



Theropod dinosaur diversity and palaeobiology in the Wealden Group (Early Cretaceous) of England: evidence from a previously undescribed tibia

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Abstract

A robust, partial right tibia of a theropod dinosaur (Natural History Museum London collections, BMNH R9385) is described for the first time. The specimen was collected at Hastings, Sussex (England) in the last century, and is among the oldest known of English Wealden Group theropods. It represents a tetanuran theropod that may have been about 3 m in total length, and is distinct from all currently known Wealden theropods for which tibiae have been described. The present specimen is significant palaeobiologically in exhibiting a series of theropod tooth marks on its caudal surface, indicating predation or scavenging by another theropod.

Abbreviations: BMNH: Natural History Museum, London; UCMP: Museum of Paleontology, University of California, Berkeley

Introduction

The Wealden Group rocks (Berriasian–Aptian, Early Cretaceous; see Kerth & Hailwood 1988) of mainland England, the Isle of Wight, and mainland Europe are famous for their diverse and abundant dinosaur fauna (Insole & Hutt 1994, Benton & Spencer 1995). In view of the fact that isolated elements are common, and that some of the nineteenth century workers who described these fossils tended to erect new taxa rather than refer new specimens to existing ones, the nomenclature and taxonomy of Wealden Group dinosaurs are complex. The dinosaur assemblage is diverse and sauropods (Charig 1980, Blows 1995), ornithopods (Galton 1974, 1975, Norman 1980, 1986, 1990a) and ankylosaurs (Blows 1987, Pereda-Suberbiola 1993) are well represented. A stegosaur (Barrett & Upchurch 1995) and a supposed pachycephalosaur (Galton 1971) are also in evidence. The historical importance of Wealden Group dinosaurs is testified by the fact that two of the very

earliest recognised of all dinosaurs, *Iguanodon* and *Hylaeosaurus*, come from Wealden strata.

Since Fox (1866) created the name *Calamospondylus oweni* for a series of vertebrae, twenty species have been erected for theropod remains from the Wealden Group. Many of these are synonyms or are based on partial or undiagnostic remains which must be regarded as nomina dubia. Taxonomic reviews include those of Ostrom (1970), Galton (1973), Norman (1990b) and Insole & Hutt (1994). Two large theropods represented by fairly complete skeletons, *Baryonyx walkeri* Charig & Milner 1986 and *Neovenator salerii* Hutt et al. 1996, have recently been added to the list of Wealden Group theropods (Charig & Milner 1986, 1990, 1997, Hutt et al. 1989, 1996). Other large Wealden Group theropods are known from fragmentary remains that were described in the last century (Lydekker 1889), and others await description (Naish & Hutt in prep., Hutt et al. in prep.).

The specimen described here is not clearly referable to any of the above-mentioned taxa and augments

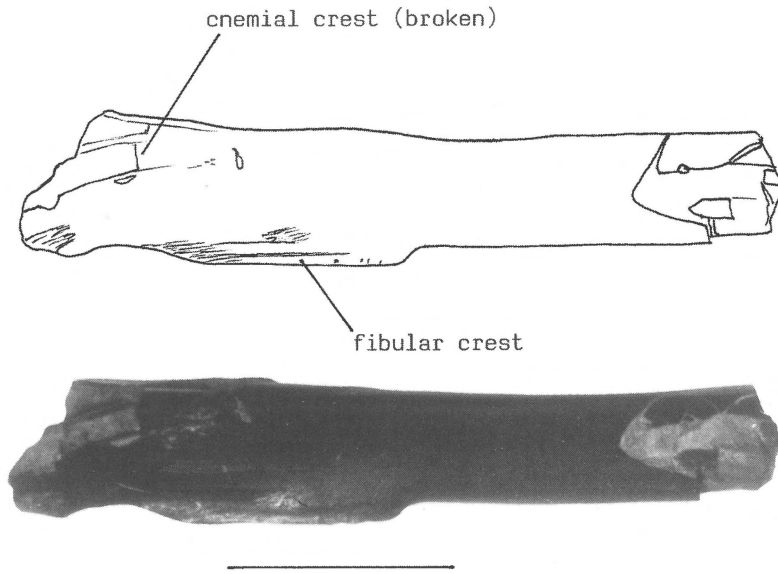


Figure 1. BMNH R9395, a partial right tibia (total length 160 mm) of a theropod dinosaur, in cranial view. Scale bar: 50 mm.

the known diversity of Wealden Group theropods. BMNH R9385 is a robust, partial right tibia of a theropod, collected in the nineteenth century from Wealden Group rocks at Hastings, England. Unlike many other fragmentary remains of Wealden Group theropods collected in the last century, it has never been described, illustrated or referred to except by Brookes (1997) in her unpublished master's thesis and, briefly, by Naish (1998).

Locality and age

Because BMNH R9385 has so far remained undescribed, no secondary source reviews its history. Fortunately, a number of letters and notes kept with the specimen allow some information to be gleaned, but data are wanting with respect to precise locational and stratigraphic detail. BMNH R9385 was evidently collected in the nineteenth century from Hastings and formed part of the Dawson Collection prior to its being added to the BMNH collections. A handwritten and undated note also reveals that it was originally obtained (and collected?) by a medical doctor, the signed name of whom is unfortunately illegible.

If BMNH R9385 was collected from an outcrop at Hastings (no further locality data are available), it

must have come from the Hastings Beds (Berriasian-Valanginian), the only Wealden Group outcrops in the area (Benton & Spencer 1995). This stratigraphic position indicates an older age than that of most other Wealden Group theropods, which come from the overlying Weald Clay and Wessex Formation. Together with various indeterminate large carnivorous dinosaurs, BMNH R9385 therefore represents one of the oldest Wealden Group theropods.

Letters and notes kept with the specimen reveal that it was previously identified as a turtle femur or bird tibiotarsus. The BMNH acquisition label identifies it as 'coelurosaur(?)'. The latter identification is evidently the most correct of the three, but while the bone is clearly of a theropod, its morphology (see below) suggests that it may not be coelurosaurian.

Description

The specimen is 160 mm long, but is missing both the proximal articular surface and its distal end (Figure 1). An approximate reconstruction of the bone can be created by continuing the shaft so that it compares in its proportions with other theropod tibiae. This suggests an approximate length of 250 mm. A tibia of similar proportions is seen in *Deinonychus antir-*

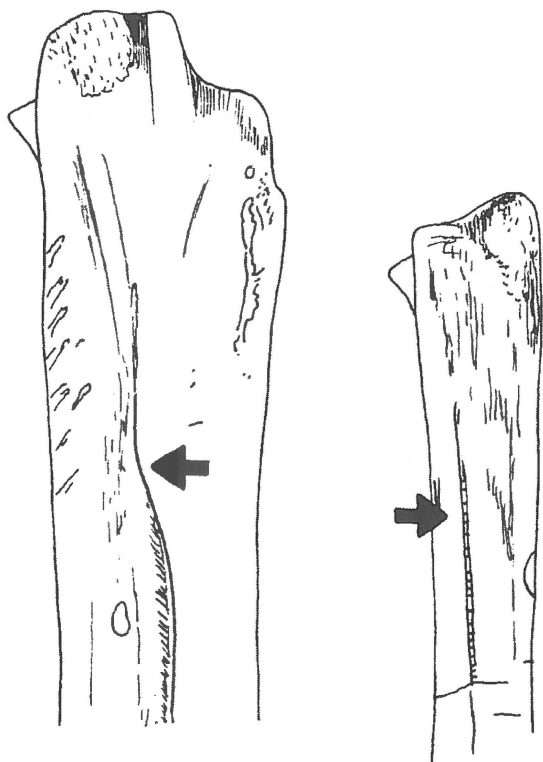


Figure 2. Lateral views of, from left to right, BMNH R9385 and BMNH R186 to show the different shapes of their fibular crests at their proximal ends (marked by the arrows). In BMNH R9385, the crest is sinuous at its proximal end, whereas it is straight in BMNH R186.

rhopus (300 mm long; see Ostrom 1969). That species was about 3 m long as an adult (Ostrom 1969), and therefore BMNH R9385 may represent an animal of a similar size.

BMNH R9385 shows a cranially-projecting cnemial crest which overhangs the cranial face of the tibial shaft, but few details can be discerned. The entire proximal apex of the crest is missing (Figure 1); only an expanse of broken bone about 4 mm wide is in its place. The cnemial crest continues distally as a ridge along the medial margin of the shaft's cranial surface, extending distally to a point adjacent to the start of the fibular crest's distalmost third (Figure 1). The ridge then smoothly tapers distally into the face of the shaft. The cranial surface of the shaft lateral to this ridge is flat, while the shaft is gently convex on its caudal surface. Breakage on the distal end of the cranial face shows that the bone's shaft is hollow.

In lateral view, the fibular crest shows a gentle sigmoidal curve at its proximal end (Figure 2). This is not an artefact of preservation because the bone is very

well preserved and is undistorted. This feature is also of importance in that it distinguishes BMNH R9385 from BMNH R186, another isolated Wealden Group theropod tibia (Lydekker 1891). In BMNH R186, the proximal part of the fibular crest is straight when viewed laterally (Figure 2).

As is evident in other theropod tibiae, there is a well-defined foramen on the caudolateral surface of BMNH R9385, slightly behind the fibular crest (Figure 3). This foramen, referred to here as the tibial foramen, is for the medullary artery. The tibial foramen in BMNH R9385 is located adjacent to a point within the fibular crest's lower third (Figure 3).

The most unusual feature of BMNH R9385 is the series of six shallow grooves on the shaft's caudal surface, aligned in parallel and oriented mediocaudally (Figure 4). The two most proximal of these grooves are somewhat indistinct, while the distal three are preceded on the shaft's lateral side (i.e., nearest the fibular crest) by small pits. Each groove is composed of fine vertical striations that are scored into the bone surface. The grooves are separated from one another by bone with a normal, smooth texture.

Identity of BMNH R9385

BMNH R9385 is theropodan because it bears both a prominent cnemial crest and a sharp-edged fibular crest (Figure 1). The tibiae of hypsilophodontids and other ornithomimids, which conceivably could be confused with theropod tibiae and must be eliminated in discussion of the identity of BMNH R9385, differ in that they do not bear a well-developed fibular crest and have a cnemial crest that curves laterally beyond the tibia's lateral margin and overlaps the proximal end of the fibula (Hulke 1882, Sternberg 1940, Galton 1974).

Holtz (1994) listed 'sharp ridge on tibia anterolaterally for clasping fibula' as an unambiguous synapomorphy (his character number 100) of the Tetanurae. This clearly refers to the fibular crest, but this feature is not synonymous with Holtz's (1994) character because some theropods possess a fibular crest that is not a sharp ridge. For example, the fibular crests illustrated for *Carnotaurus sastrei* (see Bonaparte et al. 1990), *Dilophosaurus wetherilli* (see Welles 1984), *Gojirasaurus quayi* (see Carpenter 1997), and the unnamed coelophysoid UCMP 129618 (Padian 1986) are relatively small, bump-like ridges that are not well expressed laterally. Coelophysoids and neoceratosaurs therefore lack, as coded by Holtz (1994), a

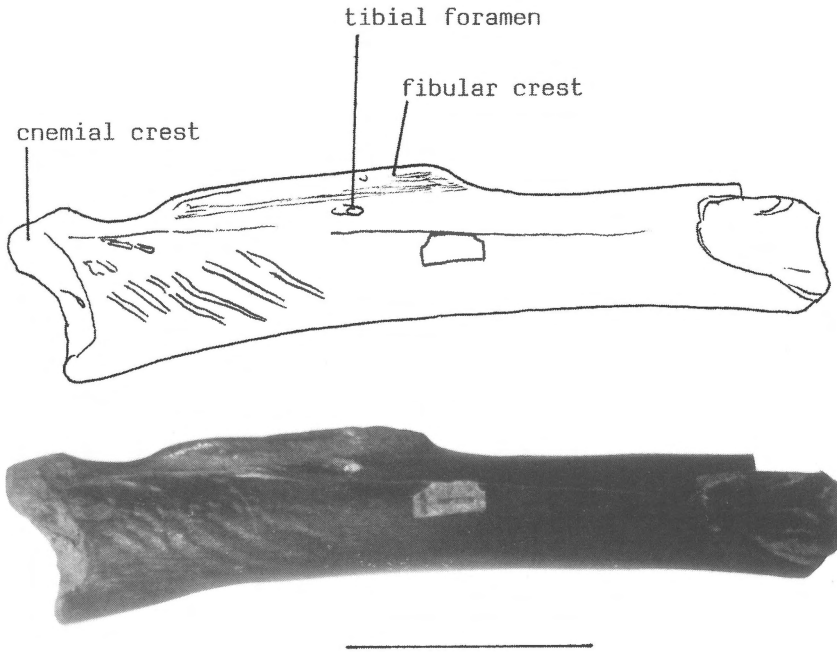


Figure 3. BMNH R9385 in caudal view. Note the position of the tibial foramen relative to the fibular crest. Scale bar: 50 mm.

sharp-ridged fibular crest, but the presence of a fibular crest does seem to be a shared derived character of coelophysoids, neoceratosaurs and tetanurans, i.e., the clade Neotheropoda of Sereno et al. (1994). Gauthier (1986) described the fibular crest as a theropodan synapomorphy, and – as his Theropoda excluded herrerasaurs and other possible basal theropods – his use of the term has obviously the same meaning as Sereno et al.'s (1994) Neotheropoda.

A sharp-ridged fibular crest does therefore appear to be a tetanuran character, as proposed by Holtz (1994), and thus BMNH R9385 is a tetanuran. Brookes (1997), who tried to elucidate the phylogenetic position of various Wealden Group theropods by comparing their characters with the character distribution proposed by Holtz (1994), also concluded that BMNH R9385 was tetanuran.

In BMNH R9385, the tibial foramen is positioned adjacent to a point within the distal third of the fibular crest (see description above). Limited discussion of this feature in other theropods suggests that a tibial foramen higher up the tibial shaft is characteristic of coelurosaurs (Osmólska et al. 1972, Kirkland et al. 1993), whereas a foramen positioned lower down appears to be the primitive theropod condition. Birds

have apparently reversed the coelurosaurian condition and have distally located tibial foramina (pers. obs.). BMNH R9385 does not appear to be avian because, even in the largest birds, the fibular crest is neither as robust nor as well expressed laterally as it is in the present specimen.

Comparisons with other Wealden Theropoda

Several other English Wealden Group theropods include tibiae as part of their known postcrania and can be compared with BMNH R9385. They are the coelurosaurian BMNH R186, and the holotypes of *Neovenator salerii* and *Baryonyx walkeri*.

A well-preserved left tibia is known for the recently described allosauroid *Neovenator salerii* from the Wessex Formation (Barremian) of the Isle of Wight (Hutt et al. 1996). Although these authors briefly described this element, it has not been figured at the time of writing. Personal observation shows it to be closely similar to the tibiae described by Gilmore (1920) and Madsen (1976) for *Allosaurus* and by Currie & Zhao (1994) for their new species, *Sinraptor dongi*. Several differences between the tibia of *N. salerii* and BMNH



Figure 4. Detail of the proximal end of BMNH R9385 in caudal view. A series of six shallow, parallel grooves run diagonally across this area.

R9385 are evident, the most noticeable of which is that in relative length of the fibular crest. In *N. salerii* and in *Allosaurus*, the fibular crest is proportionally short proximodistally, whereas it is long in BMNH R9385. BMNH R9385 is therefore not thought to be referable to *N. salerii*, nor to any member of the Allosauroidea.

The other well-known large Wealden Group theropod, *Baryonyx walkeri*, is from the upper Weald Clay (near the base of the Barremian) of Ockley, Surrey (Charig & Milner 1997). Unfortunately, the holotype does not include well-preserved tibiae (Charig & Milner 1997) and therefore no comparison can be made between BMNH R9385 and *B. walkeri*. With regard to comparisons between BMNH R9385 and the isolated theropod tibia BMNH R186 – referred by Lydekker (1891) to *Calamosaurus foxi* – the low position of the tibial foramen in BMNH R9385 is, like the slight sinuosity of the fibular crest's ridge, regarded here as being possibly of systematic importance in that it indicates that BMNH R9385 is not from the same animal. In BMNH R186, the tibial foramen is positioned more proximally in relation to the fibular crest (i.e., in a position tentatively regarded as a coelurosaurian condition), unlike in BMNH R9385. BMNH R186 is smaller and more gracile than BMNH R9385. Also, BMNH R186 comes from a higher stratigraphic horizon within the Wealden Group (viz. the Wessex Formation) than BMNH R9385.

While BMNH R9385 is regarded as referable neither to *Neovenator* nor to the coelurosaur represented by BMNH R186, the possibility that it is referable to *Baryonyx* remains open, simply because the preserved tibia of *B. walkeri* is crushed and uninformative (Charig & Milner 1997). If BMNH R9385 is of a baryonychid, it is from an individual smaller and strati-

graphically older than the holotype of *B. walkeri*, but is in agreement with phylogenetic hypotheses that baryonychids are non-coelurosaurian tetanurans (Serenio et al. 1994, Charig & Milner 1997).

The conclusions must be that BMNH R9385 is not coelurosaurian, but is tetanuran, and that it is not referable to any of the Wealden Group theropods for which tibiae are known.

Theropod diversity within the Wealden Group

Recent taxonomic revisions have tended to assume synonymy of most or all of the smaller Wealden Group theropods (Ostrom 1970, Norman 1990b, Brookes 1997). To date, the general absence of overlapping elements for the several taxa has made it impossible to either prove or disprove their synonymy.

Incomplete sacra, the types of the enigmatic form *Ornithodesmus cluniculus* and of the compsognathid *Aristosuchus pusillus*, demonstrate that certainly two small theropods are represented in the Wessex Formation of the Wealden Group. The latter species, based on the sacrum and pubes BMNH R178, is demonstrably not the same as the specimen on which *Calamospondylus oweni* is based (Fox 1866, Naish 1999). A number of other elements from the Wessex Formation also appear referable to the Compsognathidae. Material from this group has yet to be recognised from other Wealden strata, suggesting that they may be of biostratigraphic utility within the Wealden, as are a number of ornithischian taxa (Norman 1987, Pereda-Suberbiola 1993).

Isolated small theropod tibiae and femora from the Wealden Group, the subjects of an ongoing study, indicate that at least three small theropods were present.

Furthermore, some taxa based on cervical or sacral vertebrae do not appear to belong to the same theropod clades as do these limb bones.

Palaeobiological implications

The series of near-parallel tracts on the caudal surface of BMNH R9385 (Figure 4) appear to be tooth marks made by a set of serrated teeth. The question arises: what kind of animal made these tooth marks? Of known Wealden Group taxa, crocodyli-forms can be eliminated from consideration as none of the Wealden Group taxa possess serrated teeth. Denticulate teeth are seen in a variety of herbivorous dinosaurs, including such well-known Wealden Group taxa as iguanodonts and ankylosaurs, but the closely-spaced, leaf-shaped tooth crowns of these dinosaurs would not leave elongate scores such as those seen on BMNH R9385. Theropods, therefore, are the only group that cannot be eliminated from consideration, and the spacing and appearance of the tooth marks on BMNH R9385 appear wholly consistent with tooth marks made by a theropod.

The tooth marks on BMNH R9385 therefore show that another Wealden theropod had bitten the theropod represented by BMNH R9385 (Naish 1998). This may be evidence for intraspecific aggression, cannibalism, predation by another species, or opportunistic scavenging. There is no way of knowing which of these possibilities represents the correct one. This is the first reported occurrence of theropod tooth marks on a theropod bone from the Wealden Group.

Elsewhere in the global stratigraphic record, injuries inflicted on theropods by theropods are becoming increasingly well known (Rothschild & Tanke 1992, Currie & Zhao 1994, Chure & Fiorillo 1997, Harris 1998), though Fiorillo (1991) noted how rare theropod bite marks were compared to bite marks made by carnivorous mammals. That theropods did bite, injure, kill and sometimes eat other theropods, of the same or of another species, should not be at all surprising in view of the frequency of observed aggressive interactions between extant crocodylians, predatory birds, and carnivorans.

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