. Humerus with large internal cavity situated dorsally (anconally) with several smaller cavities situated ventrally. Manus proportionally long (digit II *c.* 95% humerus length) with three well-developed metacarpals. Carpals not reduced to simple elements as in tyrannosaurids.

Description

Skull. The right premaxilla is preserved (the left is absent) and is small compared to the rest of the skull elements (Figure 3). The rostral border of the premaxilla is nearly vertical with a premaxillary angle (angle between the rostral and alveolar margins of the

premaxilla: Kirkland *et al.*, 1993) of approximately 90°. The ventral alveolar margin is entire. This compares with the vertical rostral border seen in *Stokesosaurus* (Madsen, 1974), tyrannosaurids and some other theropods including *Ceratosaurus* and some megalosaurids and allosauroids. As in tyrannosaurids (Holtz, *in press*), in *Eotyrannus* the ventral ramus of the premaxilla is taller dorsoventrally than long rostrocaudally (Figure 3). Laterally the premaxilla is markedly convex and highly vascularised, with foramina linked by shallow canals. The caudal margin is incomplete. In rostral view, the conjoined premaxillae would present a broad-based triangle, tapering at 45° to its apex. In ventral view, there are four subcircular alveoli, two of which contain remnants of teeth and one a complete, erupted tooth. There is little difference in size between the alveoli. The resultant 'bite' is wide and almost horseshoe shaped (Figure 7B). The complete premaxillary tooth is D-shaped in cross section and with serrated carinae; a similar, isolated tooth would appear to be from the missing left premaxilla. The lingual face between the two carinae is flat and without vertical ridges while the labial surface is strongly convex. Both teeth have straight, conical roots.

Only a small part of the left maxilla is preserved (Figure 3). It includes the premaxillary symphysis, four complete alveoli with two replacement teeth, and the base of the nasal process. In lateral view, the maxilla is high-sided and flat craniocaudally and dorsoventrally. There are numerous foramina with linking canals. The ventral edge is straight along the preserved length. The base of the nasal process ascends at about 45°; its caudal margin is sharp and forms a precisely defined margin to the antorbital fossa. The interdental plates are small pointed processes, recalling the interdental plates on the dentary of *Troodon* (Currie, 1987), which are not clearly differentiated from the lingual surface of the maxilla. In contrast to *Neovenator* and some other theropods (where the medial alveolar margins end well above the ventral margin of the maxilla), the ventral margins of the alveoli descend almost as far as the lateral margin of the maxilla. The alveoli are in the form of narrow ellipses, each about 21 × 12 mm, and have two erupted teeth located *in situ*. Rostrally, the contact with the premaxilla is angled caudally at about 30° from the ventral margin of the maxilla.

The *in situ* maxillary tooth is laterally compressed with vertical cracking that is due to compaction. The denticles on the rostral carina are smaller than those on the caudal: there are 19–20 denticles per 5 mm on the rostral carina but 13 denticles per 5 mm on the caudal carina. The denticle size difference index

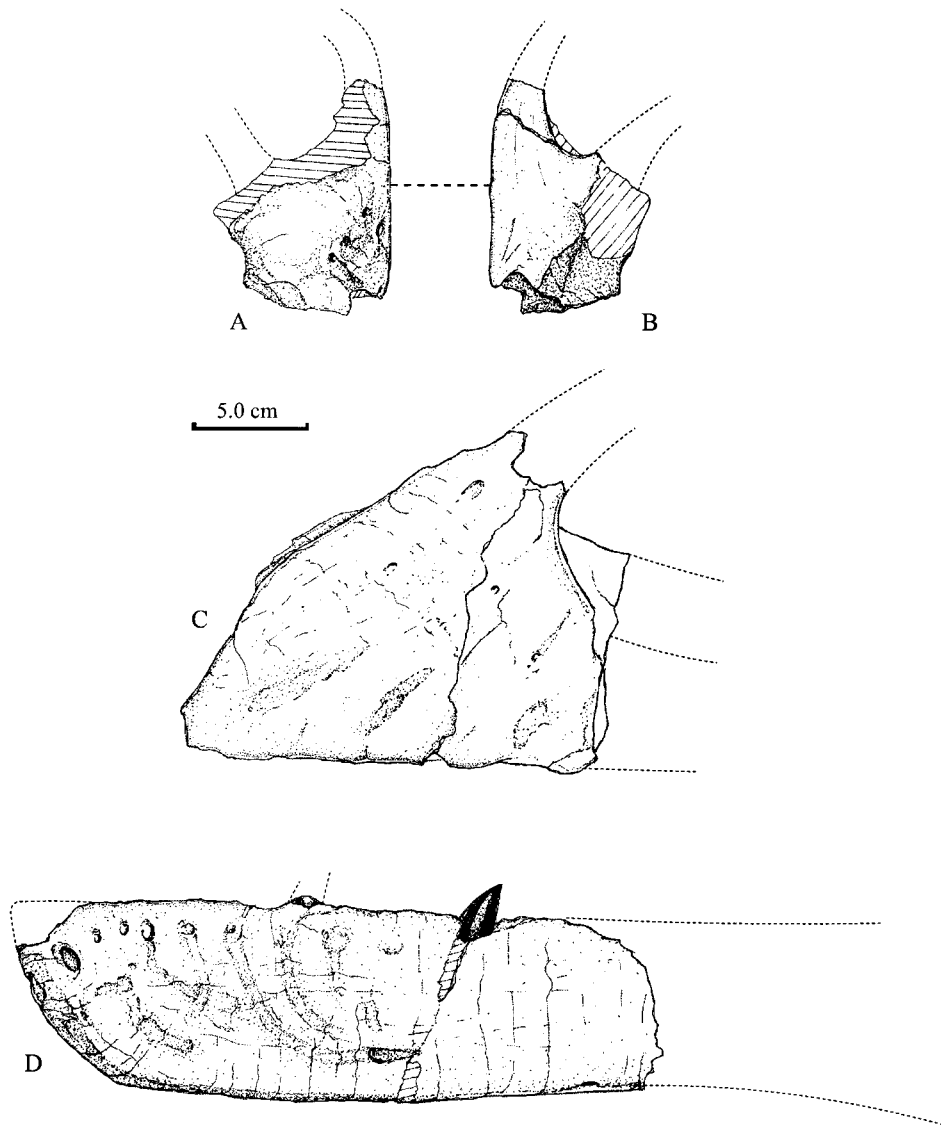


Figure 3. *Eotyrannus lengi* (MIWG 1997.550). A, right premaxilla of *Eotyrannus lengi* in lateral view. B, same in medial view. C, left maxilla in lateral view. D, left dentary of *Eotyrannus lengi* in lateral view.

(DSDI *sensu* [Rauhut & Werner, 1995](#)) is thus 1.5. This is rather high compared to tyrannosaurids (most of which have a DSDI of around 1.0) and approaches the condition seen in dromaeosaurids ([Rauhut & Werner 1995](#)). The denticles are continuous across the apex and are ‘cartouche shaped’ (*sensu* [Harris, 1998](#)).

The nasals are preserved almost complete and are fused along their length without any visible suture ([Figure 4](#)). They are 220 mm in length. In lateral view, the nasals are dorsally concave midway along their length, the caudal portion is raised by that part which would contact the lacrimal. Rostrally, the maxillary process is distorted by crushing but both it

and the base of the premaxillary process are shallow. The lateroventral surface of the maxillary process is flattened to receive the nasal process of the maxilla. This surface becomes a deep, narrow recess caudally (presumably receiving the lacrimal) on the body of the nasal. The caudal third of the nasal, the area of contact with the lacrimal, is slightly raised in the form of a low ridge. In dorsal view, the surface is highly vascularised with both large (4 mm in diameter) and small, randomly distributed, foramina. [Sues \(1977\)](#) noted the presence of similar nasal foramina in *Deinonychus*, *Velociraptor* and *Struthiomimus*. Rostrally, the dorsal surface is convex, passing into a median ridge and, just caudal to its midway point, into a wide,

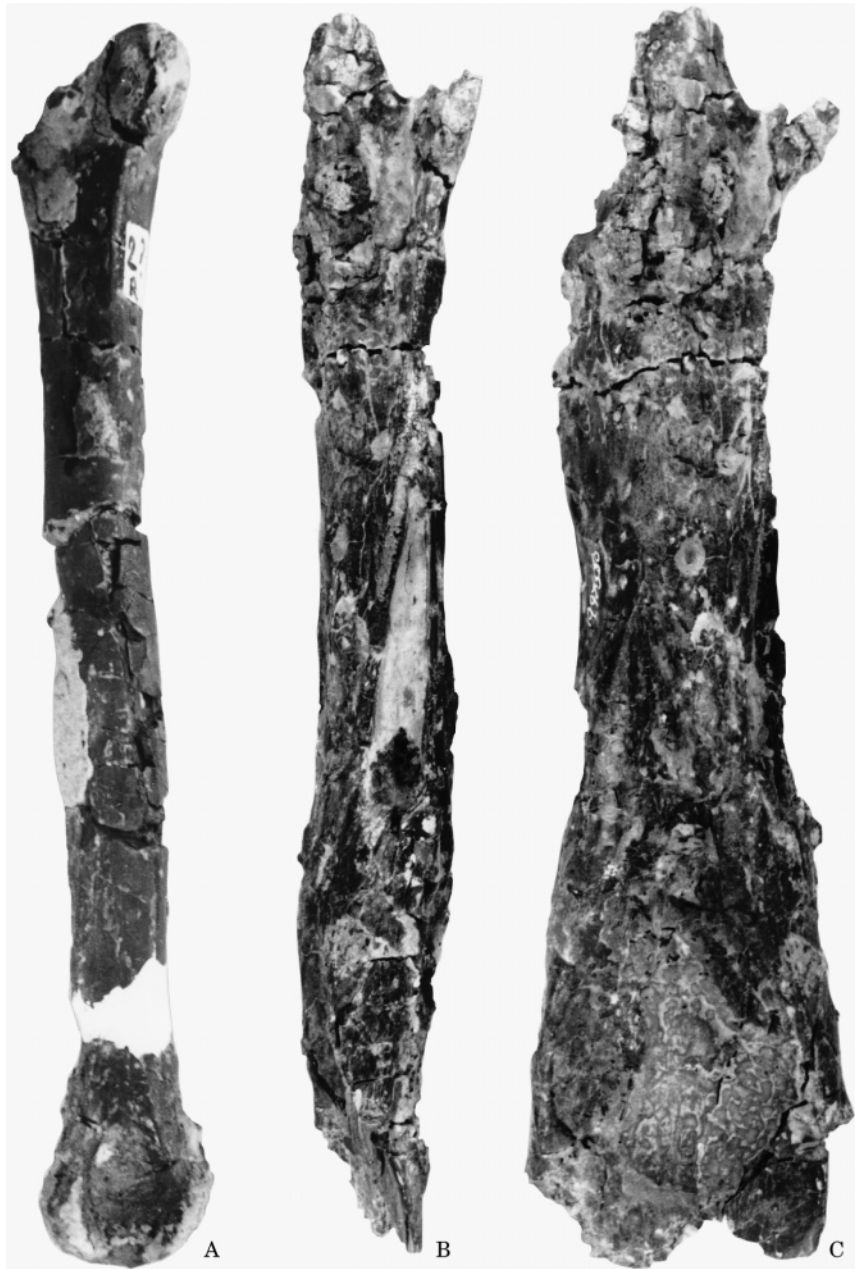


Figure 4. *Eotyrannus lengi* (MIWG 1997.550). A, right metatarsal II in medial view; $\times 1.5$. B, nasals in right lateral view; $\times 0.7$. C, nasals in dorsal view, $\times 0.7$.

shallow valley. Fused nasals are found in some other theropods including the Early Cretaceous Euroafrican *Baryonyx* (Charig & Milner, 1997) and the Late Cretaceous Madagascan abelisauroid *Majungatholus* (Sampson *et al.*, 1998). However, these taxa possess fused nasals that are distinct from those of *Eotyrannus* and other coelurosaur with fused nasals.

The incomplete right lacrimal is preserved. The preorbital bar is complete but the rostral ramus, area for postorbital contact, and ventral margin are all

damaged or missing. The gross morphology is similar to that of *Allosaurus fragilis* (Gilmore, 1920), including the position of the groove of the lacrimal duct.

The left quadrate is complete and has a dorso-ventral height of approximately 94 mm. It is robust with a broad shaft (42 mm wide across the ventral condyles) and a pterygoid process that does not extend as far rostrally as that of *Tyrannosaurus* (Carpenter, 1992); it is instead comparable superficially with that of *Sinraptor* (Currie & Zhao, 1994).

The medial condyle is larger and descends further ventrally than the lateral condyle. A raised ridge, marking the area of contact with the quadratojugal, runs the dorsoventral length of the quadrate's caudal margin. There is a shallow recess rostral to this ridge. A small foramen on the lateral surface of the pterygoid process, located within this recess, may indicate pneumaticity of the quadrate.

Both dentaries are present but the remainder of the mandibles are badly damaged. The left dentary is best preserved: it is superficially similar to that of *Deinonychus* and has almost entirely parallel dorsal and ventral borders (Figure 3). The dentary is a transversely thin element (15 mm) with a remarkably flat medial surface. There is no definite scarring to indicate the symphyseal contact with the right dentary but there are thin curving lines in the symphyseal region and a low ridge that runs along the rostral edge of the dentary's medial surface. The Meckelian groove is shallow and straight. As in the maxilla, the interdental plates are small spikes that project between the alveoli and cannot be reliably differentiated from the bone on the dentary's labial surface. The lingual alveolar margin thus resembles that of *Deinonychus* (Ostrom, 1969). In *Eotyrannus* the plates may, therefore, be fully fused or, as is the case with *Deinonychus*, reference to these structures as interdental plates may be a question of semantics (Currie, 1987, 1995; Ostrom, 1990). In lateral view, the dentary is dorsoventrally convex and exhibits several foramina linked by descending, curved and shallow canals. There are nine elliptically-shaped alveoli, one of which bears an emergent tooth. This tooth is morphologically identical to that described for the maxilla.

Axial skeleton. Several vertebrae are preserved but most are badly damaged and still partly encased in matrix. None is articulated and all neural arches are separated from their centra, an obvious indication that *Eotyrannus* was not fully grown. The axial vertebral table consists of a complete set of neurocentral processes. In dorsal view, the vertebral table is very similar to that of *Deinonychus* (Ostrom, 1969) with the postzygapophyses directed caudally and flaring laterally so that they are twice the transverse width of the prezygapophyses. The prezygapophyses project cranial to the neural canal, as in all tetanurans, and do not appear to be flexed (*sensu* Gauthier, 1986) such that the prezygapophyseal facets face craniodorsally. However, though Gauthier (1986) used 'flexed zygapophyses' as a coelurosaurian synapomorphy, this character state is not present in all taxa (Holtz, 1994; Makovicky, 1995). Notably, in the cranial cervical vertebrae of tyrannosaurids, the prezygapophyseal

facets project dorsally rather than craniodorsally. *Eotyrannus* may, therefore, share an apomorphic prezygapophyseal morphology with that of tyrannosaurids. The neural spine is low, transversely thin, and extends the entire length of the neural arch, thus being strikingly unlike the craniocaudally reduced spikes of allosauroids and dromaeosaurids (Gilmore, 1920; Currie & Zhao, 1994; Makovicky, 1995; Hutt *et al.*, 1996). Dorsally the spine is damaged so its height is unknown.

A cervical or cervico-dorsal centrum is also present and probably does not belong together with the axial spine table. This centrum is ventrally unkeeled, broader than tall, and strongly waisted at mid-length, being 50 mm long craniocaudally and 30 mm tall. It has a single large cranioventral pleurocoel on each lateral wall, 5 × 8 mm in diameter. Breaks reveal that the centrum has an internal structure of large-celled pneumatophores. The centrum is opisthocelous.

Cranial dorsal vertebrae are represented by several centra: these are elongate, narrow-waisted at mid-length and have flared articular faces that are slightly concave. Caudal dorsal centra, if correctly assigned, shorten in craniocaudal length as they approach the sacrum. A typical caudal dorsal centrum is between 45–55 mm craniocaudally: dorsal centrum 13 (if 14 are assumed) is 64 mm long and dorsal 14 is 52 mm long. The probable last sacral centrum is 71 mm long. This centrum is ventrally keeled with one small pleurocoel on each side. It was clearly unfused with adjacent vertebrae and is another indication that *Eotyrannus* was not fully grown.

Appendicular skeleton. Much of both shoulder girdles is preserved; the left is the more complete (Figure 7C). The scapular blade, missing only its distal tip, is elongate, narrow, mostly parallel-sided and about 285–295 mm long. At mid-shaft it is about 35 mm wide and curves medially to follow the lateral wall of the thorax. The proximal part of the scapula, the acromion process and glenoid cavity, is greatly expanded, being at least twice the width of the blade at mid-shaft. The left coracoid has moved a few millimetres out of articulation with the scapula: most of its margins are missing or obscured by matrix. The glenoid fossa is separated from the ventral caudal process by a U-shaped notch. The coracoid is strongly convex ventrally. Located laterally on the ventral surface is a small (6 × 8 mm in diameter) boss-like coracoid tubercle (see Norell & Makovicky, 1999). This is seen widely in other theropods including dromaeosaurids (Ostrom, 1969; Burnham *et al.*, 2000), ornithomimosaur (Osmólska *et al.*, 1972) and others, and has also been reported for the

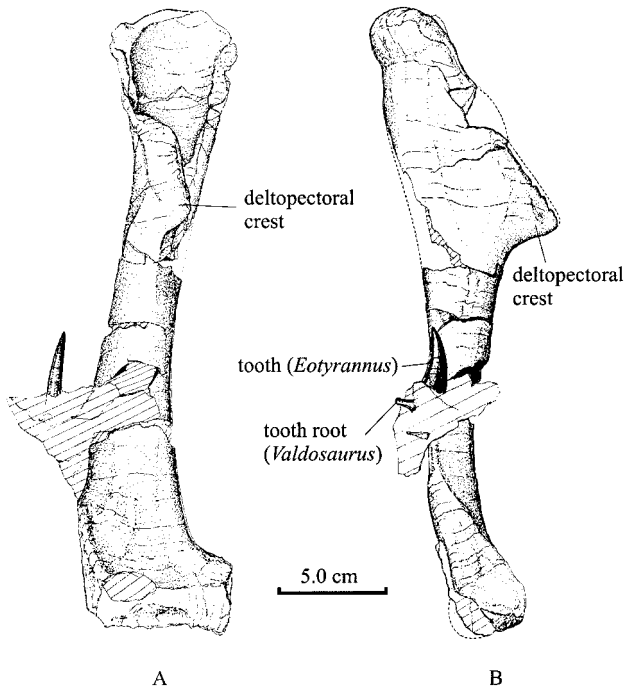


Figure 5. *Eotyrannus lengi* (MIWG 1997.550). Right humerus of *Eotyrannus lengi* in A, cranial, and B, lateral views. A single maxillary tooth of *E. lengi* and a tooth root of cf. *Valdosaurus* are attached to the matrix.

prosauropod *Massospondylus* (Ostrom, 1976; Cooper, 1981; Nicholls & Russell, 1985). Peculiarly, there is no sign of a coracoid foramen. Absence of a coracoid foramen has also been reported for the dromaeosaurid *Bambiraptor feinbergi* (Burnham *et al.*, 2000). The complete scapulocoracoid of *Eotyrannus* would have been approximately 385 mm long.

Much of the forelimbs is preserved. The right humerus (Figures 5, 6) is 235 mm long, although breaks and compaction have artificially lengthened it by 10–15 mm. It is just under two-thirds the length of the scapulocoracoid. Compared with a cast of a similar sized humerus (MIWG 2000.411) of *Allosaurus fragilis*, it is superficially similar but more gracile. The deltopectoral crest is prominent and terminates abruptly about one-third along the length of the shaft. In lateral view, the distal end of the shaft curves cranially. The humeral head is well delineated from the shaft. In cross-section, immediately distal to the deltopectoral crest, there is a large (15 × 10 mm) irregular medullary cavity and three smaller cavities (of between 2–6 mm width), two of which are circular, the third irregular. These cavities may invade the deltopectoral crest. It is tempting to suggest that these may indicate pneumaticity of the upper arm; however, the crushed state of the proximal humerus makes identification of external foramina impossible.

A probable right ulna consists of the proximal head and a fragment of shaft: only the dorsal and lateral surfaces are visible. The lateral surface is concave for the reception of the radius. The dorsal surface, the area for humeral articulation, is shallowly concave. The shaft in lateral view is concave, and in cross-section is ovoid. A fragmentary radius may be represented.

Carpals, metacarpals and phalanges from both hands are present, but almost all are difficult to orientate. Exceptions are parts of the left carpus: a complex, squarish bone compressed in one plane and with a distinct trochleated surface is present and may be the radiale. The probable dorsal and ventral surfaces are proximodistally narrow, gently concave and curved.

The metacarpus is represented by the left metacarpal I and the proximal ends of what appear to be metacarpals II and III. Metacarpal I is gracile, more elongate proportionally even than that of *Deinonychus*, and with its distal end twisted strongly medially relative to the long axis of the proximal end (Figure 7E–G). Proximally, the articular surface has a broad base and narrow apex. There is a well-developed lateral facet for contact with metacarpal II and shallow distal collateral fossae. At mid-section, the shaft is narrow. The lateral condyle is larger and more robust than the medial and the intercondylar groove is wide and deep. The medial condyle terminates about 10 mm proximal to the lateral condyle and therefore throws this digit about 40° medial to the long axis of digit II.

Various phalanges are preserved, but they are difficult to position. The most robust is 70 mm long. Its proximal articulation is deeply biconcave with a well-defined proximodorsal border. The collateral fossae are elliptical and deep and the condyles are well differentiated from the narrowly waisted shaft. Based on the size of metacarpal I, this phalanx appears to be too large to have belonged to digit I. Other preserved phalanges are less robust; of particular note is a phalanx 85 mm long. This may be phalanx II of digit II, if the usual theropod configuration is applied to *Eotyrannus*. Two manual unguals are preserved: the larger is probably from digit I and measures 103 mm (10–15 mm of its tip is missing) along the outside curve. The proximal end is expanded into a narrow, grooved articular face below which is a bulbous flexor tubercle. The ungual is laterally compressed, with both sides showing symmetrical grooves for attachment of the keratin sheath. The second, smaller ungual, probably from digit II, is less robust and less curved. It measures 95 mm along the outside curve (10–15 mm of the tip is missing), or approximately



Figure 6. Right humerus of *Eotyrannus lengi* in A, lateral; B, caudal; and C, cranial views. All $\times 0.7$.

70 mm in a straight line from the tip to the proximal articular surface.

The possible presence of all three phalanges from manual digit II allows us to calculate a length of approximately 225 mm for this digit, a length that is

about 95% of the length of the humerus. This is far higher than the second manual digit to humerus length of the tyrannosaurid *Gorgosaurus libratus* (76%, with length of ungual estimated) and even exceeds that of the dromaeosaurid *Deinonychus antirrhopus*

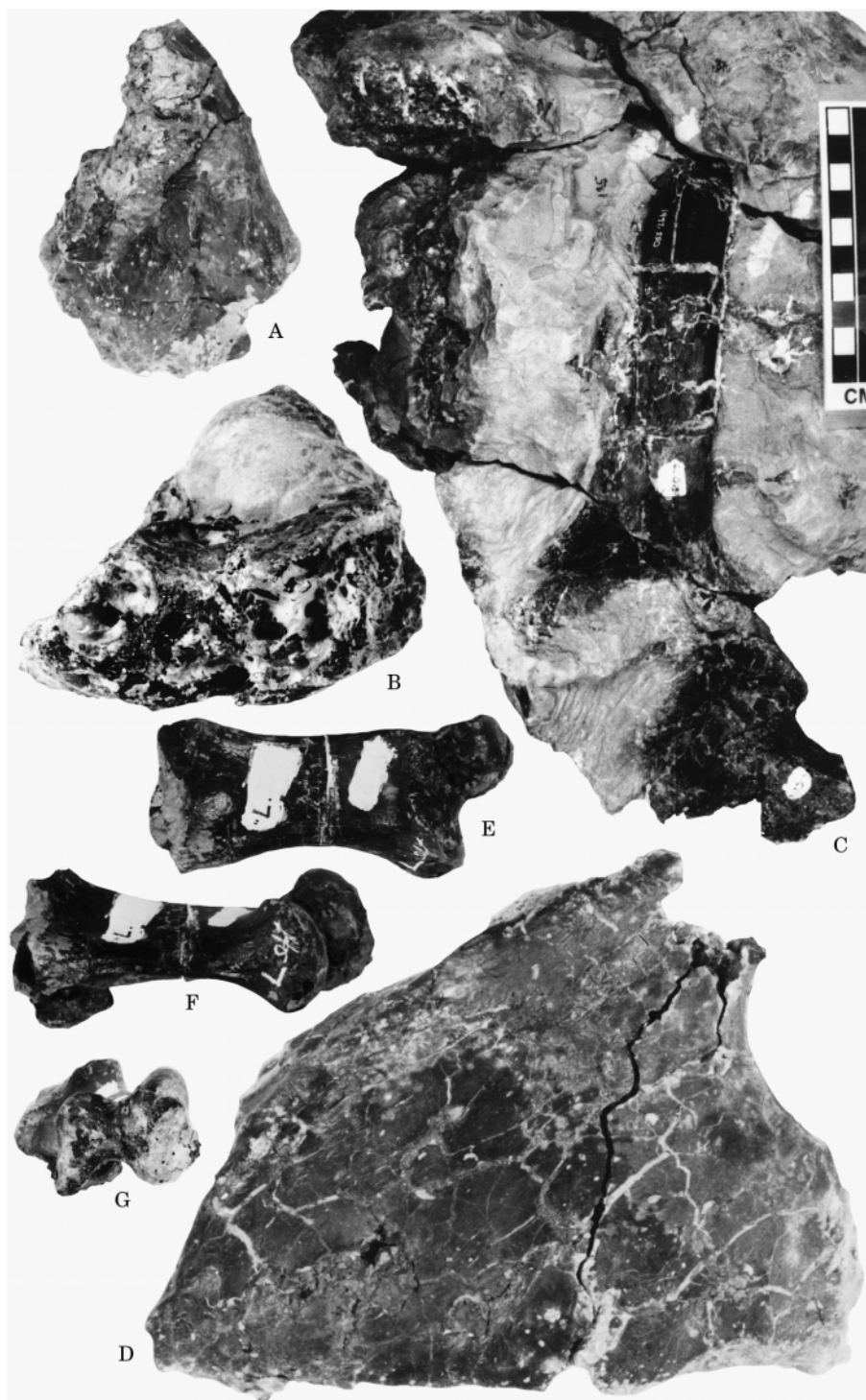


Figure 7. *Eotyrannus lengi*. A, right premaxilla in right lateral view; $\times 1$. B, right premaxilla in alveolar view; $\times 1.5$. C, left scapulocoracoid; $\times 0.5$. D, left maxilla in left lateral view; $\times 1$. E–G, metacarpal I of the left hand in dorsal, medial and distal views respectively; all $\times 1$.

(approximately 80%, based on data from more than one similar-sized specimen) (Lambe, 1917; Ostrom, 1969). Though the calculations for *Eotyrannus* are

circumstantial, they are in agreement with the elongate proportions of the complete metacarpal I and the preserved parts of the second and third metacarpals.

Eotyrannus would thus appear to have been an exceptionally long-handed theropod.

A fragment of ilium is preserved but is obscured by matrix. In cross-section it is uniformly 3–4 mm thick. No other part of the pelvic girdle is recognisable. Of the hindlimbs, only the proximal two-thirds of the left tibia is preserved and a similar portion of the left fibula. Both portions are about 350 mm in length. Several metatarsals and phalanges are also present.

The left tibia is elongate and gracile, and with a single poorly developed cnemial crest. The maximum craniocaudal width of the proximal tibia (therefore including the cnemial crest) is 95 mm. The narrowest preserved diameter of the tibial shaft is 35–38 mm. The fibular crest is short and robust and like an inverted V in cross-section. The ridge of the fibular crest does not have a flattened platform as do the tibiae of some large theropods such as the Lower Jurassic English specimens BMNH R1102 and R39496 [the latter originally part of the type material of the thyreophoran *Scelidosaurus harrisoni* (Newman, 1968)]. A large foramen (4–7 mm) is located adjacent to the distal part of the fibular crest. This indicates that Naish's (1999b) proposal that coelurosaurs may be united by a proximally located tibial foramen is incorrect. The fibula is an elongate, slender element in which the proximal third is expanded craniocaudally.

Both feet are represented by metatarsals and phalanges. Metatarsal II of the right foot is fractured and crushed, though mostly complete: its length is about 250 mm (Figure 4A). It is slender with an expanded proximal head that, in dorsal view, is semi-circular with a flattened medial facet for the reception of metatarsal three. The facet continues distally for about one-third of the length of the metatarsal. In lateral view, the cranial and caudal margins are straight and parallel and about 20 mm apart. Distally, the medial condyle is well developed but smaller than the lateral condyle. The collateral fossae are deep and wide, the lateral one especially so, with a diameter of 13 × 20 mm. The lateral condyle ends proximal to the medial condyle, directing the digit medially relative to digit three. Only distal fragments of both third metatarsals remain; they are badly damaged and insufficient of the shaft remains to support or deny an arctometatarsalian condition. Both distal fragments have wide, deep collateral fossae.

Metatarsal IV of the left pes is well preserved, about 260 mm long and also gracile. In craniomedial view, there is a strongly developed proximal concave facet for the reception of metatarsal III, which persists distally for about 50 mm. The proximal shaft has a convex cranial surface. In caudal view, the proximal head, though incomplete, is expanded

lateromedially and is shallowly concave caudally. The distal two-thirds of metatarsal IV show a flattened caudal surface and a distal expansion similar to metatarsal II.

In most theropods the most robust phalanx of the pes, although not always the longest, is phalanx I of digit III. Following this pattern it would appear that both the left and right first phalanx of digit III are preserved. Phalanx I (from the left side?) is approximately 87 mm long (allowing for crushing), elongate, and with expanded proximal and distal articulations. It is narrowest at mid-shaft where it is 9–10 mm wide. The proximal end is 35 mm in diameter and the distal end 32 mm across the condyles. The proximal articulation is deeply concave, and the insertion points for the flexor tendons are two well-defined proximal ridges on the ventral surface. Distally, there is a deep, wide pit on the dorsal surface, just proximal to the condyles. This is for an extensor tendon. The condyles are subequal, as are the large and deep collateral fossae, which are 10 mm in diameter. The various pits and ridges imply powerful flexor and extensor tendons, and perhaps a considerable range of flexion of the digits.

Other phalanges are preserved, most still embedded in the matrix. A small, isolated phalanx is tentatively identified as III or IV from digit IV of the right foot. In dorsal view, it is slightly waisted with a well-developed proximal dorsal process, a biconcave proximal articulation, well-defined collateral fossae, and with the lateral condyle slightly larger than the medial condyle. There is one preserved ungual phalanx still partly embedded in matrix. About 20 mm of the tip is missing. It is fairly strongly down-curved and probably belongs to the fourth digit.

We estimate that *Eotyrannus* had a hindlimb approximately 1.5 m in length. The material known indicates that the type specimen was an animal of 4–5 m in length. The absence of neurocentral, scapulo-coracoid and sacral fusion implies that it was not fully grown and that adults may possibly have reached much greater sizes. This raises the interesting possibility that certain large tetanuran theropod elements from the Wessex Formation may not belong to allosauroid taxa, as has been assumed, but to *Eotyrannus* instead.

6. Discussion and comparisons

Comparison with other Wealden Group theropods

Eotyrannus adds a further genus to Wealden Group theropod diversity. Several Wealden theropods should be considered *nomina dubia* as they were erected on isolated elements (Naish, 1999a, b). Unfortunately,

Eotyrannus does not resolve the status of any of these taxa, nor does it appear to be synonymous with any of them. However, several of these taxa were erected for material not represented in the *Eotyrannus* holotype.

Among the Wealden Group theropods *Eotyrannus* can be compared with *Thecocoelurus daviesi* and *Calamosaurus foxi*, both of which were erected for cervical vertebrae (Seeley, 1888; Lydekker, 1889). The presence of one well-preserved cervical neural arch of *Eotyrannus* allows comparison with these forms. BMNH R181, the incomplete holotype cervical vertebra of *Thecocoelurus daviesi*, has a distinctive hourglass-shaped ventral sulcus and ventrolateral raised edges. In these features and others (absent from the vertebrae of *Eotyrannus*) *T. daviesi* is reminiscent of the cervical vertebrae of *Chirostenotes pergracilis* (Sues, 1997) and probably represents an oviraptorosaur (Naish, 1999a; Naish & Martill, submitted). It is clear that *Eotyrannus* is not an oviraptorosaur and therefore synonymy with *T. daviesi* is improbable. The cervical neural arch known for *Eotyrannus* differs from that of *Calamosaurus* in having robust postzygapophyses that project markedly laterally and in lacking the distinctive square-shaped diapophyses of this taxon (Naish, 1999a). However, the *Calamosaurus* material does not include an axis.

Eotyrannus clearly has no close affinity with the large spinosauroid *Baryonyx* or with the allosauroids *Neovenator* or *Becklespinax*. *Ornithodesmus cluniculus* and *Aristosuchus pusillus* are both based on sacra and parts of the pelvis. Sacral vertebrae of both *O. cluniculus* and *A. pusillus* lack the ventral keel seen in *Eotyrannus* (Howse & Milner, 1993). *A. pusillus* also lacks pleurocoels on its sacral vertebrae. Furthermore, *O. cluniculus* is reminiscent of coelophysoids and abelisauroids and may not be a tetanuran while *A. pusillus* appears to represent a compsognathid (Naish, 1999c).

Phylogenetic position of Eotyrannus

The strap-like scapula, elongate manus, caudally tapering coracoid and presence of pleurocoels in the dorsal vertebrae support the inclusion of *Eotyrannus* within the Tetanurae. The elongate, narrow nasals of *Eotyrannus* also support a tetanuran affinity as narrow nasals are not present in non-tetanuran theropods (Bakker *et al.*, 1988; Charig & Milner, 1997). The presence of a flattened lateral face on the first metacarpal of *Eotyrannus* indicates that this element was closely adpressed to the second metacarpal: this is also a tetanuran character (Gauthier, 1986).

The lack of nasal participation in the antorbital fossa, presence of a markedly gracile, elongate manus,

and lack of evidence for a cranial notch between the scapula and coracoid suggest that *Eotyrannus* is a coelurosaur and not an allosauroid. The well-developed caudal projection on the coracoid appears better developed in *Eotyrannus* than that seen in allosauroids and further supports the inclusion of *Eotyrannus* within the Coelurosauria.

Comparison of Eotyrannus with other coelurosaur

The presence of fused nasals, a rostrocaudally short but dorsoventrally deep premaxilla, D-shaped premaxillary teeth and proportionally elongate tibiae and metatarsals in *Eotyrannus* immediately invite comparison with tyrannosaurids, the only other coelurosaurian group that also exhibits all of these characters (Holtz, 1994, and in press). This suggests either that *Eotyrannus* is a tyrannosaurid, or that it is closely related to the Tyrannosauridae. It is unfortunate that the *Eotyrannus* holotype does not preserve a braincase, caudal skull roof, more complete metatarsus or pelvis as these parts of the skeleton are highly apomorphic in tyrannosaurids (Holtz, 1994, and in press; Molnar *et al.*, 1990). Superficial similarities are apparent, however, between *Eotyrannus* and some other coelurosaur groups. Before examining the possible tyrannosaurid affinity of *Eotyrannus* further we discuss these other groups so that they can be eliminated from further comparison.

Like *Eotyrannus*, ornithomimosaurs possess proportionally elongate tibiae. All ornithomimosaurs however, including the basal toothed forms, have shallow premaxillae with an elongate caudal process that separate the maxilla from the nasal (Barsbold & Osmólska, 1990; Perez-Moreno *et al.*, 1994). D-shaped premaxillary teeth are known for the basal Spanish ornithomimosaur *Pelecanimimus* (Perez-Moreno *et al.*, 1994). However, these lack serrations. With the exception of the gigantic *Deinocheirus*, all known ornithomimosaurs have straightened manual unguals with weak flexor tubercles. The straight humerus with weak deltopectoral crest seen in ornithomimosaurs further suggest that *Eotyrannus* is not part of this group. Like *Eotyrannus*, ornithomimosaurs have a tuber on the coracoid (Barsbold & Osmólska, 1990; Perez-Moreno *et al.*, 1994), but so also do some other theropod groups (see below).

Superficial similarities are evident between *Eotyrannus* and troodontids. For example, troodontids have gracile hindlimbs, strongly curved manual unguals, and a dentary with nearly parallel dorsal and ventral margins. However, *Eotyrannus* lacks the waisted crown-root junction and proportionally large, apically hooked denticles seen in the teeth of

troodontids. *Eotyrannus* also lacks other key characters of this group including the long, shallow snout with low maxillae and nasals (Currie *et al.*, 1990; Norell *et al.*, 2000). *Eotyrannus* is therefore probably not a troodontid.

Based on the morphology of velociraptorines and *Sinornithosaurus*, there are a number of important differences between dromaeosaurids and *Eotyrannus*. The vertebrae of *Eotyrannus* do not possess hypapophyses, and its lacrimal is not T-shaped as it is in dromaeosaurids (Ostrom, 1969; Sues, 1977; Xu *et al.*, 1999). No dromaeosaurid has been described with medially fused or dorsally straight nasals like those of *Eotyrannus*. Xu *et al.* (1999) argued that the glenoid for the dromaeosaurid humerus is formed primarily by the scapula. This condition is clearly different from that of *Eotyrannus*.

Dromaeosaurus, known only from cranial material (Colbert & Russell, 1969; Currie, 1995), does compare favourably in some features with *Eotyrannus*. In the premaxilla, the teeth of *Dromaeosaurus* have both carinae on the lingual surface. However, the caudal carinae on these teeth is still located caudolaterally (rather than caudally) meaning that the teeth are not D-shaped in cross-section (Currie *et al.*, 1990). The maxilla of *Dromaeosaurus* preserves a prominent rostromedial process, as reported for velociraptorines (Ostrom, 1969). Although this process was apparently present in *Eotyrannus* (it appears to be broken), it is located further dorsally on the medial side of the maxilla than is the case in dromaeosaurids. While it is assumed that *Dromaeosaurus* had a T-shaped lacrimal and unfused nasals like velociraptorines and *Sinornithosaurus*, these elements are unknown for *Dromaeosaurus*. Indeed, if *Dromaeosaurus* possessed the postcranial characters noted above for the velociraptorines, an affinity with *Eotyrannus* can be eliminated.

Unlike *Eotyrannus*, compsognathids exhibit three unserrated teeth in each premaxilla (Bidar *et al.*, 1972; Ostrom, 1978). Furthermore, compsognathid premaxillae are low in lateral view and there is a diastema between the last premaxillary and first maxillary tooth. *Deltadromeus* has relatively weak humeri and a coracoid that is both markedly expanded craniocaudally and lacks the distinct caudal notch seen in the coracoid of *Eotyrannus* (Serenó *et al.*, 1996). The distinctive maxillary teeth (which have labio-lingually broad denticles that are widely separated from one another), weak deltopectoral crest and large cnemial crest of *Dryptosaurus*, an Upper Cretaceous genus allocated to the Maniraptora by Carpenter *et al.* (1997), are not suggestive of a close relationship with *Eotyrannus*. *Ornitholestes* differs from *Eotyrannus* in having

unserrated teeth (of unspecified location: Osborn, 1903, 1917), comparatively short distal hindlimb elements and a dentary that curves ventrally at its tip. *Scipionyx*, known only from a juvenile specimen, differs markedly from *Eotyrannus* in the form of its maxilla. In *Scipionyx*, the part of the maxilla rostral and ventral to the rim of the antorbital fossa is small (Dal Sasso & Signore, 1998), in marked contrast to *Eotyrannus*. *Bagaraatan* is a poorly known Mongolian coelurosaur with gracile hindlimbs (Osmólska, 1996). Unlike *Eotyrannus*, *Bagaraatan* has two cnemial crests and its dentary is of a different shape from that of *Eotyrannus*. *Nedcolbertia* from the Cedar Mountain Formation of Utah, USA, is also superficially like *Eotyrannus* in having elongate, gracile hindlimbs and a coracoid with a prominent ventral tuber (Kirkland *et al.*, 1998). The well-developed cnemial crest and elongate fibular crest on the tibia and weakly curved manual unguals that have been described for *Nedcolbertia* (Kirkland *et al.*, 1998) indicate that it is not synonymous with *Eotyrannus*.

The maxillary and dentary teeth of *Eotyrannus* are peculiar in having denticulations that are complete across the tip of the crown. Apical denticulation is also known for the allosauroids *Acrocanthosaurus* and *Neovenator*, the problematical coelurosaur *Ricardoestesia* and *Dryptosaurus*, and the tyrannosaurid *Alectrosaurus* (Carpenter *et al.*, 1997; Harris, 1998). This distribution indicates homoplasy of this character within Tetanurae. However, the presence of apically complete denticulations in a tyrannosaurid provides another character common to this group and *Eotyrannus*. An affinity between *Eotyrannus* and allosauroids can clearly be excluded, as discussed above. The holotype dentary and dentition of *Ricardoestesia* are not suggestive of a close affinity with *Eotyrannus*. In *Ricardoestesia*, the dentary is very elongate and gracile, and the teeth have denticulation on the rostral carina restricted to the tooth tip only (Currie *et al.*, 1990).

Using the character list provided by Holtz (in press) we recognise the following tyrannosaurid character states in *Eotyrannus*. The premaxillary tooth row arcade is oriented more mediolaterally than seen in other theropods; the ventral ramus of the premaxilla is taller dorsoventrally than it is long rostrocaudally; the premaxillary teeth are D-shaped in cross-section (Figure 8) with both carinae placed along the same plane perpendicular to the skull axis; the premaxillary teeth are smaller than the lateral teeth (17 mm crown height in premaxillary teeth compared to 25–28 mm crown height in lateral teeth); the nasals are fused; the acromial expansion is well developed and more than twice the midshaft width of the scapula. Holtz (in



Figure 8. Left premaxillary tooth in oblique lingual view; $\times 2$.

press) also notes that in tyrannosaurids the tibiae and metatarsals are proportionally elongate. These elements are slender in *Eotyrannus* but their proportions with respect to other hindlimb elements cannot yet be tested. The conclusion that *Eotyrannus* is closer to tyrannosaurids than to other coelurosaurs is thus the most likely option.

Position within Tyrannosauroidea of Eotyrannus

The presence of elongate, well-developed forelimbs and elongate cervical vertebrae in *Eotyrannus* suggest that, if it is closely related to tyrannosaurids, it is a primitive form compared to *Tyrannosaurus*, *Albertosaurus* and their relatives (the Tyrannosaurinae of Paul, 1988, and Holtz, 1994, and in press). These forelimb and vertebral characters, together with the ventrally straight margin of the maxilla and lack of both nasal rugosities and incassate lateral teeth, suggest that *Eotyrannus* is not a member of the group defined by members of the Tyrannosaurinae. Comparisons with aublysodontines, the less specialised sister group to the tyrannosaurines (Paul, 1988; Holtz, 1994, and in press), are therefore warranted. Following Holtz (in press) we recognise the Aublysodontinae for *Aublysodon molnari*, the Kirtland Shale aublysodontine and *Alectrosaurus olseni*.

Like other tyrannosaurids, aublysodontines possess fused nasals but, in contrast to *Eotyrannus*, a median suture is present rostrally (Molnar, 1978). Furthermore, unlike *Eotyrannus*, the premaxillary teeth of aublysodontines lack serrations and have a series of vertical ridges, described by Lehman & Carpenter (1990) as a bilobed median ridge, on the flattened lingual face between the two carinae (Molnar & Carpenter, 1989; Currie *et al.*, 1990). In contrast to *Eotyrannus*, aublysodontine dentaries have a

distinctive 'step' near the symphyseal region that results in an upturned rostral tip (Molnar, 1978; Paul, 1988). The lack of aublysodontine characters in *Eotyrannus* indicates that it is not part of the group defined by *Aublysodon molnari*, the Kirtland Shale aublysodontine and *Alectrosaurus olseni*.

Exclusion of *Eotyrannus* from both the Aublysodontinae and Tyrannosaurinae suggests that it may represent the sister-taxon to the aublysodontine+tyrannosaurine clade. This hypothesis is supported by the fact that some of the tyrannosaurid character states present in *Eotyrannus* are morphologically intermediate between those of non-tyrannosaurid coelurosaurs and those of tyrannosaurids. For example, while the premaxillary tooth row arcade of *Eotyrannus* is oriented more mediolaterally than in non-tyrannosaurid theropods, it is not as mediolaterally oriented in *Eotyrannus* as it is in tyrannosaurines (the condition of this character is presently unknown for aublysodontines) (Osborn, 1912; Paul, 1988; Holtz, in press). Similarly, the difference between the rostrocaudal length and dorsoventral height of the premaxilla's ventral ramus is not as marked in *Eotyrannus* as it is in aublysodontines or tyrannosaurines, nor is the disparity between the premaxillary and lateral teeth as great in *Eotyrannus* as it is in aublysodontines and tyrannosaurines.

If the Tyrannosauridae is defined as a node-based taxon encompassing aublysodontines and tyrannosaurines (Holtz, in press), exclusion of *Eotyrannus* from this clade results in its exclusion from the Tyrannosauridae. A different interpretation of tyrannosaurid taxonomy is given by Sereno (1998) where the Tyrannosauridae is restricted to *Tyrannosaurus* and all taxa closer to it than to aublysodontines or *Nanotyrannus*. This definition is problematical in that most other workers regard aublysodontines as tyrannosaurids (Paul, 1988; Currie *et al.*, 1990; Lehman & Carpenter, 1990; Holtz, in press); furthermore, *Nanotyrannus* is probably synonymous with *Tyrannosaurus* (Carr, 2000). Our favoured hypothesis is, therefore, that *Eotyrannus* is a non-tyrannosaurid tyrannosauroid and the possible sister taxon to the Tyrannosauridae (Aublysodontinae+Tyrannosaurinae). Confirmation of this hypothesis awaits parsimony analysis.

Implications for tyrannosauroid evolution

Identification of *Eotyrannus* as a tyrannosauroid is interesting in the context of tyrannosauroid biogeography and macroevolution. The presence of an apparently basal tyrannosauroid in Europe is noteworthy as most other evidence suggests an

Asian origin for the Tyrannosauridae (Holtz, 1994; Buffetaut *et al.*, 1996; Manabe, 1999). However, the presence of *Stokesosaurus*, regarded by some workers as a possible tyrannosaurid or tyrannosaurid relative (Madsen, 1974; Paul, 1988), in the Upper Jurassic Morrison Formation of the western USA, suggests that early tyrannosauroid biogeography could have been more complex than this and that basal tyrannosauroids might have been more widespread.

Small teeth from the Upper Jurassic of Guimarota, Portugal identified as tyrannosaurid by Zinke (1998), suggest the presence of the Tyrannosauroidea in Europe prior to the Early Cretaceous. However, identification of these teeth is controversial and they could belong to another theropod taxon with D-shaped teeth. A fragmentary ilium also from Guimarota has been attributed to *Stokesosaurus*. This also indicates the presence of tyrannosaurids pending a review of this taxon (Rauhut, 2000). *Eotyrannus* is the first reported substantial European material that can be attributed to the Tyrannosauroidea.

A tyrannosauroid identity for *Eotyrannus* would also seem to confirm Holtz' (1994) suggestion that early relatives of tyrannosaurids were gracile 'tyrannoraptors' with elongate, well-developed forelimbs and grasping hands. However, *Eotyrannus* would appear to have been a large animal. This could suggest that early evolution of the Tyrannosauroidea occurred at large body size. Alternatively, *Eotyrannus* could represent a phylogenetic increase in body size independent from that which occurred later in derived tyrannosaurids.

7. Taphonomy and preservation

The following account is based on examination of the assemblage of bones as preserved in several portions of matrix that fit together. Together, these portions of matrix form one large and irregular concretionary mass. Broken edges of the concretionary mass suggest that some material is missing, perhaps lost to coastal erosion, while more material may well remain within the cliff exposure. Thus the account of the taphonomy is limited in scope.

The bones of *Eotyrannus* form part of an assemblage comprising associated but disarticulated dinosaur bones partially enclosed within concretionary siderite. *Eotyrannus* is associated with skeletal elements of cf. *Valdosaurus* sp. Some skeletal elements are almost in natural articulation with their adjacent elements, but most parts of the skeleton are disarticulated. The bones are preserved mainly as three-dimensional elements, but some localised crushing as well as cracking of elements has occurred. Some bones display fractured ends that are post-mortem but preburial,

suggestive of damage by trampling. Internally, void spaces are either partially empty or filled with diagenetic euhedral pyrite, overlain by white/grey calcite and white barite. Calcite also fills some compactional cracks of long bones. The bones are dark brown to black, and apart from the slight cracking are in a good state of preservation.

The disarticulated nature of the skeletal elements, while still retaining a spatial relationship with adjacent elements, indicates little movement after decomposition of the ligaments. The assemblage may therefore represent the remains of disrupted carcasses rather than a transported assemblage of unrelated elements. The association of elements of three different animals is less easy to explain. Such associations are, however, a relatively common occurrence for dinosaur discoveries in the plant debris beds of the Wessex Formation.

The plant debris beds represent flood events in which large volumes of transported forest litter comprising both small (mm-sized) and large (m-sized) pieces of wood were stranded in chaotic masses on the floodplains of the Wessex Formation. Although it is possible that herds of dinosaurs living on the floodplain were decimated by such floods, there is little evidence to support mass mortality. Isolated skeletons are, however, relatively frequently encountered in the plant debris beds, and probably represent individual drowning events. Presumably large carcasses would have generated considerable odours during decomposition on a subtropical, humid floodplain. With their probable superb sense of smell (cf. Brochu, 2000), theropod dinosaurs would have been attracted to such carcasses. Carcasses could have become battlegrounds if several theropods were simultaneously attracted to a site and competition between theropods may have resulted in deaths, thereby adding additional material to the site. Scavenger activity could also have resulted in disarticulation and also account for trampling damage. Support for this scenario is, admittedly, circumstantial.

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