

# The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England

Steven C. Sweetman

*School of Earth and Environmental Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK*

Received 20 March 2003; accepted in revised form 30 January 2004

---

## Abstract

Velociraptorine dromaeosaurid dinosaur teeth are reported for the first time from the Wessex Formation (Early Cretaceous, Barremian) of the Isle of Wight, southern England. They represent the second record of the Dromaeosauridae in Britain and the first of this clade from strata of the British Wealden Group.

© 2004 Elsevier Ltd. All rights reserved.

*Keywords:* Cretaceous; Barremian; Dinosaur; DSDI; Isle of Wight; Teeth; Theropoda; Velociraptorinae

---

## 1. Introduction

The Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, southern England, yields a diverse dinosaur fauna (Martill and Naish, 2001). In addition to ankylosaurs, ornithopods, sauropods, rare stegosaurs and the problematic *Yaverlandia bitholus* Galton, 1971 (Sullivan, 2000), the fauna also includes a number of theropods known from both isolated elements and partially articulated skeletons. The latter comprise the allosauroid *Neovenator salerii* Hutt et al., 1996 and the basal tyrannosauroid *Eotyrannus lengi* Hutt et al., 2001. Among taxa represented by isolated elements are: baryonychid spinosauroids known from isolated teeth (Martill and Hutt, 1996); a possible oviraptorosaur, *Thecocoelurus daviesi* Seeley, 1888 (Naish and Martill, 2002) known from an incomplete cervical vertebra; the coelurosaurs *Aristosuchus pusillus* Owen, 1876 (Naish, 1999a,b) represented by the sacrum and pubes of one individual and possibly by ungual phalanges, dorsal and caudal vertebrae and partial limb

bones from several others (Lydekker, 1888; Galton, 1973; Naish, 2000), *Calamosaurus foxi* Lydekker, 1889, represented by two associated cervical vertebrae; and *Calamospondylus oweni* Fox in Anon., 1866a (Anon., 1866b; Naish, 2002), which is based on a sacrum the whereabouts of which is currently unknown. The synsacrum named *Ornithodesmus chuniculus* Seeley, 1887a (Seeley, 1887b) has been compared with troodontid and dromaeosaurid coelurosaurs (Howse and Milner, 1993; Norell and Makovicky, 1997) and coelophysoids (Makovicky, 1995; Naish, 1999c). Although some features of the sacral vertebrae of *O. chuniculus* are similar to those of dromaeosaurids (Norell and Makovicky, 1997), Naish et al. (2001) argued that the lack of dorsoventrally flattened transverse processes precludes this referral. If, however, *O. chuniculus* is a dromaeosaurid with an estimated overall length of ca. 1.5 m (Naish et al., 2001), it would appear to have been rather small to have accommodated all but perhaps one of the teeth described herein, unless the specimen concerned represents a juvenile. Wealden strata near Bexhill, on the mainland of southern England, have also produced fragmentary remains that may be referable to a dromaeosaurid (D. Naish, pers. comm. 2003), although this remains to be confirmed.

---

*E-mail address:* [steven.sweetman@port.ac.uk](mailto:steven.sweetman@port.ac.uk)

## 2. Geological and palaeoenvironmental setting

Inland exposures of the Wessex Formation are poor but there are extensive coastal exposures on the south-west coast of the Isle of Wight in the core of the Brighstone Anticline between Compton Bay and Cowleaze Chine, and in the core of the Sandown Anticline in Sandown Bay on the south-east coast (Fig. 1). Estimates for the total thickness of exposed sediments of the Wessex Formation vary between about 170 and 190 m owing in part to difficulty in estimating the throw on a significant fault in Compton Bay and minor faults elsewhere in the section. However, Stewart (1978, 1981) estimated the thickness to be 180 m and borehole data (Falcon and Kent, 1960) proved a total thickness of 592 m for strata of the Isle of Wight Wealden Group as a whole. The exclusively non-marine Wessex Formation is entirely of Barremian age (Allen and Wimbledon, 1991) although it has been proposed that the Hauterivian-Barremian boundary may lie at the level of the Pine Raft, which is exposed at low tide on the foreshore at Hanover Point (NGR SZ 379837) (Harding, 1986; Hughes and McDougall, 1990). The Wessex Formation is overlain by about 70 m of lagoonal strata which comprise the upper Barremian to ?lowermost Aptian Vectis Formation (Stewart et al., 1991) (Fig. 2).

The Wessex Formation comprises massive varicoloured mudstones, interpreted as overbank deposits, interbedded with sandstones and subordinate intraformational conglomerates, crevasse splay deposits, and plant debris beds (sensu Oldham, 1976) in which a number of facies associations have been recognised (Stewart, 1978, 1981; Daley and Stewart, 1979; Insole and Hutt,

1994). These sediments were deposited on a low gradient, near-coast floodplain by a high sinuosity river flowing from west to east within a confined east–west, fault-bounded valley (Stewart, 1978, 1981; Daley and Stewart, 1979; Stoneley, 1982; Chadwick, 1985; Ruffell, 1992; Insole and Hutt, 1994; Radley, 1994; Wright et al., 1998; Underhill, 2002).

The diversity of habitats available within the Wessex Basin was considerable, although seasonal aridity (Ruffell and Batten, 1990) may have rendered large areas of the floodplain inhospitable at times and significantly reduced its large herbivore-carrying capacity during periods of drought (Insole and Hutt, 1994; Allen, 1998). The large and small vertebrate material recovered from the plant debris beds demonstrates that the flood events responsible for their formation gathered the bones, teeth and carcasses of animals from a variety of habitats before depositing them in depressions on the floodplain. Moreover, Insole and Hutt (1994) concluded that plant debris beds were produced by local storm events (contra Stewart 1978, 1981). If this were the case, the fauna present in these beds would be of local origin.

The microvertebrate fauna comprises mammals, dinosaurs, crocodiles, turtles, pterosaurs, lepidosaurs, lissamphibians, and chondrichthyan and osteichthyan fishes (Freeman, 1975; Butler and Ford, 1975; Buffetaut and Ford, 1979; S.E. Evans, pers. comm. 2003; Sweetman, in prep.). Post-depositional anoxia within the plant debris beds was conducive to preservation of bones and teeth, but the durability of theropod teeth (Argast et al., 1987) may account for their relative abundance in comparison to other dinosaur teeth and their common occurrence in the intraformational conglomerates. In

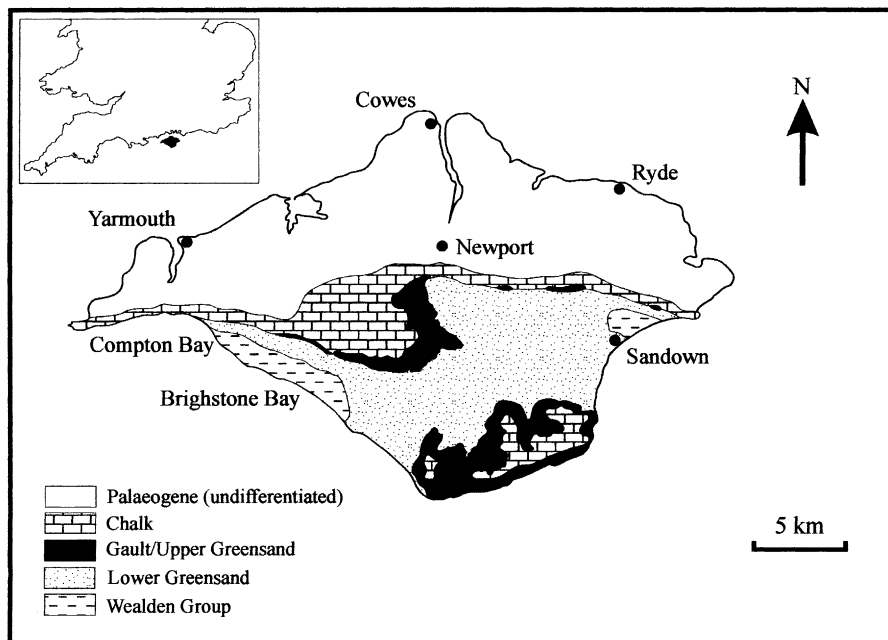


Fig. 1. Location and outline geological maps of the Isle of Wight.

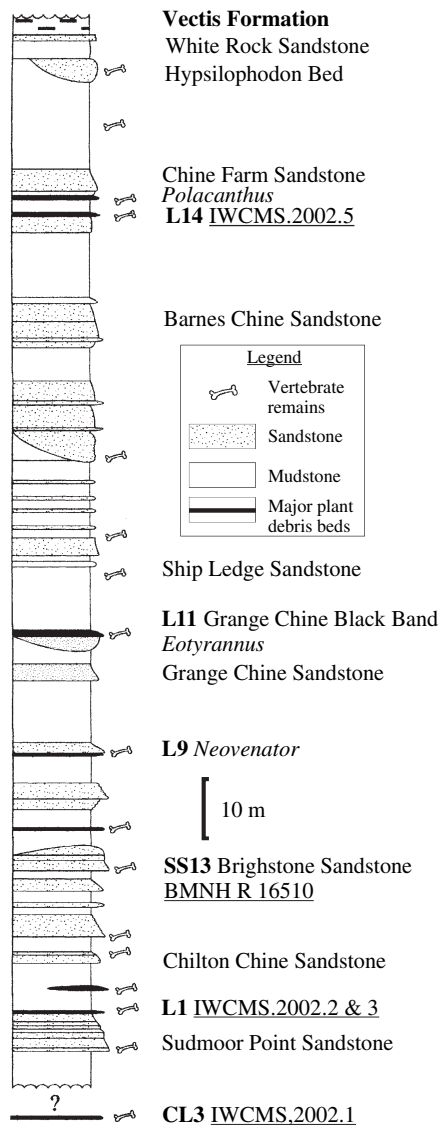


Fig. 2. Schematic lithological log for the Wessex Formation between Sudmoor Point (NGR SZ 392827) and Barnes High (NGR SZ 438807) on the south-west coast of the Isle of Wight (based in part on Stewart, 1978).

contrast to the plant debris beds, the conglomerates are well cemented and difficult to process for microvertebrates. In view of this and the abundance of both large and small vertebrate remains within the plant debris beds (see Freeman, 1975; Butler and Ford, 1975; Buffetaut and Ford, 1979; Martill and Naish, 2001; S.E. Evans, pers. comm. 2003), work currently in progress on the microvertebrate fauna of the Wessex Formation has concentrated on processing bulk samples from these beds.

### 3. Material and methods

Surface prospecting of the Wessex Formation yielded a number of large theropod teeth. Bulk sediment

samples were also collected from plant debris beds and the position of each sample was recorded using a Garmin 12 satellite GPS receiver. The samples were processed using a bulk screening machine (Ward, 1981) modified for use with re-circulated water. After processing, the residues were divided into two fractions using a sieve with mesh size 6 (ca. 2.8 mm). When dry, fossils from the fraction with particles >2.8 mm in size were picked by eye. The finer fraction was retained for further processing and the recovery of microvertebrate material. Digital images of specimens were obtained using a scanning electron microscope and digital macro-photography. Low acceleration voltages were used in order to avoid excessive charging and to obtain satisfactory images of uncoated specimens. Measurements were taken using either digital image capture, analysis and processing software (SemAfore version 4.00, Insinööri J. Rimpä Oy), a binocular microscope incorporating an optical micrometer, or micrometer callipers.

### 4. Theropod dental morphology and taxonomy

The use of theropod tooth morphology for taxonomic purposes has been examined by a number of workers (Currie et al., 1990; Rauhut and Werner, 1995; Sankey et al., 2002). Currie et al. (1990) have shown that analysis of theropod tooth morphology is reliable for diagnosing taxa to familial, and in some cases to higher, taxonomic levels. Rauhut and Werner (1995) refined these methods further by including an analysis of the difference in denticle size between the mesial and distal carinae of individual teeth. This has been shown to be independent of tooth size and also of potential value for taxonomic purposes. Tooth measurements were taken using the criteria established by Currie et al. (1990) and Farlow et al. (1991). Tooth curvature was measured according to the method of Sankey et al. (2002) and the denticle size difference index (DSDI) calculated following Rauhut and Werner (1995). Where possible, denticles were counted over carinae lengths of 5 mm. When this was not possible, counts were made over the largest possible carina length consistent with an accurate denticle count for the purpose of calculating DSDIs. Alternatively, the length of carina occupied by a minimum of ten denticles was measured digitally. In all cases the denticle count per 1 mm carina unit length was calculated and used to calculate DSDIs (Table 1).

*Institutional abbreviations.* BMNH, The Natural History Museum, London; IWCMS, Isle of Wight County Museum Service; MIWG, Museum of Isle of Wight Geology. Specimens with MIWG accession numbers are now in the collections of the Isle of Wight County Museum Service.

Table 1  
Theropod tooth measurements and denticle counts

Number	Taxon	TCH	CBW	CBL	MDC	DDC	DSDI
IWCMS.2002.1		16	4	6.5–7	4.8	3.5	1.37
IWCMS.2002.2		8.5	2	5	–	6.25	–
IWCMS.2002.3		–	–	–	3.8	2.7	1.41
IWCMS.2002.4		–	–	–	4.4	3.2	1.38
BMNH R 16510		>21.5	6	10	4.8	3	1.60
	<sup>1</sup> <i>Nuthetes destructor</i>	1.5–16	1.5–4.2	3–6	6–10	4.5–8	1.14–1.55 mean 1.35
MIWG.1997.885	<sup>2</sup> <i>Eotyrannus lengi</i>	20–26		11–15	3.7–4.2	3.2–3.7	1.03–1.31 mean 1.16
MIWG.6348	<sup>2</sup> <i>Neovenator salerii</i>	8–45	7.5–12	10.5–20	2.7–3.2	2.6–3.8	0.78–1.11 mean 0.98
	<sup>3</sup> Isle of Wight baryonychid spinosauroids				3.5	3.5	1.00
	<sup>4</sup> <i>Tyrannosaurus</i>						0.77–1.16 mean 0.96
	<sup>4</sup> <i>Aublysodon</i>						0.94–1.2 mean 1.04
	<sup>4</sup> <i>Dromaeosaurus</i>						0.81–1.13 mean 0.96
	<sup>4</sup> <i>Deinonychus</i>						1.31–2.33 mean 1.75
	<sup>4</sup> <i>Saurornithoides</i>						1.19–2.00 mean 1.57

Abbreviations: CBL, crown basal length, mm; CBW, crown basal width, mm; DDC, distal carina denticle count per 1 mm unit length; DSDI, denticle size difference index (ratio of MDC/DDC); MDC, mesial carina denticle count per 1 mm unit length; TCH, tooth crown height, mm.

1, after Milner, 2002; 2, measurements taken January 2003; 3, data from Martill and Hutt, 1996 and pers. obs.; 4, after Zinke and Rauhut, 1994.

**Nomenclature.** No standardised nomenclature for the description of theropod dinosaur teeth is apparent in the literature (see Smith and Dodson, 2003, for a review) and the following nomenclature, which follows proposals made by Smith and Dodson (2003), is used here: mesial, towards the premaxillary and mandibular symphyses; distal, away from the premaxillary and mandibular symphyses; lingual, towards the tongue; labial, towards the lips; apical, towards the tip of the tooth; basal, towards the base of the tooth; crown basal length (CBL), length of the base of the crown measured along the mesiodistal axis. Labiolingual and apicobasal compression of the basal profile of denticles and apicobasal expansion of denticle tips refer to orientation with respect to the tooth.

## 5. Descriptions

Five teeth are described, all of which exhibit broadly similar gross morphology. In none of the specimens is anything other than a vestige of the root preserved and this, together with tooth tip and denticle wear, indicates that all specimens, including those in which the base of the crown is missing, are shed teeth. All specimens are strongly labiolingually compressed and moderately to strongly mesiodistally recurved. Except where removed by wear, denticles are present along the entire length of

distal carinae, which occupy the entire distal margin of tooth crowns. Mesial carinae occupy apically approximately half of the mesial crown margin of all specimens and denticles are present on all except IWCMS.2002.2 (Fig. 3). In all cases labiolingual compression of the crown indicates that the specimens represent lateral teeth, but it is not possible to ascertain from which jaw they originate (Farlow et al., 1991; Fiorillo and Currie, 1994). Beyond the basal extremity of mesial carinae the mesial margin of all crowns is U-shaped in cross section with a progressively increasing radius of curvature basally. Mesial carinae are unflexed and divide the mesial margin of the crown symmetrically. Where present, mesial denticles are considerably smaller than those present on the distal carinae. The distal carinae of complete crowns are somewhat sinusoidal in distal view, being slightly flexed lingually in the middle of the crown. All specimens appear to be unaffected by crushing indicating that flexion of the distal carina is a primary feature. Denticles are of uniform size along most of the mesial and distal carinae but apically and basally they become progressively very small. Wear of the tooth tip is present in all specimens and has removed the most apical denticles and breached the enamel to form a wear facet (Fig. 3). The facet is orientated obliquely towards the mesial carina and fewer denticles have been removed from distal carinae than from mesial carinae. Bases of denticles on distal carinae are apicobasally compressed and strongly rectangular in outline. In contrast, those on

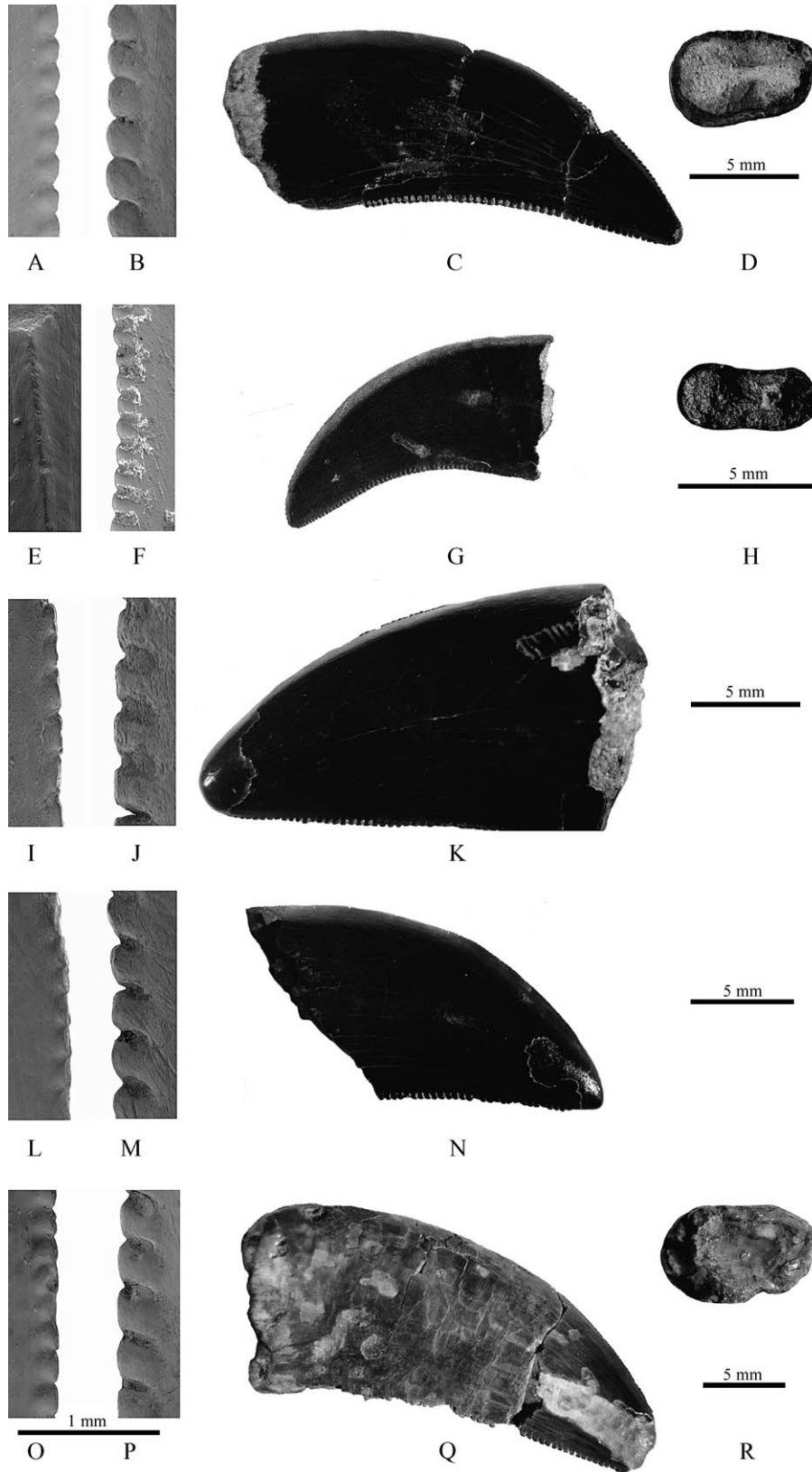


Fig. 3. A–D, IWCMS.2002.1. A, Mesial denticulation in lingual view; B, distal denticulation in labial view; C, tooth crown in lingual view; D, basal profile. E–H, IWCMS.2002.2. E, Mesial carina in mesial view showing apical enamel rugosity; F, distal denticulation in labial view; G, tooth crown in labial view; H, basal profile. I–K, IWCMS.2002.3. I, Mesial denticulation in ?lingual view; J, distal denticulation in ?labial view; K, partial tooth crown in ?labial view. L–N, IWCMS.2002.4. L, Mesial denticulation in ?lingual view; M, distal denticulation in ?labial view; N, partial tooth crown in ?lingual view. O–R, BMNH R 16510. O, Mesial denticulation in lingual view; P, distal denticulation in labial view; Q, tooth crown in lingual view; R, basal profile. Mesial margin of all basal profiles to the left. Scale bars on the right apply to tooth crowns and basal profiles where both are shown.



mesial carinae are either labiolingually compressed or approximately square in basal profile (Fig. 4).

Distal denticles are waisted in labial and lingual views and interdenticle pits are oval in outline on the labial and lingual surfaces of the crown (Fig. 3). No extension of interdenticle pits onto the lingual and labial surfaces of the crown is apparent below the base of denticles. Distal denticle tips are somewhat inflated apicobasally and convex, and axe-like in lateral profile. In teeth with asymmetrical curvature of labial and lingual surfaces, the labial and lingual surfaces of distal denticles follow the curvature of the underlying tooth wall and are also asymmetrical in distal view, being more expanded on the labial side of the carina. Tooth enamel is finely reticulate although reticulation is less pronounced basally. Apico-basally orientated cracking of the enamel is present to a greater or lesser extent in all specimens. Faint ridges indicate growth lines but no colour banding is evident. The ridges are either concave basally towards the midline of the crown or form straight lines across the

crown. In either case, their mesial and distal margins are orientated approximately perpendicular to the carinae. Striations attributable to feeding activity are variably evident as further discussed below.

#### 5.1. Specimen IWCMS.2002.1

This tooth (Fig. 3A–D) was collected in 1972 from the second of three lignitic bands in Compton Bay depicted by White (1921) and later assigned bed number CL3 by Stewart (1978) (Fig. 2). CL3 is a typical plant debris bed (Oldham, 1976; Insole and Hutt, 1994), occurring ca. 50 m above the base of the exposed Wessex Formation (Stewart, 1978) and is lenticular in nature. The bed is poorly developed in current cliff exposures, much of it having been removed by erosion since the specimen was collected. However, removal of recent beach deposits by winter storms occasionally provides foreshore exposures of the bed as originally described by White (1921). Based on foreshore exposures in the

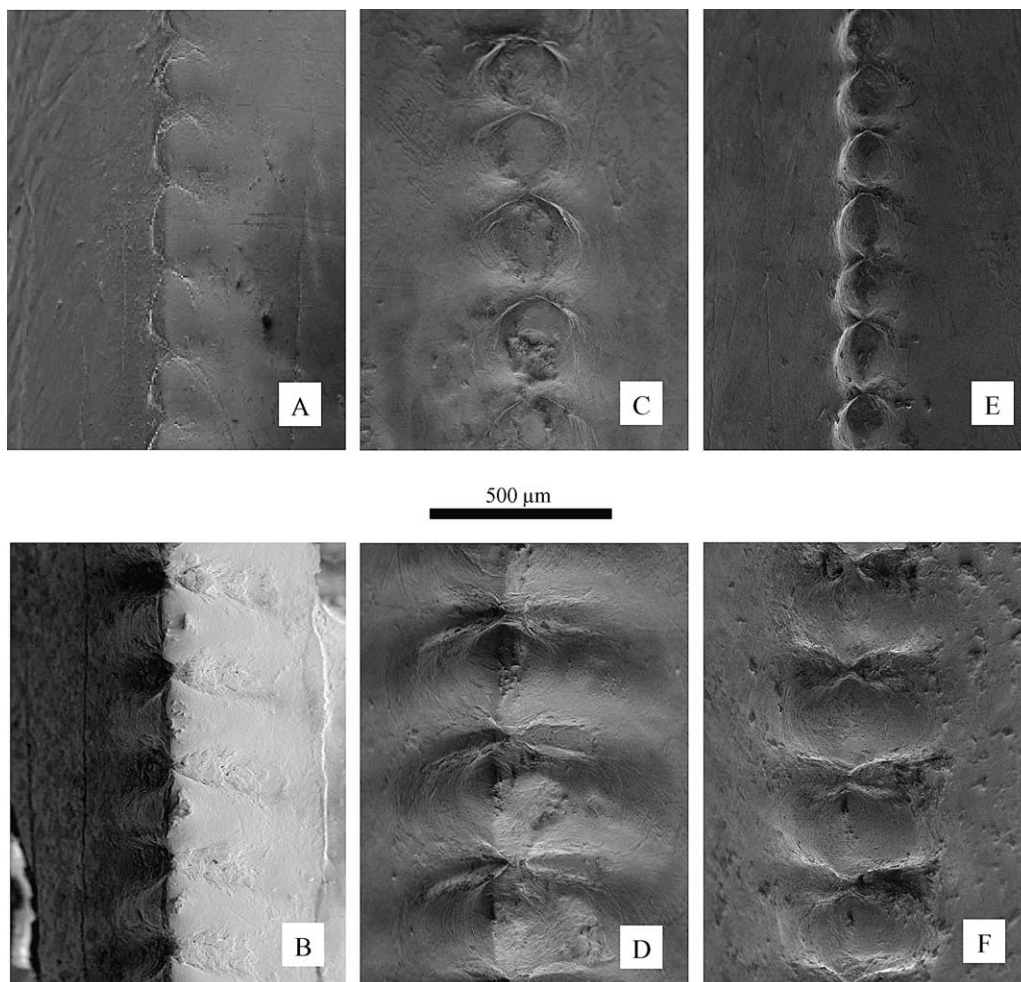


Fig. 4. A, B, IWCMS.2002.1. A, Mid-carina mesial denticulation in mesial view; B, mid-carina distal denticulation in distal view. C, D, IWCMS.2002.3. C, Mid-carina mesial denticulation in mesial view; D, mid-carina distal denticulation in distal view. E, F, BMNH R 16510. E, Mid-carina mesial denticulation in mesial view; F, apical mid-carina distal denticulation in distal view; mid-carina denticulation damaged (Fig. 3Q) but measurable for the purpose of calculating DSDI.

winter of 2001–2002 the site of collection is taken to be NGR SZ 3775 8395.

Preserved crown height is ca. 16 mm, but slight damage to the base of the crown and an apical wear facet indicate that originally crown height would have been somewhat greater; CBL is estimated in view of damage to the base of the crown at ca. 6.5–7 mm; basal labiolingual crown width is 4 mm; mesial denticle count per 1 mm unit length is 4.8; distal denticle count per 1 mm unit length is 3.5; DSDI is 1.37; the tooth is moderately to strongly recurved with a curvature of 3.35 mm. Mesial denticles are orientated ca. 20 degrees apically and, while the tips of all denticles were probably originally chisel-like (Fig. 4A), wear along most of the carina gives the impression that the denticle tips are hemispherical in mesial view. Part of the basal end of the distal carina is missing rendering determination of denticle morphology impossible for this region.

In contrast to the mesial carina, denticles on the distal carina are inclined ca. 15 degrees apically. A plane through the carinae divides the tooth into two unequal halves. The labial side is generally convex but becomes almost flat towards the middle of the crown. The lingual side, while convex apically and along the mesial margin, becomes progressively less so distobasally. From approximately 3 mm below the tip of the crown the distal margin of the tooth is slightly concave. The concavity is crescent shaped, being most pronounced in the middle of the distal half of the crown and is lost at the extreme basal end. Individual distal denticles are only slightly taller than wide, with a height to basal width ratio close to 1 for unworn denticles. A number of striations attributable to feeding activity can be seen on the labial and lingual surfaces of the crown. These occur in two distinct sets, one aligned approximately parallel to the orientation of the interdentine slits between the distal denticles and another, all with parallel alignment, which form an acute angle apically as they meet the distal carina. Approximately 1.5 mm of the root is preserved and, although partially filled with matrix, a well-developed resorption pit is present. In cross section the base of the crown is sub-rectangular and lacks any constriction on either the lingual or labial side (Fig. 3D). The mesial and distal margins of the base are rounded and the distal margin is slightly narrower than the mesial margin.

### 5.2. Specimen IWCMS.2002.2

IWCMS.2002.2 (Fig. 3E–H) was collected in 2002 by bulk processing of a sample from a basal conglomerate associated with a plant debris bed occurring immediately above the Sudmoor Point Sandstone Member (Fig. 2), at beach level to the north-west of Chilton Chine; NGR SZ 40747 82188. The plant debris bed, which occurs higher in the section than CL3, was

assigned bed number L1 by Stewart (1978). However, difficulties involved in correlating between Compton Bay and Brighstone Bay, due to lateral lithological variability and discontinuity, render their precise relationship problematic.

The measured crown height is 8.5 mm; CBL is 5 mm; maximum basal labiolingual width is 2 mm; there is a prominent mesial carina that is only slightly worn, except close to the apical end where approximately 1 mm has been removed. The mesial carina forms a sharp edge with its basal termination on the mesial margin of the crown well defined. Rugosity of the mesial carina enamel immediately below the wear facet suggests that denticles may have been present at the apical extremity but otherwise they are absent (Fig. 3E). If the apical rugosity does represent denticulation, at least six denticles are present, but no trace of denticles can be seen in the underlying dentine on the wear facet immediately apical to the rugosity. The distal denticle count per 1 mm unit length is 6.25 and denticles are either orientated perpendicular to the tooth margin or inclined at a shallow angle apically. Unworn denticles are only slightly taller than wide in labial and lingual views, with a height to basal width ratio close to 1. The tooth is strongly recurved, with a curvature of 2.75 mm. Both sides of the tooth are convex, with the convexity more pronounced labially. Shallow concave depressions are developed towards the base of the crown on both the lingual and labial surfaces. Tooth enamel is very finely reticulate in a band around the base of the crown. This band is a little over 2 mm wide towards the mesial margin and ca. 1 mm towards the distal margin and the apical extremity may perhaps represent the gum line. Despite the presence of a wear facet at the apex of the crown; striations attributable to feeding activity could not be detected on either the lingual or the labial surfaces. No portion of the root is preserved and a well-developed resorption pit is present in the base of the crown, which is sub-rectangular in cross section. The lateral depressions occurring towards the base of the crown on both the lingual and labial sides extend to reach the base and produce a central constriction in the basal profile (Fig. 3H). The mesial and distal margins of the base are rounded and the distal margin is slightly narrower than the mesial margin.

### 5.3. Specimen IWCMS.2002.3

This tooth (Fig. 3I–K) was collected in the early 1990s from the same site of collection as IWCMS.2002.2. IWCMS.2002.3 is the apical part of a shed tooth which when complete would have been the largest of those described here. The preserved part has a height of 20 mm but it is not possible to estimate the tooth crown height from this measurement; basal length is 12 mm and basal width is 7 mm; mesial denticle count per 1 mm

unit length is 3.8; distal denticle count per 1 mm unit length is 2.7; DSDI is 1.41. Loss of the basal part of the tooth occurred ca. 6 mm beyond the basal extremity of the mesial carina. Mesial denticles are generally uncompressed and appear hemispherical in mesial view, and it is clear that they were substantially shorter than those present on the distal carina. Wear renders measurement of mesial denticle orientation difficult but they appear to be inclined ca. 22 degrees apically. All distal denticles are affected by wear to a greater or lesser extent and denticle tip morphology cannot be fully determined. Distal denticles are inclined ca. 15 degrees apically. Many fine striations attributable to feeding activity are evident on the lingual and labial surfaces of the tooth. These occur in two sets, one aligned approximately parallel to the orientation of the interdenticle slits between the distal denticles, and another, all with parallel alignment, which form an obtuse angle apically as they meet the distal carina. The latter set is orientated approximately at right angles to those present on IWCMS.2002.1.

#### 5.4. Specimen IWCMS.2002.4

This tooth was collected from the Wessex Formation by a local collector but the exact provenance is currently unknown. IWCMS.2002.4 (Fig. 3L–N) is the broken apical part of a shed tooth. The mesial surface of the crown is strongly convex mesially whereas the distal carina is slightly concave mesially. Breakage occurred ca. 4 mm beyond the basal extremity of the mesial carina and before breakage the crown was intermediate in size between IWCMS.2002.2 and IWCMS.2002.3. The height of the preserved crown fragment is ca. 18 mm; mesial denticle count per 1 mm unit length is 4.4; distal denticle count per 1 mm unit length is 3.2; DSDI is 1.38. Mesial denticle morphology cannot be fully determined due to wear but the basal outline of denticles is similar to that observed in IWCMS.2002.1 and 3, and BMNH R 16510 (Fig. 4) and the denticles appear to be similarly inclined apically. The distal carina extends from the tip of the crown below a wear facet to the point of breakage. It divides the crown symmetrically in this portion of the tooth and provides no guidance as to which is the lingual and which the labial surface. No flexion of the distal carina is apparent, although this may have been present in that part of the crown now lost. Distal denticles are inclined somewhat variably ca. 16 degrees apically. Striations attributable to feeding activity are as described for IWCMS.2002.3.

#### 5.5. Specimen BMNH R 16510

This specimen (Fig. 3O–Q) was found in a loose block of intraformational conglomerate from the foreshore north-west of Grange Chine, approximately at NGR SZ

414819. The block is believed to be derived from a conglomerate occurring at the base of the Brighstone Sandstone, bed number SS13 of Stewart (1978) (Fig. 2). Although damaged and somewhat worn and abraded, accurate mid-carina denticle counts could be made for both the mesial and distal carinae. This tooth shares many characters in common with IWCMS.2002.1 but differs from it in being somewhat larger; having a higher DSDI (Table 1) reflected in denticle basal profiles (Fig. 4); and having a mid-distolingual surface that is slightly convex rather than concave. Despite these differences, the gross crown morphology, denticle morphology, denticle inclination and flexion of the posterior carina indicate that it is referable to the same taxon as IWCMS.2002.1 (Fig. 3). Striations attributable to feeding activity are evident on the lateral surfaces of the crown and, while those orientated parallel to the interdenticle slits are clearly to be seen, the orientation of a second set cannot be ascertained with confidence due to damage, abrasion and the presence of randomly orientated scratches acquired during transport prior to burial.

## 6. Taxonomic position

In addition to demonstrating that analysis of theropod tooth morphology is a potentially reliable method of diagnosing taxa to family, and in some cases to higher, taxonomic level, Currie et al. (1990) also concluded that theropod teeth show little ontogenetic variation. Juvenile teeth display the same features as those of adults, but on a smaller scale. It is necessary, therefore, to consider whether or not the smaller specimens described above could represent juvenile teeth of large Wessex Formation theropods for which teeth are known. In the case of the larger specimens, it is also necessary to consider whether or not these could represent part of the normal range of variation within the tooth rows of these theropods.

A DSDI of 1.5 for teeth of the basal tyrannosauroid *Eotyrannus lengi* was reported by Hutt et al. (2001) and all suitably preserved teeth pertaining to *E. lengi* (MIWG.1997.550) were re-examined in this study. The DSDI of 1.5 for *E. lengi* is based on measurements taken from a left maxillary tooth that is partially erupted from the extreme rostral end of the maxilla. This DSDI is considered to be unreliable because measurements were taken close to the apical ends of the carinae where denticle size is decreasing at different rates on the mesial and distal carinae. Four teeth could be accurately measured and provided reliable DSDIs of 1.03, 1.06, 1.25 and 1.31 with a mean of 1.16, which is close to the range expected for a tyrannosauroid based on measurements from Upper Cretaceous taxa (Table 1). Teeth of *E. lengi* can be distinguished from the specimens described here by: lower DSDI; distal denticles significantly higher than wide, with a height to basal width



ratio of  $> 1.5$  for unworn denticles; denticles with similar labial and lingual profiles on mesial and distal carinae of all teeth, and denticle tips only slightly inflated apicobasally and chisel-like on both carinae; denticles only slightly waisted and interdenticle pits therefore U-shaped rather than oval; basal extremity of the mesial carina considerably raised above the mesial tooth margin giving the impression of a constriction in the tooth margin below termination of the mesial carina; distal carina unflexed.

The described specimens can be readily distinguished from all teeth of *Neovenator salerii* (Hutt et al., 1996) on the basis of their DSDI. Mesial and distal denticle counts were made for seven of the most complete teeth forming part of the holotype series (MIWG.6348) (Table 1). All *N. salerii* teeth produced low DSDIs, with the highest value (1.11) obtained from the largest tooth (crown height 45 mm). The lowest values were obtained from the smallest teeth. In contrast to the specimens described here, but as seen in teeth of *Eotyrannus lengi*, all *N. salerii* teeth bear denticles with similar labial and lingual profiles on both the mesial and distal carinae.

The described specimens can be easily distinguished from all teeth referred to baryonychid spinosauroids (Martill and Hutt, 1996; Charig and Milner, 1997) on the basis of DSDI, enamel texture, lack of fluting, denticle morphology and substantially greater labiolingual compression of the crowns than that seen in baryonychid spinosauroids. Even juvenile teeth of baryonychid spinosauroids, some of which are almost as labiolingually compressed as IWCMS.2002.1, lack fluting, and are occasionally moderately recurved, can be readily distinguished from those of other theropod teeth from the Wessex Formation on the basis of their enamel texture and denticle morphology (pers. obs.).

Comparison of the DSDIs of the specimens described here with values for other theropod taxa (Table 1) indicates that these specimens can be referred to the Velociraptorinae (sensu Currie et al., 1990). Lack of denticles on the mesial carinae of teeth attributable to velociraptorine dromaeosaurids has been reported for several taxa including *Nuthetes* from the Lower Cretaceous (Berriasian) of the UK and *Saurornitholestes* from the Upper Cretaceous of the USA, and appears to be a function of tooth position within the dental arcade (Currie et al., 1990; Milner, 2002; Sankey et al., 2002). Gross crown morphology, distal denticle morphology and the presence of an unflexed and well-defined mesial carina, support tentative referral of IWCMS.2002.2 to the Velociraptorinae.

## 7. Comparisons with other European velociraptorine dromaeosaurids

Until recently, the taxonomic position of *Nuthetes destructor* from the Purbeck Limestone Formation

(Berriasian) of mainland southern England remained equivocal. Milner (2002) re-examined this material and concluded, on the basis of many of the above-mentioned characters, that *N. destructor* is a velociraptorine dromaeosaurid and therefore the first confirmed record of a British dromaeosaur.

The large tooth sample size available for *N. destructor* indicates that the DSDI for this taxon lies within the range 1.14–1.55. The considerably smaller sample from the Wessex Formation produces a range of 1.37–1.60 but indicates a mean value in excess of that determined for *N. destructor*. In contrast to *N. destructor* and other European Late Jurassic and Early Cretaceous velociraptorines (Rauhut and Zinke, 1995; Canudo et al., 1997; Zinke 1998; Milner, 2002; Rauhut, 2002), denticles on the mesial and distal carinae of Isle of Wight specimens are inclined apically. Even allowing for the fact that the Purbeck teeth may represent juveniles (Milner, 2002), this factor precludes the Isle of Wight teeth being referred to *Nuthetes*.

Elsewhere in Europe isolated teeth with velociraptorine dromaeosaurid affinities have been reported from the Kimmeridgian at Guimarota, Portugal (Zinke, 1998), from the Barremian at Uña and Castellote, Spain (Rauhut and Zinke, 1995; Canudo et al., 1997; Rauhut, 2002), and from the Upper Cretaceous at four localities in southern France (Buffetaut et al., 1986). The considerably larger size of the Isle of Wight velociraptorine specimens and differences in denticle morphology, including their apical orientation, suggest they cannot be referred to any of these. Postcranial material referable to dromaeosaurs with possible velociraptorine affinities has also been reported from the Maastrichtian at Fox-Amphoux and Roques-Hautes, Provence, southern France and from the Upper Cretaceous of Romania (Le Lœuff et al., 1992). However, until teeth are found, no comparisons can be made with velociraptorines from the Isle of Wight.

## 8. Conclusions

The new specimens described here can be readily distinguished from other theropod teeth from the Wessex Formation, including those of *Eotyrannus lengi* for which a revised mean DSDI of 1.16 has been established. They can be referred to the Velociraptorinae (sensu Currie et al., 1990) on the basis of their DSDI, and represent the first record of the Velociraptorinae in the British Wealden Group. While IWCMS.2002.1 and BMNH R 16510 can be referred to the same taxon, sufficient differences exist between these specimens and the others described here to warrant caution in referring all to the same taxon. A larger tooth sample size is required in order to ascertain whether the differences observed relate to tooth position within the dental

arcade or to taxonomic differences. Denticle morphology and orientation indicate that the Isle of Wight specimens cannot be referred to the velociraptorine *Nuthetes* from the Berriasian of mainland England or to velociraptorine dromaeosaurids from continental Europe. Furthermore, based on tooth sizes, the Isle of Wight specimens might represent a taxon (or taxa) that was large in the context of Dromaeosauridae as a whole and possibly comparable in size to *Utahraptor* from the Barremian of the western US (Kirkland et al., 1993).

Among the considerable number of small theropod teeth recovered to date from bulk screening of plant debris beds in the Wessex Formation only IWCMS.2002.2 may be referred to the Velociraptorinae, indicating that juveniles are extremely rare. This is in contrast to *Nuthetes destructor* from the Purbeck Limestone Formation, which appears to be represented predominantly by teeth of juveniles of that taxon (Milner, 2002). The lack of small teeth pertaining to velociraptorine dromaeosaurids in the Wessex Formation may indicate that they were breeding elsewhere, only venturing onto the Wessex Formation floodplain, perhaps seasonally, as adults. However, at present this remains speculative.

### Acknowledgements

The National Trust and English Nature are thanked for their help and permission to collect samples. The Isle of Wight County Museum Service provided access to specimens and assistance in the field. Private collectors Mr. M. Green, Mr. K. Simmonds and Mr. J. Winch are thanked for making available specimens in their collections and for invaluable discussions and assistance in the field. Mr. M. Simpson generously donated specimens (IWCMS.2002.3 and 4 and BMNH R 16510) from his private collection and provided assistance in the field. I thank Mr. R. Loveridge, University of Portsmouth, for technical assistance and the production of photographs; Dr. D. Martill, University of Portsmouth, for his support and encouragement; Mr. D. Naish, University of Portsmouth, for invaluable discussions and access to his library; and Dr. P. Barrett, The Natural History Museum, London, for his very helpful review of the first draft of this paper. The award of a research scholarship by the University of Portsmouth is gratefully acknowledged.

### Addendum

While this manuscript was in review, a further tooth (IWCMS.2002.5) referable to a velociraptorine dromaeosaur was recovered from a bulk sample taken from bed number L14 (Fig. 2) near the top of the Wessex Formation at Barnes High (NGR SZ 43787 81026). It

bears many similarities to IWCMS.2002.2 but the presence of denticles can be discerned in the dentine on the apical half of the mesial carina. Distal denticles are well preserved but only four mesial denticles could be measured. The DSDI for this specimen, the accuracy of which is limited by the small number of mesial denticles counted, is 1.6. The specimen serves to demonstrate that velociraptorine dromaeosaurs were present throughout the period of deposition of most, if not all, of the exposed Wessex Formation.

### References

- Anon., 1866a. Another Wealden reptile. *Athenaeum* 10, 740.
- Anon., 1866b. Another new Wealden reptile. *Geological Magazine* 3, 383.
- Allen, P., 1998. Purbeck–Wealden (Early Cretaceous) climates. *Proceedings of the Geologists' Association* 109, 197–236.
- Allen, P., Wimbledon, W.A., 1991. Correlation of NW European Purbeck–Wealden (non-marine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research* 12, 511–526.
- Argast, S., Farlow, J.O., Gabel, T.R.M., Brinkman, D.L., 1987. Transport-induced abrasion of fossil reptilian teeth: implications for the existence of Tertiary dinosaurs in the Hell Creek Formation, Montana. *Geology* 15, 927–930.
- Buffetaut, E., Ford, R.L.E., 1979. The crocodylian *Bernissartia* in the Wealden of the Isle of Wight. *Palaeontology* 22, 905–912.
- Buffetaut, E., Marandat, D., Sigé, B., 1986. Découvert de dents de deinonychosaurus (Saurischia, Theropoda) dans le Crétacé Supérieur du Sud de la France. *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 303, 1393–1396.
- Butler, P.M., Ford, R., 1975. Discovery of Cretaceous mammals on the Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society* 6, 662–663.
- Canudo, J.I., Cuenca-Bescó, G., Ruiz-Omenaca, J.I., 1997. Dinosaurios dromeosáuridos (Saurischia: Theropoda) en el Barremiense Superior (Cretácico Inferior) de Castellote, Teruel. *Geogaceta* 22, 39–42.
- Chadwick, R.A., 1985. End Jurassic–early Cretaceous sedimentation and subsidence (late Portlandian to Barremian), and the late Cimmerian unconformity. In: Whitaker, A. (Ed.), *Atlas of Onshore Sedimentary Basins in England and Wales: Post Carboniferous Tectonics and Stratigraphy*. Blackie, London, pp. 52–56.
- Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum, London, Geology* 53, 11–70.
- Currie, P.J., Rigby, J.K., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge, pp. 107–125.
- Daley, B., Stewart, D.J., 1979. Weekend field meeting: the Wealden Group in the Isle of Wight. *Proceedings of the Geologists' Association* 90, 51–54.
- Falcon, N.L., Kent, P.E., 1960. Geological results of petroleum exploration in Britain 1945–1957. *Memoir of the Geological Society of London* 2, 56 pp.
- Farlow, J.O., Brinkman, D.L., Abler, W.L., Currie, P.J., 1991. Size, shape and serration density of theropod dinosaur lateral teeth. *Modern Geology* 16, 161–198.
- Fiorillo, A.R., Currie, P.J., 1994. Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. *Journal of Vertebrate Paleontology* 14, 74–80.

- Freeman, E.F., 1975. The isolation and ecological implications of the microvertebrate fauna of a lower Cretaceous lignite bed. *Proceedings of the Geologists' Association* 86, 307–312.
- Galton, P.M., 1971. A primitive dome-headed dinosaur (Ornithischia: Pachycephalosauridae) from the Lower Cretaceous of England and the function of the dome of pachycephalosaurids. *Journal of Paleontology* 45, 40–47.
- Galton, P.M., 1973. A femur of a small theropod dinosaur from the Lower Cretaceous of England. *Journal of Paleontology* 47, 996–997.
- Harding, I.C., 1986. An Early Cretaceous dinocyst assemblage from the Wealden of southern England. *Special Papers in Palaeontology* 35, 95–109.
- Howse, S.C.B., Milner, A.R., 1993. *Ornithodesmus*—a maniraptoran theropod dinosaur from the Lower Cretaceous of the Isle of Wight, England. *Palaeontology* 36, 425–438.
- Hughes, N.F., McDougall, A.D., 1990. New Wealden correlation for the Wessex Basin. *Proceedings of the Geologists' Association* 101, 85–90.
- Hutt, S., Martill, D.M., Barker, M.J., 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1996, 635–644.
- Hutt, S., Naish, D., Martill, D.M., Barker, M.J., Newbury, P., 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research* 22, 227–242.
- Insole, A.N., Hutt, S., 1994. The palaeoecology of the dinosaurs of the Weald. *Proceedings of the Geologists' Association* 87, 443–446.
- Kirkland, J.I., Gaston, R., Burge, D., 1993. A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. *Hunteria* 2 (10), 1–16.
- Le Lœuff, J., Buffetaut, E., Mechin, P., Mechin-Salessy, A., 1992. The first record of dromaeosaurid dinosaurs (Saurischia, Theropoda) in the Maastrichtian of southern Europe: palaeobiogeographical implications. *Bulletin de la Société Géologique de France* 163, 337–343.
- Lydekker, R., 1888. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part 1, Ornithosauria, Crocodylia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria. *British Museum (Natural History)*, London, 309 pp.
- Lydekker, R., 1889. On a coelurid dinosaur from the Wealden. *Geological Magazine* 6, 119–121.
- Makovicky, P.J., 1995. *Phylogenetic aspects of the vertebral morphology of Coelurosauria (Dinosauria: Theropoda)*. Unpublished MSc thesis, University of Copenhagen, 303 pp.
- Martill, D.M., Hutt, S., 1996. Possible baryonychid teeth from the Wessex Formation (Lower Cretaceous, Barremian) of the Isle of Wight, England. *Proceedings of the Geologists' Association* 107, 81–84.
- Martill, D.M., Naish, D. (Eds.), 2001. *Dinosaurs of the Isle of Wight*. *Field Guides to Fossils*, vol. 10. *Palaeontological Association*, London, 433 pp.
- Milner, A.C., 2002. Theropod dinosaurs of the Purbeck Limestone Group, southern England. *Special Papers in Palaeontology* 68, 191–201.
- Naish, D., 1999a. *Studies on Wealden Group theropods: an investigation into the historical taxonomy and phylogenetic affinities of new and previously neglected specimens*. Unpublished MPhil thesis, University of Portsmouth, 184 pp.
- Naish, D., 1999b. Fox, Owen and the small Wealden Group theropods *Calamospondylus* and *Aristosuchus*. *Journal of Vertebrate Paleontology* 19 (Supplement to No. 3), 66A.
- Naish, D., 1999c. Theropod dinosaur diversity and palaeobiology in the Wealden Group (Early Cretaceous) of England: evidence from a previously undescribed tibia. *Geologie en Mijnbouw* 78, 367–373.
- Naish, D., 2000. A small, unusual theropod (Dinosauria) femur from the Wealden Group (Lower Cretaceous) of the Isle of Wight, England. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2000, 217–234.
- Naish, D., 2002. The historical taxonomy of the Lower Cretaceous theropods (Dinosauria) *Calamospondylus* and *Aristosuchus* from the Isle of Wight. *Proceedings of the Geologists' Association* 113, 153–163.
- Naish, D., Martill, D.M., 2002. A reappraisal of *Thecocoelurus daviesi* (Dinosauria: Theropoda) from the Early Cretaceous of the Isle of Wight. *Proceedings of the Geologists' Association* 113, 23–30.
- Naish, D., Hutt, S., Martill, D.M., 2001. Saurischian dinosaurs 2: theropods. In: Martill, D.M., Naish, D. (Eds.), *Dinosaurs of the Isle of Wight*. *Field Guide to Fossils*, vol. 10. *The Palaeontological Association*, London, pp. 242–309.
- Norell, M.A., Makovicky, P.J., 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215, 1–28.
- Oldham, T.C.B., 1976. The plant debris beds of the English Wealden. *Palaeontology* 19, 437–502.
- Owen, R., 1876. *Monograph of the fossil Reptilia of the Wealden and Purbeck formations. Supplement 7. Crocodylia (Poikilopleuron), Dinosauria (Chondrosteosaurus)*. *Palaeontographical Society London, Monographs* 30, 1–7.
- Radley, J.D., 1994. Stratigraphy, palaeontology and palaeoenvironment of the Wessex Formation (Wealden Group, Lower Cretaceous) at Yaverland, Isle of Wight, southern England. *Proceedings of the Geologists' Association* 105, 199–208.
- Rauhut, O.W., 2002. Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research* 23, 255–263.
- Rauhut, O.W., Werner, C., 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift* 69, 475–489.
- Rauhut, O.W., Zinke, J., 1995. A description of the Barremian dinosaur fauna from Uña with a comparison to that of Las Hoyas. II International Symposium on Lithographic Limestones, Lleida-Cuenca, Spain. *Extended abstracts*. *Universidad Autónoma de Madrid*, pp. 123–126.
- Ruffell, A.H., 1992. Early to mid-Cretaceous tectonics and unconformities of the Wessex Basin (southern England). *Journal of the Geological Society*, London 149, 443–454.
- Ruffell, A.H., Batten, D.J., 1990. The Barremian–Aptian arid phase in western Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 80, 197–212.
- Sankey, J.T., Brinkman, D.B., Guenther, M., Currie, P.J., 2002. Small theropod and bird teeth from the Late Cretaceous (late Campanian) Judith River Group, Alberta. *Journal of Paleontology* 76, 751–763.
- Seeley, H.G., 1887a. On a sacrum apparently indicating a new type of bird, *Ornithodesmus cluniculus* Seeley. *Quarterly Journal of the Geological Society of London* 43, 206–211.
- Seeley, H.G., 1887b. On a sacrum apparently indicating a new type of bird (*Ornithodesmus cluniculus* Seeley), from the Wealden of Brook [report of Seeley 1887a]. *Geological Magazine* 4, 236.
- Seeley, H.G., 1888. On *Thecospondylus daviesi* (Seeley), with some remarks on the classification of the Dinosauria. *Quarterly Journal of the Geological Society of London* 44, 79–87.
- Smith, J.B., Dodson, P., 2003. A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23, 1–12.
- Stewart, D.J., 1978. *The sedimentology and palaeoenvironment of the Wealden Group of the Isle of Wight, Southern England*. Unpublished PhD thesis, Portsmouth University, 347 pp. + appendices.
- Stewart, D.J., 1981. A field guide to the Wealden Group of the Hastings area and the Isle of Wight. In: Elliot, T. (Ed.), *Field Guides to Modern and Ancient Fluvial Systems in Britain and Spain*. *International Fluvial Conference*, University of Keele, pp. 3.1–3.32.

- Stewart, J.D., Ruffell, A., Wach, G., Goldring, R., 1991. Lagoonal sedimentation and fluctuating salinities in the Vectis Formation (Wealden Group, Lower Cretaceous) of the Isle of Wight, southern England. *Sedimentary Geology* 72, 117–134.
- Stoneley, R., 1982. The structural development of the Wessex Basin. *Journal of the Geological Society, London* 139, 545–552.
- Sullivan, R.M., 2000. *Prenocephale edmontonensis* (Brown and Schlaikjer) new comb. and *P. brevis* (Lambe) new comb. (Dinosauria: Ornithischia: Pachycephalosauria) from the Upper Cretaceous of North America. In: Lucas, S.G., Heckert, A.B. (Eds.), *Dinosauria of New Mexico*. New Mexico Museum of Natural History and Science, Bulletin 17, 177–189.
- Underhill, J.R., 2002. Evidence for structural controls on the deposition of the Late Jurassic–Early Cretaceous Purbeck Limestone Group, Dorset, southern England. *Special Papers in Palaeontology* 69, 12–40.
- Ward, D.J., 1981. A simple machine for bulk processing of clays and silts. *Tertiary Research* 3, 121–124.
- White, H.J.O., 1921. A short account of the Geology of the Isle of Wight. *Memoirs of the Geological Survey of the United Kingdom*. HMSO, London, 219 pp.
- Wright, J.L., Barrett, P.M., Lockley, M.G., Cook, E., 1998. A review of the Early Cretaceous terrestrial vertebrate track-bearing strata of England and Spain. In: Lucas, S.G., Kirkland, J.I., Estep, J.W. (Eds.), *Lower and Middle Cretaceous Terrestrial Ecosystems*. New Mexico Museum of Natural History and Science, Bulletin 14, 143–153.
- Zinke, J., 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72, 179–189.
- Zinke, J., Rauhut, W.M., 1994. Small theropods (Dinosauria, Saurischia) from the Upper Jurassic and Lower Cretaceous of the Iberian Peninsula. *Berliner Geowissenschaftliche Abhandlungen E* 13, 163–177.