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Bicentennial Review

Dinosaurs of Great Britain and the role of the Geological Society of London in their discovery: basal Dinosauria and Saurischia

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Abstract: Beginning with Buckland's 1824 description of *Megalosaurus*, the Geological Society of London played a leading role during the 19th century discovery of dinosaurs in Britain. Here we review the society's role and assess the current knowledge of saurischian dinosaurs in the country. Of Britain's 108 dinosaur species (excluding *nomina nuda* and objective synonyms), 32% have been named in the pages of Society publications. Britain has a rich and diverse dinosaur record ranging from the Rhaetian to the Cenomanian, and includes a surprising taxonomic diversity. Alleged Lower and Middle Triassic dinosaurs from Britain are suspect or erroneous. Sauropodomorphs represent all of the major clades and several have their earliest global appearances in the British record (Diplodocoidea, Rebbachisauridae and Titanosauria), implying that this region was biogeographically important for this group. The British theropod record is diverse, and includes the earliest spinosaurids, carcharodontosaurids and coelurosaurs. Although some specimens are represented by near-complete skeletons, much material is fragmentary and indeterminate, and *c*. 54% of British dinosaur taxa are considered *nomina dubia*. In part this high number results from the genesis of dinosaur science in Britain and the corresponding obsolescence of supposedly diagnostic characters.

Dinosaurs were first described by 19th century British scientists working on fossils discovered in England (e.g. Torrens 1997, and references therein), and the Geological Society of London played a pivotal role in establishing the scientific study of dinosaurs. With an emphasis on the role of the Society, we here review the history, geological occurrence and systematics of British dinosaurs.

In 1824, William Buckland announced the discovery of *Megalosaurus* from the Stonesfield Slate of Oxfordshire (Buckland 1824). This seminal paper includes the first scientific description (Fig. 1) of the animals that later became the Dinosauria (Owen 1842). Although many early papers were often little more than descriptions of isolated bones or teeth, they set the foundation for what was to become one of the most popular strands of vertebrate palaeontology. In the latter half of the 19th century, the *Quarterly Journal of the Geological Society of London* became the leading journal in which studies on British dinosaurs were published. A remarkable 35 dinosaur taxa, representing 32% of the 108 dinosaurs that we recognize as valid or as *nomina dubia*, have been named in Society publications. (A list of these taxa is available online at http://www.geolsoc.org.uk/SUP18267. A hard copy can be obtained from the Society Library.) Although we include Aves within Dinosauria, we have restricted our listing to the Mesozoic. Because many British dinosaur finds have been highly incomplete, many taxa have been erected on material now considered inadequate. What were regarded as species-defining characters (autapomorphies in modern parlance) have turned out to be characters defining larger groups (synapomorphies in modern parlance); to adapt the term of Wilson & Upchurch (2003), they have become obsolete features.

Despite the fragmentary nature of much British dinosaur material, and the fact that many names based on this material are now considered *nomina dubia*, it remains of scientific value in that much of it is diagnostic at higher taxonomic levels. Even fragmentary remains can provide important data on the occurrence and distribution of clades. However, it is misleading to imply that all British dinosaur taxa, or all of those erected within Society publications, were erected for poor specimens. Some of the best represented and best known British dinosaurs (*Hypsilophodon foxii* Huxley 1869, *Cumnoria prestwichii* (Hulke, 1880*a*) and *Mantellisaurus atherfieldensis* (Hooley, 1925)) were published in the *Quarterly Journal*.

Dinosaur localities in Britain

Here we present a brief summary of the dinosaur-bearing strata and localities in Britain. General locality maps are available in the Supplementary Publication (see p. 000).

Upper Triassic dinosaur localities

Several suspect or erroneous discoveries have been claimed from the Lower and Middle Triassic, but the oldest British forms are probably Rhaetian. These include, in the Bristol district, abundant remains of the basal sauropodomorph *Thecodontosaurus* (Benton *et al*. 2000), and in South Wales, coelophysoid and *Thecodontosaurus* material from the Vale of Glamorgan (Kermack 1984; Fraser 1994; Rauhut & Hungerbühler 2000; Yates 2003). *Thecodontosaurus* material has also been reported from an unspecified location in Avon (Yates 2003), and from the Westbury Formation of Newark-Upon-Trent, Nottinghamshire (Martill & Clarke 1994). The latter record is erroneous, however, and should be regarded as Archosauria indet. Other reports of

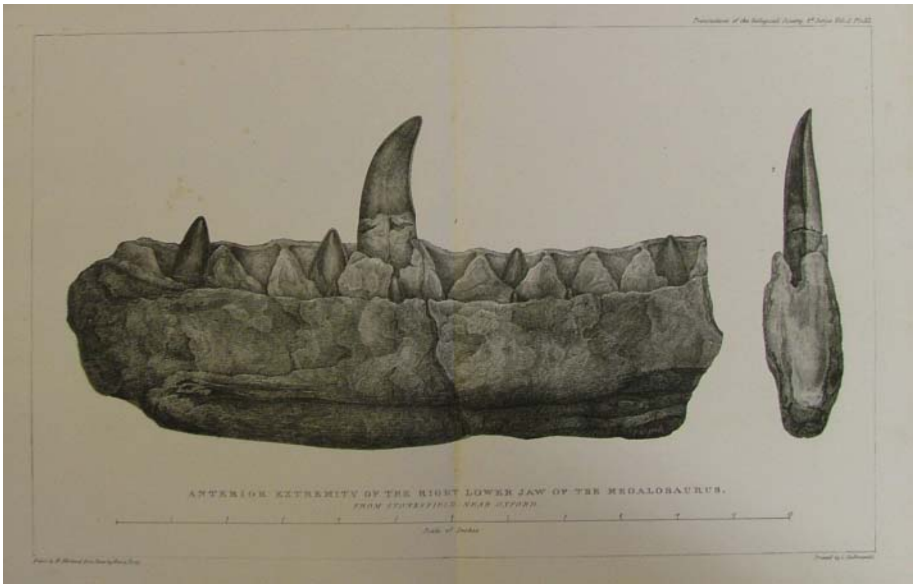

Fig. 1. The famous right dentary (OUM J.13505) of *Megalosaurus bucklandii* Ritgen, 1826 from the Taynton Limestone Formation of Stonesfield, Oxfordshire, in (left) lingual view and (right) in transverse view at mid-length. Originally published by Buckland (1824, plate XL).

the taxon from Somerset and Gloucestershire (Storrs 1994) lack the diagnostic characters of *Thecodontosaurus* and should be regarded as Sauropodomorpha indet.

Dinosaur tracks probably produced by theropods and basal sauropodomorphs (possibly plateosaurs) are known from Newton Nottage and from The Bendricks, Vale of Glamorgan (Sollas 1879; Tucker & Burchette 1977; Lockley *et al*. 1996).

Lower Jurassic dinosaur localities

Exposures of the Lower Jurassic Lias Group of southern England between Lyme Regis and Charmouth have yielded dinosaurs, the best being partial and near-complete skeletons (Fig. 2) of the thyreophoran *Scelidosaurus harrisonii*, some of which preserve soft tissues (Martill 1991; Martill *et al*. 2000). Fragmentary theropod remains have also been reported from these localities (see below). Evidence from ammonites suggests that most *Scelidosaurus* specimens come from the Woodstone Nodule Bed in the Charmouth Mudstone Formation.

Dinosaur remains have been recovered from clay pits in Warwickshire (Woodward 1908) and Leicestershire (Andrews 1921). von Huene (1926*a*) referred to a theropod femur from the Upper Lias of Whitby, and a posterior dorsal vertebra from the Toarcian jet rock of the Whitby Mudstone Formation, probably from a large theropod, was referred by Owen (1842) to *Streptospondylus* (see below).

Elsewhere, Benton *et al*. (1995) reported a partial theropod tibia from the Sinemurian part of the Upper Broadford Beds Formation of the Isle of Skye, Scotland, a marine formation that may have been deposited close to the palaeoshoreline. Irish dinosaur fragments from the Lower Jurassic mudstones of the Antrim coast include fragments of probable theropod femur and scutes from a thyreophoran likened to *Scelidosaurus* (Crowther & Simms 1997; Parkes 2001).

Fig. 2. A new, fully articulated and nearly complete skeleton of the thyreophoran *Scelidosaurus harrisonii* Owen, 1861. This specimen was collected from the Charmouth Mudstone Formation of the Black Ven landslip between Lyme Regis and Charmouth in Britain's Jurassic Coast World Heritage Site. Photograph by kind courtesy of D. Sole. Total length is *c*. 2 m.

Middle Jurassic dinosaur localities

Middle Jurassic strata on the Dorset coast are mostly marine and dinosaur remains occur infrequently (Evans & Milner 1994). On the Yorkshire coast much of the Middle Jurassic is in sandy or silty fluvio-deltaic facies. Although dinosaur bones are rare here, footprints are well known (Brodrick 1909; Sarjeant 1970; Whyte & Romano 1993, 1994), especially from the Aalenian Saltwick Formation. Evidence for probable theropods is preserved, and large tracks named *Deltapodus brodricki* Whyte & Romano 1994 are probably of thyreophoran identity (McCrea *et al*. 2001).

Most Middle Jurassic British dinosaurs are from inland exposures. Near Stonesfield, Oxfordshire, sandy limestones contained *Megalosaurus* and *Iliosuchus* (Metcalf & Walker 1994; Benton & Spencer 1995). The Bathonian White Limestone Formation at Ardley Quarry in Oxfordshire has yielded Britain's largest trackway site: sauropod and large theropod trackways provide new data on locomotion and palaeobiology (Day *et al*. 2002*a*, *b*, 2004). Wide-gauge sauropod trackways here are significant, as these are thought to have been produced by titanosaurs, one of the youngest sauropod clades (Wilson & Sereno 1998; Wilson & Carrano 1999; Upchurch *et al*. 2004).

Between 1887 and 1905, five dinosaur genera were recovered from the Middle Callovian Peterborough Member of the Oxford Clay Formation in clay pits between Yaxley, Peterborough and Whittlesey, including two sauropods, a stegosaur, an ankylosaur and an ornithopod (Leeds 1956; Martill 1988). Clay pits in the Upper Callovian Stewartby Member of the Oxford Clay Formation near Oxford yielded the theropod *Eustreptospondylus* (Phillips 1871; Walker 1964).

In the English Midlands, the partial skeleton of a sauropod was recovered from the Bajocian Rutland Formation of Great Casterton, Rutland (Jones 1970; Upchurch & Martin 2002). Elsewhere, only scrappy remains have been reported, among them a sauropod from the Aalenian Northampton Sands Formation of Northamptonshire (Reid 1984: although it should be noted that Reid regarded this unit as Lower Bajocian).

In Scotland, Marker & Barrow (1908) noted a possible dinosaur vertebra from the Hugh Miller Reptile Bed of Eigg. On Skye, Andrews & Hudson (1984) reported a probable ornithopod footprint in the Bathonian Lealt Shale Formation, and tridactyl dinosaur tracks were described from the Bathonian Valtos Sandstone Formation (Clark & Barco Rodriguez 1998; Marshall 2005). The Valtos Sandstone Formation has also yielded dinosaur bones, including two theropod caudal vertebrae, a rib, and a sauropod limb bone. The Bajocian Bearreraig Sandstone Formation on Skye has yielded thyreophoran forelimb elements (Clark 2001).

Upper Jurassic dinosaur localities

Notable finds include an iguanodontian ornithopod from the Kimmeridge Clay Formation of Oxfordshire and a partial stegosaur from the same formation near Swindon (Hulke 1880*a*, 1887). Oxfordian Oxford Clay dinosaurs include *Metriacanthosaurus parkeri* from the Weymouth Member (formerly Upper Oxford Clay) of Weymouth, Dorset. Holtz *et al*. (2004*a*) and Weishampel *et al*. (2004) incorrectly stated that *M. parkeri* is from the Corallian Oolite Formation. The overlying Ampthill Clay of the Midlands has also yielded dinosaurs (Seeley 1869).

Kimmeridgian dinosaurs from the Dorset coast include sauropods, theropods and stegosaurs. Remains from inland clay pits include, at Swindon, *Dacentrurus* and *Bothriospondylus* (Owen 1875), and at Cumnor, near Oxford, the camptosaurid *Cumnoria prestwichii* (Hulke 1880*a*). In Cambridgeshire, Kimmeridgian dinosaurs have been recovered from clay pits at Roswell near Ely and, in Norfolk, from canals at Denver Sluice. Isolated dinosaur remains, including sauropod vertebrae referred to *Cetiosaurus*, teeth referred to '*Cetiosaurus*' *humerocristatus*, and theropod metatarsals, have been reported from Tithonian 'Portland Stone' exposures in Dorset, Buckinghamshire, Oxfordshire and Wiltshire by Delair & Wimbledon (1995). Those workers also mentioned teeth from the Portland Stone of the Vale of Wardour referred to *Megalosaurus*, *Camarasaurus*, *Diplodocus*, *Iguanodon* and others (Delair & Wimbledon 1995), but it is unlikely that any of these identifications are correct.

Lower Cretaceous dinosaur localities

In southern England, on the Isle of Purbeck, limestones yield abundant and diverse vertebrate remains. Teeth from embryonic or hatchling macronarian sauropods, and dinosaur eggshell fragments, are known from both the Lulworth and Durlston formations (Ensom 2002), and Purbeck dinosaurs include the possible dromaeosaurid *Nuthetes destructor*, the heterodontosaurid *Echinodon becklesii*, the camptosaurid *Camptosaurus hoggii* and fragmentary remains of indeterminate large theropods, nodosaurids and sauropods (Milner 2002; Norman & Barrett 2002). Dinosaur tracks are well known from the Purbeck Limestone Group (Charig & Newman 1962; Delair 1966) and indicate the presence of sauropods, large theropods, ankylosaurs and iguanodontians (e.g. Lockley & Wright 2001, and references therein).

The Lower Cretaceous of southern England is also noted for the dinosaur-bearing Hastings Beds Group, Weald Clay Group and Wealden Group of Kent, Sussex, and the Isle of Wight (Radley 2004). On the Isle of Wight, dinosaur remains including those of sauropods, theropods, ankylosaurs and ornithopods are well known from coastal outcrops of the Barremian to Lower Aptian Wessex and Vectis formations of the Wealden Group (Martill & Naish 2001*a*). Among these are the best known and best preserved of British dinosaurs: *Neovenator salerii*, *Polacanthus foxii*, *Hypsilophodon foxii* and *Mantellisaurus atherfieldensis*. These units also preserve a good trackway record (Martill & Naish 2001*b*). Dinosaur remains have also been reported from the Aptian Lower Greensand and the Albian Upper Greensand (Swinton 1936; Stroh 1949).

In West and East Sussex, exposures of the Hastings Beds Group and Weald Clay Group have yielded material of large theropods and iguanodontians (Owen 1855, 1858*a*, *b*; Naish 2003). Their trackways are known from the Hastings area and elsewhere in Sussex (Parkes 1993). Quarries near Cuckfield have yielded iguanodontian material (Norman 1987), including that acquired by Mantell. Clay pits around Horsham and Bexhill continue to yield dinosaur material (Cooper 1995).

The Hastings Beds Group in Kent also produces dinosaur remains (Seeley 1882; Norman 1987), but it was from the Aptian Kentish Rag (part of the Lower Greensand Formation) that the famous 'Mantel-Piece' *Iguanodon* specimen was obtained (Mantell 1834; Norman 1993). Titanosauriform and ankylosaur material is known from the Kent Lower Greensand (Owen 1884; Pereda Suberbiola & Barrett 1999). In Surrey, partial and near-complete skeletons have been discovered from the Weald Clay Group, including the holotype of *Baryonyx walkeri* at Smokejack's Brickworks near Ockley (Charig & Milner 1986, 1997).

In Oxfordshire, records of dinosaurs in the Faringdon Sponge Gravels at Faringdon are probably derivatives from the Kimmeridgian (Benton & Spencer 1995) rather than Lower Cretaceous examples.

Elsewhere (south Midlands, East Anglia, Lincolnshire, south Yorkshire), Lower Cretaceous strata are represented by shallow marine facies and only rarely yield vertebrates. Indeterminate bones and sauropod and theropod teeth have been reported from the Purbeck Beds of Aylesbury, Buckinghamshire (Hudleston 1887; Lydekker 1893*a*; Woodward 1895; Benton & Spencer 1995). In Bedfordshire, the Aptian Potton Sands have yielded *Iguanodon* and the stegosaur *Craterosaurus pottonensis* (Seeley 1874; Galton 1981). In Cambridgeshire, probable Albian dinosaurs occur in the Cenomanian Cambridge Greensand, an unusual remanié deposit where vertebrates occur as derived fossils in phosphate nodules. Dinosaurs present include indeterminate sauropods, ankylosaurs and iguanodontians as well as the nodosaurid *Anoplosaurus curtonotus* and the hesperornithine *Enaliornis* (Seeley 1879; Pereda Suberbiola & Barrett 1999; Unwin 2001; Galton & Martin 2002*a*, *b*). In North Yorkshire, the Berriasian Speeton Clay Formation has yielded iguanodontian remains referred to *Camptosaurus hoggii* (Norman & Barrett 2002).

Upper Cretaceous dinosaur localities

Few Upper Cretaceous British localities produce dinosaur remains, probably because of an absence of non-marine facies. This is in marked contrast to central and southern Europe, where fluvio-lacustrine Upper Cretaceous strata are rich in dinosaurs (e.g. Buffetaut *et al*. 1991, 1997). The few British specimens include an iguanodontian tooth from the Totternhoe Stone of Hitchin, Hertfordshire (Newton 1892), conventionally identified as hadrosaurid, and indeterminate titanosaurs and nodosaurids from the lower Cenomanian Upper Greensand at Folkestone (Le Loeuff 1993; Pereda Suberbiola & Barrett 1999).

A systematic review of British dinosaurs

The genesis of dinosaur science in Britain resulted in the creation of many names that are today considered inadequate in terms of establishing taxonomic validity (see supplementary information; see p. 000). Ideas on British taxa were sometimes revised several or many times as knowledge improved, and the results are convoluted synonymy lists. Partly for this reason, we know of only one published review devoted to the British dinosaur fauna (Swinton 1934). Others, however, have incorporated British taxa into large-scale reviews of global dinosaur diversity (e.g. Steel 1969, 1970; Olshevsky 1991; Weishampel *et al*. 2004). In view of inconsistencies in the literature, we have used the original spellings proposed for specific names, although this results in an apparent inconsistency within our own text. A large number of British dinosaur species have been incorrectly allocated to a genus (e.g. most species referred to *Cetiosaurus* and *Ornithopsis*) and, in most cases, it is the type species alone that should be regarded as being correctly associated with the generic name. All other designations to generic level should be assumed to be historical artefacts and, following convention, we use quotation marks.

Possible dinosaurs

Several specimens claimed to be dinosaurian have been reported from Triassic strata, and two form the basis of named taxa. *Saltopus elginensis* von Huene, 1910, although probably a dinosauriform, is unlikely to be dinosaurian (Rauhut & Hungerbühler 2000; Langer 2004). Far more dinosaur-like is *Agnosphitys cromhallensis* Fraser *et al*., 2002 from the Upper Triassic fissure deposits of Cromhall Quarry, Avon. Though the *Agnosphitys* holotype is an ilium, material including a maxilla, a tooth, two astragali and a humerus is also referred to the taxon. Although Fraser *et al*. (2002) noted that the fully developed brevis fossa, perforate acetabulum and ascending astragalar process of *Agnosphitys* are dinosaur-like, those workers concluded that the taxon should be regarded as a dinosauromorph that might, in future, prove to be part of Dinosauria. Langer (2004) regarded *Agnosphitys* as a *nomen dubium* and drew attention to the disassociated nature of the referred material. However, he argued that the type specimen and some of the referred material are probably dinosaurian.

Basal sauropodomorphs

Although conventionally classified together within a group termed Prosauropoda, recent studies indicate that 'prosauropods' represent an assemblage of basal sauropodomorphs and basal sauropods, but with some forming a clade for which the name Prosauropoda can be used (Sereno 1998; Yates & Kitching 2003; Galton & Upchurch 2004). One of the most basal sauropodomorphs is *Thecodontosaurus* Riley & Stuchbury, 1836, represented by two species from the British Upper Triassic. Two other archosaurian species named for Durdham Down material, *Paleosaurus cylindrodon* and *P. platyodon* (both of which have their own complex synonymies), have often been regarded as synonymous with, or closely related to, *T. antiquus*. Benton *et al*. (2000) showed that these names were based on non-diagnostic non-dinosaurian teeth.

Thecodontosaurus has also been reported from the ?Rhaetian fissure fill deposits of Pant-y-ffynnon Quarry, Vale of Glamorgan and, although initially referred to as *Thecodontosaurus* sp. (Kermack 1984), has been shown to represent a new species, *T. caducus* Yates, 2003. *T. caducus* possesses pneumatic foramina on its cervical vertebrae and lacks the autapomorphies of *T. antiquus* (a projecting medial tubercle on the proximal part of the humerus and downcurved preacetabular process on the ilium).

Specimens allegedly referable to Plateosauria, the only sauropodomorph clade unambiguously associated with the name Prosauropoda (as a result of its anchoring on *Plateosaurus* (Sereno 1998; Galton & Upchurch 2004)), have been reported from Britain. Von Huene (1907–1908, 1932) referred material from Wedmore, Somerset, to the German species *Gresslyosaurus ingens* Rütimeyer, 1856, and Swinton (1934) referred various (unspecified) fragments from Glastonbury to the same taxon. Although *G. ingens* is generally regarded as a *nomen dubium* (Galton & Upchurch 2004), Moser (2003) argued that it is diagnostic and valid. However, the Wedmore material does not belong to this taxon and was later made the type of the melanorosaurid *Camelotia borealis* (see below). Although Swinton (1934) may have been referring to the same material, there is no evidence that the Glastonbury material he listed belonged to *G. ingens*. Two tooth-based taxa from the Westbury Formation, *Avalonianus sanfordi* Seeley, 1898, and *Picrodon herveyi* Seeley, 1898, have been referred at times to *Gresslyosaurus* (von Huene 1907–1908, 1932; Swinton 1934) but should be regarded as Archosauria indet.

Martill & Dawn (1986) reported *Plateosaurus* from the Rhaetian of Staple Pit in Newark-Upon-Trent, Nottinghamshire. Although at least some references to *Gresslyosaurus* and *Plateosaurus* in Britain are confused references to *Camelotia* (Clark

1993), material such as that from Staple Pit lacks the characters needed to refer it to Sauropodomorpha, let alone to *Plateosaurus*, and are regarded by Galton (2005) as Saurischia indet.

Sauropoda

Although many British sauropod fossils are poor and, where named, should be regarded as *nomina dubia*, many can be classified within higher-level taxa. They show that Britain had a diverse sauropod assemblage and that some groups make their earliest geological appearance in British strata. The general phylogenetic pattern of the sauropod radiation is largely agreed (Upchurch 1998; Wilson & Sereno 1998; Wilson 2002; Upchurch *et al*. 2004; Taylor & Naish 2005) but the inclusiveness of Sauropoda has changed as some Upper Triassic and Lower Jurassic taxa now seem to be basal members of the clade, rather than prosauropods (Yates 2003, 2004; Yates & Kitching 2003; Upchurch *et al*. 2004). Among these is *Camelotia borealis* Galton, 1985 from the Rhaetian Westbury Formation of Wedmore Hill, Somerset. *Camelotia* has been regarded as a melanorosaurid (Galton 1985), a group of large quadrupedal sauropodomorphs otherwise restricted to the southern hemisphere.

All other British sauropods belong to Eusauropoda (Upchurch 1995; Upchurch *et al*. 2004). The oldest British representative of this group is an indeterminate form from the Aalenian Northampton Sands Formation of Northamptonshire. Used by Reid (1984) for histological study, it was suggested by Hunt *et al*. (1994) and Weishampel *et al*. (2004) to be a possible brachiosaurid. The specimen would be the oldest member of this group worldwide, and the oldest reported macronarian and neosauropod, if this is correct.

The earliest named sauropod is *Cetiosaurus*, described by Owen (1841*a*) but misidentified as crocodilian. Thirteen species from the British Jurassic and Cretaceous (Benton & Spencer 1995; Upchurch & Martin 2003; Weishampel *et al*. 2004) have been referred to this genus and only recently has their taxonomic status been resolved (Upchurch & Martin 2002, 2003). The outcome is that *C. oxoniensis* Phillips 1871, from the Bajocian–Bathonian Forest Marble Formation of Oxfordshire, has been proposed as the type species, seven of the referred species are *nomina nuda* or *nomina dubia* and, in addition to *C. oxoniensis*, three species represent valid taxa, none of which are close enough to *C. oxoniensis* to warrant inclusion in the same genus (Upchurch & Martin 2002, 2003). These are '*C.*' *brevis* Owen, 1842, '*C.*' *glymptonensis* Phillips, 1871 and '*C.*' *humerocristatus* Hulke, 1874 (see below). *C. oxoniensis* is part of a clade (Cetiosauridae) located near the base of Eusauropoda (Upchurch *et al*. 2004), although earlier studies had found it to be closer to the eusauropod clade Neosauropoda (Upchurch 1995, 1998; Upchurch & Martin 2002). Long used as a taxonomic dumping ground for assorted taxa, Cetiosauridae has been defined as the clade including all those sauropods more closely related to *Cetiosaurus* than to *Saltasaurus* (Upchurch *et al*. 2004).

Most isolated material referred to *Cetiosaurus* lacks diagnostic characters and should be regarded as Eusauropoda indet. Some appears to represent distinct sauropod taxa that are too poorly known to be named or identified: the Stow-on-the-Wold (Gloucestershire) material referred to *Cetiosaurus* by Reynolds (1939), for example, differs from *C. oxoniensis* in having a straight, rather than posterodorsally curved, ischium. *Cardiodon rugulosus* Owen, 1844 (although with the generic name coined by Owen 1841*b*), named for a tooth (currently of unknown whereabouts) from the Forest Marble Formation of Bradford-on-Avon, Wiltshire, has been regarded as a possible senior synonym of *Cetiosaurus* given that it is highly similar to alleged *C. oxoniensis* teeth (e.g. Lydekker 1890*b*; Steel 1970). Upchurch & Martin (2003) showed that the *Cardiodon* tooth is different from supposed *C. oxoniensis* teeth (atypically, *Cardiodon* has a convex lingual surface), and there are no grounds for synonymy. *Cardiodon* remains Eusauropoda *incertae sedis*.

The 1968 discovery of a *Cetiosaurus* from the Bajocian Rutland Formation of Rutland (Fig. 3) has improved our understanding of this sauropod. Although intimated to represent a new species (Martill & Clarke 1994), the Rutland cetiosaur is referable to *C. oxoniensis* (Upchurch & Martin 2002). An isolated braincase from the Bathonian of Oxford has also ben referred to *Cetiosaurus* (Galton & Knoll 2006).

Besides *C. oxoniensis*, the Forest Marble Formation yielded '*C.*' *glymptonensis*, based on nine caudal vertebrae from Glympton, Oxfordshire (although within the boundaries of Northamptonshire when named by Phillips (1871)). These vertebrae are proportionally elongate and possess diagnostic lateral ridges: features suggesting that '*C.*' *glymptonensis* is a diplodocoid, and a valid taxon that requires a new generic name (Upchurch & Martin 2003; Upchurch *et al*. 2004). The Bathonian age of '*C.*' *glymptonensis* makes it the oldest diplodocoid.

A sauropod discovered at Peterborough, '*Ornithopsis*' *leedsii* Hulke, 1887, probably came from the Callovian Kellaways Formation (Martill 1988). It was established on vertebrae, rib and pelvic fragments and, although lacking autapomorphies, can be referred to Brachiosauridae (Upchurch & Martin 2003). A second specimen referred to '*O.*' *leedsii* by Woodward (1905), also from Peterborough and from the Oxford Clay Formation,

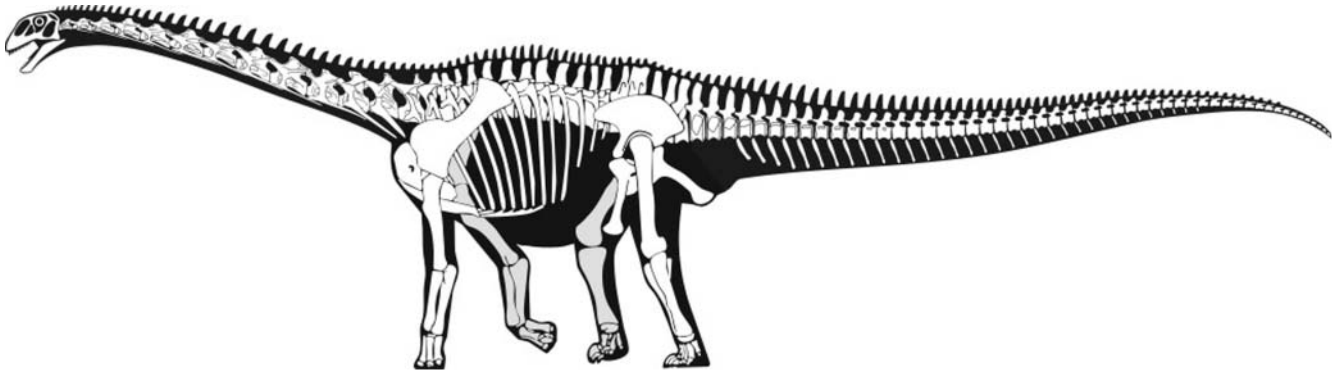

Fig. 3. Reconstructed skeleton of the Rutland dinosaur, a cetiosaurid discovered in 1968 and recently shown to be referable to *Cetiosaurus oxoniensis*. Reconstruction kindly supplied by Mark Evans. Total length *c*. 14.5 m.

was given its own genus (*Cetiosauriscus* von Huene, 1927) but incorrectly regarded as the type specimen of '*O.*' *leedsii*. To circumvent this problem, Charig (1980, 1993) renamed it *Cetiosauriscus stewarti* Charig, 1980. It includes dorsal, sacral and caudal vertebrae, a scapulocoracoid and forelimb, a partial ilium, a left hindlimb, and chevrons (Fig. 4). A distal tail segment referred to *C. stewarti* cannot be reliably associated with the taxon. Although conventionally regarded as a diplodocoid (Charig 1980; Upchurch *et al*. 2004), Rauhut *et al*. (2005) found *C. stewarti* to be part of a clade that included *Mamenchisaurus* and *Omeisaurus*, two Middle or Upper Jurassic Chinese taxa. Mamenchisauridae Young & Chao, 1972, a clade that we here diagnose as all those sauropods closer to *Mamenchisaurus constructus* Young, 1954 than to *Saltasaurus loricatus* Bonaparte & Powell, 1980, is the oldest name for this clade. Some European fossils, including the holotype of '*Ornithopsis*' *greppini* von Huene, 1922 from the Kimmeridgian of Switzerland, and an unnamed taxon known only from an enormous proximal caudal vertebra from the Tithonian–Berriasian of Spain, have been regarded as close relatives of *C. stewarti* on the basis of similarly proportioned caudal vertebrae (Meyer & Thüring 2003; Royo-Torres & Cobos 2005).

A taxon from the Kimmeridge Clay of Weymouth, Dorset, '*Cetiosaurus*' *humerocristatus* Hulke, 1874 is based on a gracile humerus that would have exceeded 1500 mm when complete (Hulke 1874; Lydekker 1888). Representing a brachiosaurid, '*C.*' *humerocristatus* appears to be diagnosable based on its degree of elongation and the distal prolongation of its deltopectoral crest (Upchurch & Martin 2003) and this taxon also needs a generic name. A phalanx and partial pubis from the Kimmeridge Clay referred to '*C.*' *humerocristatus* cannot be reliably assigned to this taxon (Lydekker 1888; Martill *et al*. 2006). A second Kimmeridge Clay brachiosaurid humerus, the holotype of '*Ornithopsis*' *manseli* Lydekker, 1888, was also, like '*O.*' *leedsii*, probably incorrectly assigned to the genus. The '*O.*' *manseli* humerus appears to have been similar to the '*C.*' *humerocristatus* holotype (Lydekker 1888) and the two may be synonymous. Various unassociated Kimmeridge Clay vertebrae, limb elements and dermal scutes were referred by Seeley (1869) to *Gigantosaurus megalonyx* Seeley, 1869. Most of these cannot be identified beyond Sauropoda and none exhibit autapomorphies (Martill *et al*. 2006). However, a caudal vertebra referred to this species was suggested by Upchurch (1993) to belong to a diplodocid diplodocoid.

Several dorsal and sacral vertebrae from the Kimmeridge Clay of Wiltshire were named *Bothriospondylus suffossus* Owen, 1875. Although often regarded as a brachiosaurid, this name is a *nomen dubium* and it cannot be identified beyond Neosauropoda (Upchurch 1993; Salgado & Calvo 1997). *B. robustus* Owen, 1875 from the Bajocian–Bathonian Forest Marble Formation of Wiltshire (suggested by Owen (1875) to perhaps represent a new genus, for which he proposed the name *Marmarospondylus*), is a *nomen dubium* based on a vertebral centrum that might be of macronarian identity (Upchurch 1993).

Wealden sauropods include *Pelorosaurus conybeari* (Melville, 1849) from the Hastings Beds Group of Cuckfield, East Sussex, another form represented by a large non-diagnostic humerus (Naish & Martill 2001; Upchurch & Martin 2003). Caudal vertebrae found adjacent to the humerus were included by Owen (1842) in '*Cetiosaurus*' *brevis*, together with Barremian Isle of Wight vertebrae shown by Melville (1849) to belong to an iguanodontian. Melville (1849) renamed the Cuckfield vertebrae '*C.*' *conybeari*, and it was to this species that Mantell (1850) referred the humerus. Melville's renaming is not justifiable

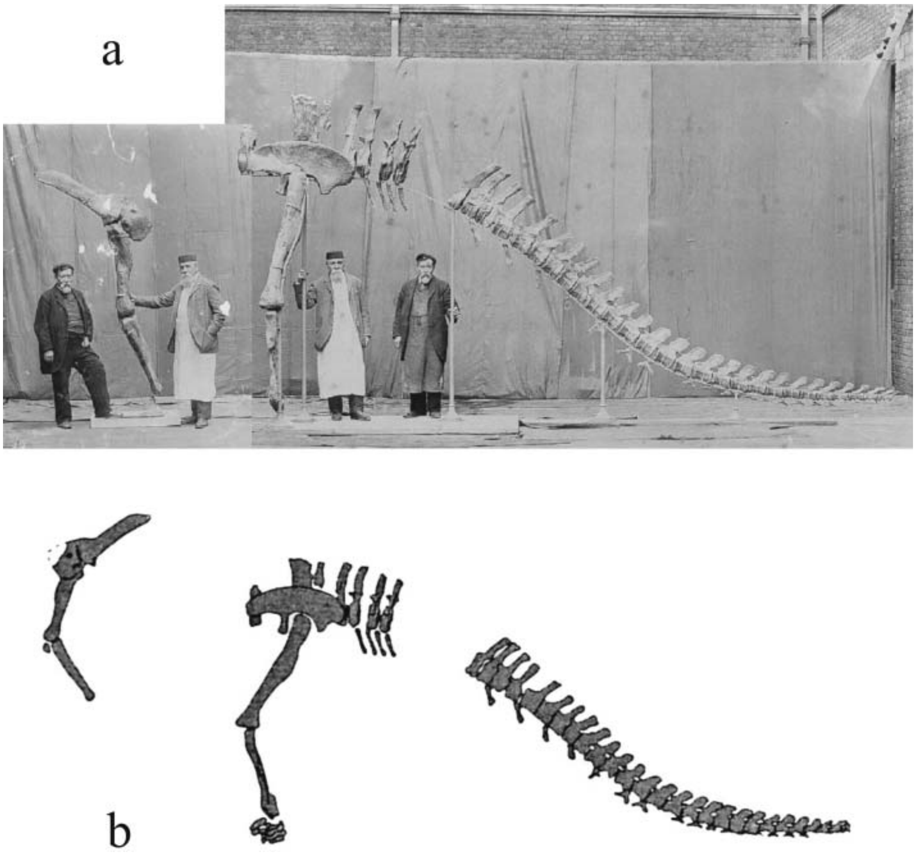

Fig. 4. (**a**) Composite photograph showing mounted partial skeleton of *Cetiosauriscus stewarti*, a possible mamenchisaurid sauropod from the Oxford Clay Formation of Peterborough, as assembled at the then British Museum (Natural History). Collage by J. Liston, from photographs held by the Leeds Family and used with their kind permission (original images believed to be taken by the British Museum (Natural History), now lost). (**b**) Diagrammatic representation of same, from Martill & Clarke (1994).

however, and *P. conybeari* is a junior objective synonym of '*C.*' *brevis*. Although this is the first named *Cetiosaurus* species that is not a *nomen dubium* (and thus technically the type species), the name *Cetiosaurus* is usually associated with *C. oxoniensis* and the most sensible course of action is to petition the International Commission on Zoological Nomenclature to make this the type species (Upchurch & Martin 2002, 2003). Although the *P. conybeari* humerus is brachiosaurid-like, it differs in having a less prominent deltopectoral crest. Furthermore, the '*C.*' *brevis* caudal vertebrae are titanosaur-like in at least one feature: the absence of a hyposphenal ridge. Upchurch *et al*. (2004) therefore proposed that this material be allocated to Titanosauriformes *incertae sedis*.

A second Wealden species referred to *Pelorosaurus*, '*P.*' *becklesii* Mantell, 1852, is from the Hastings Beds Group of Hastings, and consists of a humerus, radius and ulna, and associated skin impressions. The bones are robust and show that this taxon is a titanosaur (Upchurch 1995; Upchurch *et al*. 2004), although whether the material is diagnostic is arguable. The skin impressions reveal subrounded to subhexagonal, non-overlapping scales with a papilliform texture (Hooley 1917; Czerkas 1994). An unusual sauropod vertebra, also from the Hastings Beds Group of Hastings, was described by Lydekker (1893*b*) and represents a new taxon. An isolated metacarpal from Bexhill Beach, derived from the Hastings Beds Group, has been identified as that of a diplodocid (Anonymous 2005; M. Bonnan, pers. comm.).

The Isle of Wight's Wessex Formation has yielded nine sauropod genera and 11 species with an unnamed diplodocoid represented by fragmentary evidence (Charig 1980; Naish & Martill 2001). Most of these names are based on non-overlapping material that lacks autapomorphies, and all but two (*Oplosaurus armatus* Gervais, 1852 and *Ornithopsis hulkei* Seeley, 1870) should be regarded as *nomina dubia* (Naish & Martill 2001; Upchurch *et al*. 2004). The presence of three tooth morphologies (represented by *Oplosaurus armatus*, '*Pleurocoelus*' *valdensis* Lydekker, 1889 and Rebbachisauridae indet.) indicates that at least three taxa were present. The name '*Pleurocoelus*' *valdensis* has been attached to teeth and vertebral centra from the Hastings Beds Group and Wessex Formation (Lydekker 1889, 1890*a*), as well as for teeth from Spain and Portugal (Ruiz-Omeñaca & Canudo 2005). Although conventionally regarded as a *nomen dubium* (Naish & Martill 2001), Ruiz-Omeñaca & Canudo (2005) argued that, whereas there is no reason to regard '*P.*' *valdensis* as congeneric with the North American *P. nanus* (the type species), it is a diagnosable brachiosaurid. The presence of rebbachisaurids in the Wessex Formation is based on isolated teeth (illustrated by Naish & Martill 2001) similar to those of *Nigersaurus taqueti* from the Aptian–Albian Tegama Group of Niger (Sereno *et al*. 1999; Sereno & Wilson 2005). This is the earliest global record of Rebbachisauridae.

Brachiosaurids are securely identified in the Wessex Formation on the basis of isolated cervical and dorsal vertebrae, and the undescribed Barnes High skeleton, all of which share derived characters with *Brachiosaurus* (Blows 1995; Upchurch 1995; Naish & Martill 2001; Naish *et al*. 2004*a*). Although diagnostic Wessex Formation brachiosaurid material has been referred to *Eucamerotus foxi* Blows, 1995 (Fig. 5a and b), this is inappropriate. A cervical vertebra with a centrum 745 mm long (Fig. 5d) represents a brachiosaurid similar to *Sauroposeidon proteles* Wedel *et al*., 2000 from the Aptian–Albian Antlers Formation of the USA (Naish *et al*. 2004*a*), although whether this giant form is conspecific with material referred to *E. foxi* cannot be determined. *Ornithopsis hulkei* Seeley, 1870, also from the Wessex Formation, has been regarded as a brachiosaurid distinct from *E. foxi* (Blows 1995). Upchurch *et al*. (2004) noted that brachiosaurid characters were lacking from the holotype (an incomplete dorsal centrum) but that, as the centrum contained coarsely cancellous bone, it should perhaps be regarded as an indeterminate titanosauriform. The characters reported as diagnostic for this specimen (Blows 1995; Upchurch *et al*. 2004) are suspect (Naish & Martill 2001), and the validity of *O. hulkei* requires re-evaluation. A second vertebra, from the Hastings Beds Group, was used by Seeley, (1870) in establishing *O. hulkei* but later formed the holotype of *Bothriospondylus elongatus* Owen, 1875. *B. elongatus* is a *nomen dubium* based on indeterminate material. '*O.*' *eucamerotus* Hulke, 1882, based on pelvic elements from the Wessex Formation, is a non-diagnostic titanosauriform.

Oplosaurus armatus Gervais, 1852, based on a large tooth, was regarded as a brachiosaurid by Naish & Martill (2001) but suggested to be camarasaurid by Canudo *et al*. (2002). The Wessex Formation's *Chondrosteosaurus gigas* Owen, 1876, based on two cervical vertebrae, has also been regarded as a camarasaurid but its camellate internal structure shows that it is better identified as a basal titanosauriform (M. Wedel, pers. comm.). A second *Chondrosteosaurus* species, *C. magnus* Owen 1876, was erected for an incomplete Wessex Formation vertebra (BMNH R98) that lacks informative characters and should be regarded as Sauropoda indet.

Wessex Formation caudal vertebrae referred by Lydekker (1887, 1888) to *Titanosaurus*, a *nomen dubium* based on Indian material, were given their own species ('*T.*' *valdensis* von Huene, 1929) and genus (*Iuticosaurus* Le Loeuff, 1993). These specimens are titanosaurian but cannot be diagnosed (Naish & Martill 2001; Wilson & Upchurch 2003). Isle of Wight caudal vertebrae from the Albian Upper Greensand ('*Titanosaurus*' *lydekkeri* von Huene, 1929), are also Titanosauria indet. A sauropod pelvis and sacrum from the Lower Greensand of Luccombe Chine (Stroh 1949; Blows 1995; Naish & Martill 2001) can be referred to Titanosauriformes.

A fourth British sauropod based (in part) on a humerus is *Dinodocus mackesoni* (Owen, 1884) from the Aptian–Albian Lower Greensand of Hythe, Kent. Named for poorly preserved pelvic and limb fragments originally described as from a pliosaur, its humerus is much like that of *Pelorosaurus* and, although some researchers have synonymized the two, they lack shared derived characters. It seems prudent to identify *Dinodocus* as Titanosauriformes indet.

Britain's youngest sauropod is *Macrurosaurus semnus* Seeley, 1876 from the Cenomanian Cambridge Greensand of Cambridgeshire, but again it is a *nomen dubium* that cannot be identified beyond Titanosauria indet. *M. semnus* was based on 25 caudal vertebrae from Barnwell and another 15 from Barton; other elements include an ungual, more caudal vertebrae, and a partial foot (Seeley 1876*a*). The latter specimen was identified as belonging to an ankylosaur and, combined with other material, formed the basis of *Acanthopholis platypus* Seeley, 1869. Although from a sauropod, the material cannot be identified more precisely (Pereda Suberbiola & Barrett 1999).

Theropoda

Theropods are all those saurischians more closely related to birds than to sauropods (Sereno 1998). Excluding birds, British theropod fossils range in age from Norian or, at least, Rhaetian to Barremian. Given that the first non-avian theropod to be recognized was a British fossil (Buckland 1824), Britain has a

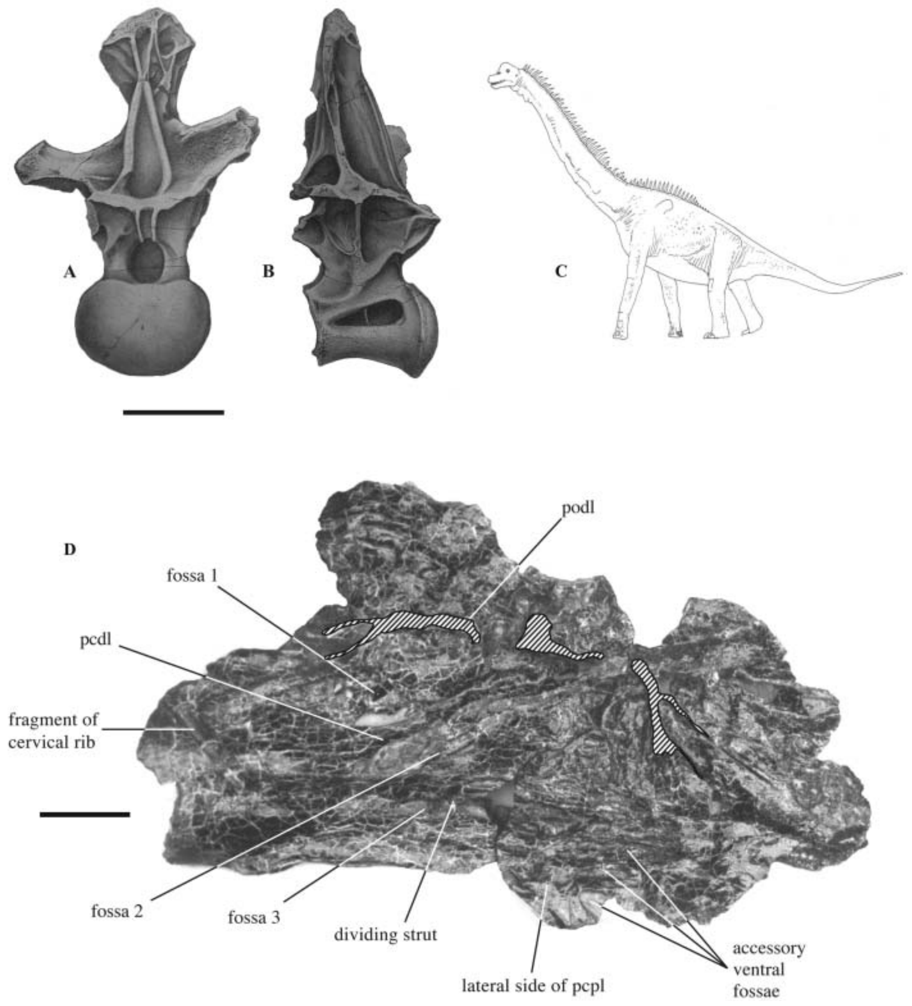

Fig. 5. Brachiosaurid dorsal vertebra from the Wessex Formation of the Isle of Wight, in (**a**) anterior and (**b**) right lateral views, after Hulke (1880*b*). This well-preserved vertebra (BMNH R88) was referred by Blows (1995) to his taxon *Eucamerotus foxi* and shares derived characters with *Brachiosaurus*. Scale bar is 20 cm. (**c**) Life restoration of the Upper Jurassic brachiosaurid *Brachiosaurus*. Total length *c*. 25 m. (**d**) The large brachiosaurid cervical vertebra MIWG.7306. Representing the largest British dinosaur, it also shares derived characters with *Brachiosaurus*. pcdl, posterior centrodiapophyseal lamina; pcpl, posterior centroparapophyseal lamina; podl, postzygodiapophyseal lamina. Scale bar is 10 cm.

particularly important place in the history of theropod research. Our theropod fossil record is rich with most major clades represented, some by well-preserved and reasonably complete remains.

One of the most basal theropod clades, Coelophysoidea, is represented by specimens from Wales, Scotland and England. The Welsh material consists of a pelvis, femur and vertebrae from the (probably) Norian fissure fillings of the Vale of Glamorgan. This material is similar to that of the coelophysid coelophysoid *Syntarsus*, a Hettangian–Pliensbachian genus from the USA and southern Africa, and was tentatively referred to it by Rauhut & Hungerbühler (2000), despite its greater age. Irmis (2004) expressed scepticism about this identification, noting that the only character linking the Pant-y-ffynnon specimen with *Syntarsus* (a pubic fenestra adjacent to the obuturator foramen) is widely distributed, and Rauhut (2003*a*) reported its presence in diverse coelophysoids. Rauhut & Hungerbühler (2000) also noted that the Pant-y-ffynnon material is similar to *Procompsognathus* from the Norian of Germany, and might belong to this taxon instead.

A second Welsh theropod that might also be a member of Coelophysoidea, a natural mould of a dentary named ‘*Zanclodon*’ *cambrensis* Newton, 1899, is from the Rhaetian of the Vale of Glamorgan (Fig. 6a). *Zanclodon* Plieninger, 1846, a *nomen dubium*, was named for a jaw fragment probably from a crurotarsan: the referral of the Rhaetian theropod to this taxon is therefore incorrect. ‘*Z.*’ *cambrensis* lacks autapomorphies and is also a *nomen dubium*, and there is even uncertainty over which theropod clade it belongs to (Steel 1970; Molnar *et al*. 1990; Rauhut & Hungerbühler 2000; Holtz *et al*. 2004*a*). The shape of the interdental plates and a strong overall similarity to the dentaries of *Liliensternus* and *Dilophosaurus* suggest that identification of ‘*Z.*’ *cambrensis* as a coelophysoid or near-coelophysoid is most likely. A vertebral centrum from Lavernock, Vale of Glamorgan, has been suggested to belong to ‘*Z.*’ *cambrensis* (Storrs 1994). The best known English coelophysoids are *Sarcosaurus woodi* Andrews, 1921 and *S. andrewsi* von Huene, 1932. *Sarcosaurus* has a complex taxonomic history (Carrano & Sampson 2004). *S. woodi*, named for a partial pelvis, femur and vertebral centrum, is from the Lower Lias Group in Leicestershire, with a probable second specimen described from the Lower Lias Group in Warwickshire (von Huene 1932). Although often assumed to be Sinemurian (Carrano & Sampson 2004; Weishampel *et al*. 2004), the ammonite fauna suggests that the Leicestershire beds are of latest Rhaetian and Hettangian age (Martin *et al*. 1986). *S. andrewsi* was named for a tibia from Wilmcote, Warwickshire that was given a second name, *Magnosaurus woodwardi*, in the paper where it was first named (von Huene 1932). Carrano & Sampson (2004) suggested the use of *S. andrewsi* for the specimen, though they noted that no derived characters demonstrate its referral to *Sarcosaurus*. Although *Sarcosaurus* was identified as non-tetanuran by several researchers (Paul 1988*a*; Rowe & Gauthier 1990), the strong similarity of its femur to that of *Liliensternus*, combined with other simila-

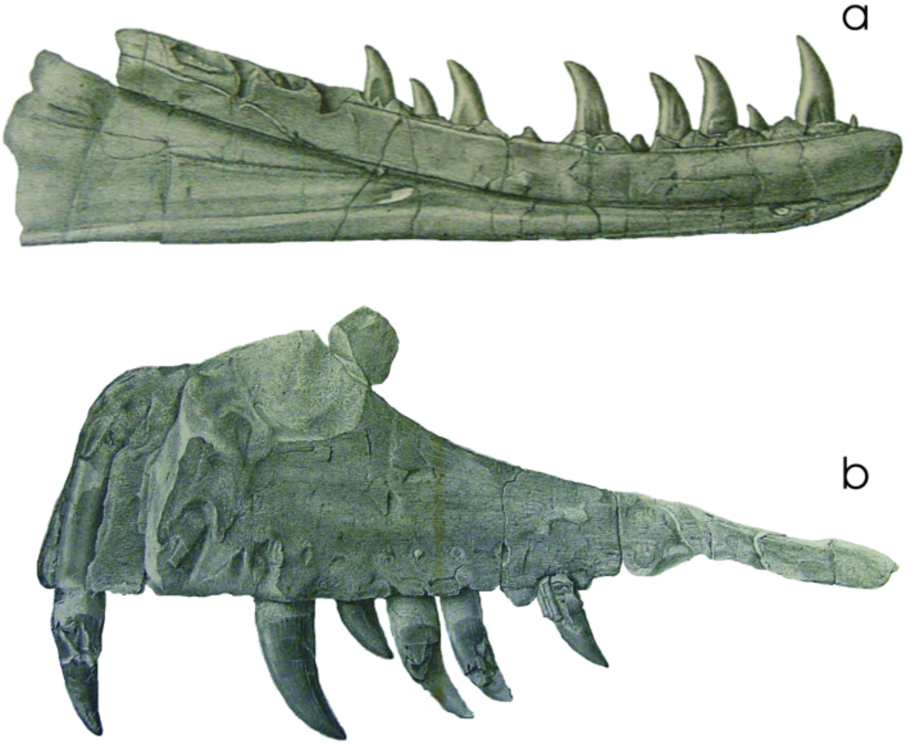

Fig. 6. (**a**) Natural mould of the dentary of a basal theropod from the Rhaetian of the Vale of Glamorgan; the holotype of '*Zanclodon*' *cambrensis* Newton, 1899. Actual specimen is 275 mm long. (**b**) Maxilla of a large theropod from the Taynton Limestone Formation of Oxfordshire. Decribed by Huxley (1869), this specimen (OUM J13506) appears to belong not to *Megalosaurus*, but to an additional, unnamed large theropod. Actual specimen is *c*. 480 mm long.

rities, has allowed allocation to Coelophysoidea (Carrano & Sampson 2004). However, autapomorphies have yet to be recognized for *Sarcosaurus* and it is a *nomen dubium*.

British coelophysoids are also represented by the distal part of a left tibia from the Sinemurian part of the Upper Broadford Beds Formation of the Isle of Skye (Benton *et al*. 1995). A caudal vertebra from the Isle of Skye has the same degree of elongation as coelophysoid caudal vertebrae and also possesses the short prezygapophyses and distally located neural spine characteristic of this group. Finally on coelophysoids, it should be noted that some Triassic suchians converged on theropods to such a high degree that their bones have been misidentified as belonging to coelophysoids (Nesbitt & Norell 2006). Some isolated 'coelophysoid' elements may, therefore, be of non-dinosaurian identity.

Basal tetanurans

Members of Tetanurae, the theropod clade that includes carnosaurs and coelurosaurs, are represented in British rocks as old as the Sinemurian. An ungual, incomplete femur, and articulated distal portion of femur and proximal tibia, all from the Lower Lias Group of Charmouth, Dorset and originally described by Owen (1861) as belonging to *Scelidosaurus* (Fig. 2), belong to a tetanuran. Newman (1968) assumed these remains to belong to a megalosaurid. A theropod tooth (25 mm long) from the Lower Lias Group of Lyme Regis, referred to *Zanclodon* by Lydekker (1888), was named '*Megalosaurus*' *lydekkeri* von Huene, 1926 and referred by von Huene (1932) to *Magnosaurus* (see below). '*M*.' *lydekkeri* is a *nomen dubium* and von Huene (1926*a*) only differentiated it on the basis of its 'falciform curvature': it should be classified as Theropoda indet.

Von Huene (1926*a*, *b*) described various remains from the Aalenian–Bajocian Inferior Oolite Formation of Nethercomb, Dorset, as belonging to '*Megalosaurus*' *nethercombensis* von Huene, 1923. He hinted that this species might deserve its own genus, and later named it *Magnosaurus* (von Huene 1932). Waldman (1974) argued that this taxon should be returned to *Megalosaurus* but Holtz *et al*. (2004*a*) retained *Magnosaurus*, noting that it differs from *Megalosaurus* in the shape of the tibia. Rauhut (2003*a*) found *M. nethercombensis* to share dentary characters with *Eustreptospondylus oxoniensis* Walker, 1964 and thus referred the latter to *Magnosaurus*. A number of other theropod elements from the Inferior Oolite Formation, including teeth from Selsby Hill in Gloucestershire, Daston in Northamptonshire, and Stanton in Wiltshire, as well as a femur from the Forest Marble of Enslow Bridge in Oxfordshire, were referred (without reason) to *M. nethercombensis* by Steel (1970).

Another taxon probably incorrectly referred to *Megalosaurus* is '*M*.' *hesperis* Waldman, 1974 from the Bajocian Upper Oolite of Sherbourne, Dorset. Known from various cranial bones described by Owen (1883), recent reviews have concluded that, although probably a valid taxon, '*M*.' *hesperis* does not preserve enough information to allow reliable identification within Tetanurae (Holtz *et al*. 2004*a*).

The type species of *Megalosaurus*, *M. bucklandii* Ritgen, 1826 from the Bathonian Taynton Limestone Formation of Stonesfield, Oxfordshire, remains controversial. Although most workers have assumed that the dentary OUM J.13505 (Fig. 1) is the type specimen (Swinton 1955; Molnar *et al*. 1990; Allain 2002; Allain & Chure 2002), *Megalosaurus* was originally named for an assortment of bones regarded by Buckland (1824, p. 390) as having 'belonged to several individuals of various ages and sizes'. Delair & Sarjeant (2002, p. 194) argued that these remains 'were the scattered remnants of a single individual, coming to light over a period of several decades', but this is difficult to accept as clear size discrepancies are evident. Two taxa are represented by the postcranial remains of *Megalosaurus* (Allain & Chure 2002; Rauhut 2003*a*; Day & Barrett 2004), some of which, most notably 'sigmoidal' femora with a distal extensor groove, may belong together with the *M. bucklandii* dentary. Straight femora from Stonesfield, possessing a robust anterolateral ridge connected to the anterior trochanter, appear to belong to a non-tetanuran theropod (Day & Barrett 2004), possibly an abelisauroid.

Furthermore, a maxilla (OUM J13506) referred to *Megalosaurus* by Huxley (1869), and used by Phillips (1871) in the first ever reconstruction of a theropod skull, differs from megalosaurid maxillae in lacking a subrectangular rostral process (Fig. 6b). Bakker *et al*. (1992) proposed that this maxilla belonged to a sinraptorid. However, the absence of a subrectangular rostral process on the maxilla is not unique to sinraptorids: rather, it is a plesiomorphy widespread in basal theropods. Although the maxilla probably does not belong to a megalosaurid, it lacks characters that allow it to be identified beyond Theropoda and it may also belong to an abelisauroid.

Given that *Megalosaurus* was generally regarded as the only large predatory dinosaur for most of the 19th and early 20th century, it is understandable that much material from the Jurassic and Cretaceous was referred to it. At least some of the Bathonian material, such as that from the Sharp's Hill, Chipping Norton and Forest Marble formations of Gloucestershire, Oxfordshire and Wiltshire (e.g. Reynolds 1939; Metcalf & Walker 1994), may belong to *M. bucklandii*, but many '*Megalosaurus*' elements should be regarded as Tetanurae indet. until restudy allows more confident identification.

Also from the Taynton Limestone Formation of Stonesfield is *Iliosuchus incognitus* von Huene, 1932, known only from three small ilia (Galton 1976; Galton & Molnar 2005). The lateral vertical ridge dorsal to the acetabulum seen in *Iliosuchus* has led several workers to speculate on affinities between this taxon and other theropods with the same character. Foster & Chure (2000) showed that *Iliosuchus* differs from other ridge-bearing taxa in possessing additional ridges anterior and posterior to the main ridge. Rauhut (2003*b*) suggested that *Iliosuchus* might be a basal tyrannosauroid, and also noted that the elongate pubic peduncle of one specimen suggests a coelurosaurian identity. Conversely, Holtz *et al*. (2004*a*) noted that the large supracetabular crest of *Iliosuchus* is unlike that of tyrannosauroids and reminiscent of non-tetanurans. The distal end of a small theropod tibia from the Taynton Limestone Formation was described by Galton & Molnar (2005). It probably belonged to a basal tetanuran, and perhaps to *Iliosuchus*.

A partial skull and postcranium from the Callovian part of the Oxford Clay Formation of Wolvercote, Oxfordshire was described by Phillips (1871) as referable to *Streptospondylus* Meyer, 1832. The latter, named for Jurassic French material, was proposed as a sub-genus of the crocodyliform *Steneosaurus* but, because the composite skull material included in the type species (*S. altdorfensis* Meyer, 1832 from Calvados, France), has since been excluded from it, only the theropod vertebrae that were combined with this composite skull remain in this taxon (Walker 1964; Allain 2001). Although *Streptospondylus* is therefore a valid theropod genus, the name was applied to various dinosaur remains during Victorian times, not all of which proved to be of theropod identity. Walker (1964) recognized that the Wolvercote specimen should be separated from *Streptospondylus*, and named it *Eustreptospondylus oxoniensis* Walker, 1964. *Eustreptospondylus* is a spinosauroid (Rauhut 2003*a*; Holtz *et al*. 2004*a*) with the most recent view being that it is part of the megalosaurid clade Eustreptospondylinae (Holtz *et al*. 2004*a*). Rauhut (2003*a*) proposed that *E. oxoniensis* and *Magnosaurus nethercombensis* share derived characters of the dentary and are congeneric. The portrayal in a television series of *E. oxoniensis* as an island-dwelling dwarf was based on the erroneous assumption that the juvenile holotype represented an adult (Martill & Naish 2000).

Another basal tetanuran initially referred to *Megalosaurus* (von Huene 1923, 1926*a*, *b*), *Metriacanthosaurus parkeri* (Walker, 1964) from the Oxfordian part of the Oxford Clay Formation of Weymouth, Dorset, is based on vertebrae and pelvic and hindlimb elements. Although *Metriacanthosaurus* was named for its tall neural spines, these are not in fact taller than those of many other tetanurans. Molnar *et al*. (1990) suggested that the species could be diagnosed on the basis of the 'angled' dorsal margin of the ilium and the lateral ridge present on the ischium, and both characters appear to be autapomorphic. *Metriacanthosaurus* is similar to the Asian sinraptorid *Yangchuanosaurus* and Paul (1988*a*) treated it as a senior synonym of *Yangchuanosaurus*. Although this proposal has not been accepted, it does seem that *Metriacanthosaurus* is a sinraptorid. The claim that *Lourinhanosaurus antunesi* Mateus, 1998 from the Upper Jurassic of Portugal might be Europe's first recognized member of Sinraptoridae (Mateus 1998) is therefore incorrect.

Various theropod remains have been reported from the Kimmeridge Clay Formation. With the exception of an as-yet-undescribed specimen that represents a new taxon, discovered between Chapman's Pool and Kimmeridge Bay (H. P. Powell, pers. comm.), all are fragmentary. An incomplete tooth from Foxhangers, Wiltshire, was referred to the French species '*Megalosaurus*' *insignis* Eudes-Deslongchamps, 1870 by Lydekker (1888). Von Huene (1932) and Swinton (1934) referred this taxon to *Aggiosaurus* but the type species of that genus, *A. nicaeensis* Ambayrac, 1913, is a crocodyliform (Buffetaut 1982). '*M.*' *insignis* is a *nomen dubium*, and its type material (destroyed during World War II according to Powell (1987)), and the Foxhangers tooth, should be regarded as Theropoda indet. Several other Kimmeridge Clay theropod fragments, some from very large animals, were identified as megalosaurid by Powell (1987). At least some of them (e.g. the tibia OUM J13568) can be identified as far as Tetanurae.

Baryonyx walkeri Charig & Milner, 1986 from the Barremian Upper Weald Clay Formation of Ockley, Surrey, has proved integral to the reinterpretation of the carnosaur clade Spinosauridae. An identification of *Baryonyx* as a spinosaurid by Paul (1988*a*) and Buffetaut (1989) was initially resisted by Charig & Milner (1990), but new data have confirmed this relationship (Sereno *et al*. 1998; Milner 2001; Sues *et al*. 2002; Rauhut 2003*a*). *Baryonyx* is the sister-taxon to Spinosaurinae, a clade that includes *Spinosaurus* and *Irritator* from the Upper Cretaceous of Africa and Brazil (Sereno *et al*. 1998). *Suchomimus tenerensis* Sereno *et al*., 1998, is probably congeneric with *Baryonyx*. Isolated British baryonychine material is known from the Hauterivian Ashdown Beds Formation of East Sussex and from the Isle of Wight's Wessex Formation (Martill & Hutt 1996; Charig & Milner 1997; Naish *et al*. 2001). These records represent either cf. *Baryonyx* or *Baryonyx* sp., and because they differ in detail from the teeth of *B. walkeri* it is possible that they represent additional baryonychine taxa.

Neovenator salerii Hutt *et al*., 1996 shares derived characters with the carcharodontosaurids, a group of large-bodied allosauroids from Africa and North and South America, and groups with them in phylogenetic analyses (Harris 1998; Rauhut 2003*a*; Holtz *et al*. 2004*a*). *Neovenator* is thus a basal carcharodontosaurid according to a definition of this taxon (Sereno 1998), and the first European member of this clade. It negates the idea that the most basal members of this clade are South American (Novas *et al*. 2005).

Possible other Wealden allosauroid taxa include *Becklespinax altispinax* (Paul, 1988*b*) and *Valdoraptor oweni* (Lydekker, 1889). The former, based on three articulated dorsal vertebrae with tall, robust neural spines (Fig. 7) from the Hastings Beds Group of Battle, East Sussex, has a complex taxonomic history (von Huene 1926*a*, *b*; Paul 1988*a*; Olshevsky 1991). *Valdoraptor* is based on a partial metatarsus originally referred to *Hylaeosaurus* (Owen 1858*b*), then referred to *Megalosaurus* (Lydekker 1889), and finally given its own genus (Olshevsky 1991). *V. oweni* possesses a proportionally short metatarsus (its original total length is verified by a referred and undescribed isolated mt II) in which mt II is mediolaterally compressed and with a prominent dorsolateral ridge. This morphology is diagnostic and, in answer to Holtz *et al*. (2004*a*), the possibility that *V. oweni* might be synonymous with *Neovenator* or *Eotyrannus* can be excluded. Isolated allosauroid material, including the proximal end of a tibia more robust than that of *Neovenator*, is known from the Hastings Beds Group (Naish 2003) and might be referable to *Becklespinax*.

Coelurosauria

Based on a well-preserved but incomplete skull from the Great Oolite Group of Minchinhampton, Gloucestershire, *Proceratosaurus bradleyi* (Woodward, 1910) was first described by Woodward (1910) as a new species of *Megalosaurus*. Von Huene (1926*a*, *b*) erected *Proceratosaurus* for the taxon and reconstructed the missing parts of the skull based on those of *Ceratosaurus*. Walker (1964) noted that ‘there appears to be no reason to presume any particularly close relationships between *Proceratosaurus* and *Ceratosaurus*’ (p. 127) and Paul (1988*a*, *b*) proposed that, although a nasal horn was present in *P. bradleyi*, it was different from that of *Ceratosaurus*. The incorporation of *P. bradleyi* into cladistic phylogenies of Theropoda has shown that it is a coelurosaur, and one of the most basal members of the clade (Holtz 2000; Rauhut 2003*a*; Holtz *et al*. 2004*a*). It is also the oldest verified coelurosaur, given that alleged coelurosaurs of greater age (Zhao & Xu 1998) are not securely identified.

Two pedal phalanges from the Kimmeridge Clay of Fleet, Dorset, currently in a private collection, have been identified as representing an ornithomimid (Brokenshire & Clarke 1993), a group otherwise unknown both from the Jurassic and from Europe. The identification is unlikely given the poor quality of the material (Martill *et al*. 2006).

The youngest major coelurosaurian clade, Maniraptora, has some of its earliest global occurrences in the British fossil record. Troodontid- and dromaeosaurid-like teeth from the Bathonian Forest Marble Formation of Kirtlington, Oxfordshire, resemble more confidently identified Cretaceous specimens of these groups (Evans & Milner 1994). Maniraptorans may also be present in the Berriasian Lulworth Formation. *Nuthetes destructor* Owen, 1854, based on a partial dentary and also known from isolated teeth, all from the Isle of Purbeck, has been interpreted as a dromaeosaurid (Milner 2002). *Nuthetes* has also been reported from the Purbeck Limestone Group of Wiltshire and Sussex (Benton & Spencer 1995). An incomplete metatarsal III from the Isle of Purbeck was suggested by Milner (2002) to belong to a eumaniraptoran, possibly an adult *Nuthetes*. However, the specimen lacks the markedly convex distal end seen in the metatarsals of this group, and should be identified as Theropoda indet.

One of Britain’s few alleged Mesozoic birds, *Wyleyia valdensis* Harrison & Walker, 1973, is from the Weald Clay Group of Henfield, West Sussex. Based on an incomplete humerus, it should be regarded as a *nomen dubium*, and there has been debate over its claimed avian status (Norman 1990; Zhou *et al*. 1992; Kurochkin 1995). Naish (2002) argued for avian status on the basis of the presence of a proximal ligamental furrow and

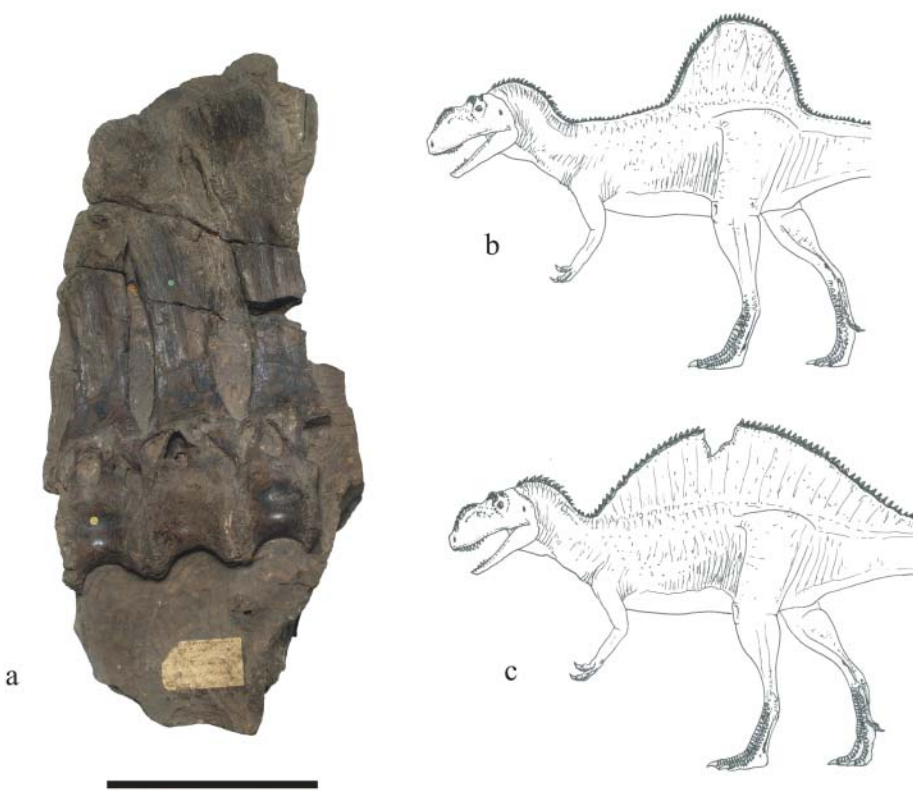

Fig. 7. (**a**) BMNH R1828, the three dorsal vertebrae that form the holotype of *Becklespinax altispinax*. The peculiar difference in the height of the neural spines in this specimen, coupled with their interpretation as posterior dorsal vertebrae, suggests two possibilities for how their owner may have looked in life. Scale bar 20 cm. (**b**) Speculative life restoration restoring the neural spines as supporting a sail present only on the posterior dorsal, sacral and anterior caudal vertebrae. (**c**) Speculative life restoration restoring the neural spines as supporting a more extensive sail that was damaged during life.

distal notch for the brachialis anticus. It is doubtful, however, as to whether even these characters are uniquely avian and *Wyleyia* may be better regarded as Maniraptora indet.

The Isle of Wight's Wessex Formation has yielded several coelurosaurs, most of which can be referred to specific clades. Two taxa traditionally regarded as being based on the same specimen, *Calamospondylus oweni* Fox *in* Anonymous, 1866 and *Aristosuchus pusillus* (Owen, 1876), were named for different specimens (Naish 2002), although the holotype of the former is lost. *A. pusillus* was named for a sacrum, partial pubes and other elements and is highly similar to compsognathids, and specifically to *Compsognathus* from the Upper Jurassic of Germany, France, and Portugal (Seeley 1887; Naish *et al*. 2004*b*). *A. pusillus* is provisionally regarded as a valid compsognathid taxon.

Often confused with *C. oweni* is *Calamosaurus foxi* Lydekker, 1889 (not *Calamosaurus foxii* [*sic*] as stated by Naish *et al*. 2001), based on two small opisthocoelous cervical vertebrae. Although suggested to be a compsognathid (Naish *et al*. 2001), the close similarity of *C. foxi* to the basal tyrannosauroid *Dilong paradoxus* from Lower Cretaceous China (Xu *et al*. 2004) indicates that *C. foxi* may be a basal tyrannosauroid.

Based on a sacrum, *Ornithodesmus cluniculus* Seeley, 1887, long regarded as congeneric with the pterosaur *Istiodactylus latidens*, represents a coelurosaur, and probably a dromaeosaurid (Norell & Makovicky 1997). Howse & Milner (1993) proposed that *O. cluniculus* was a troodontid, but the 'troodontid' specimen they used for comparison was a dromaeosaurid. Other isolated Wessex Formation coelurosaur elements have been reported (e.g. Galton 1973; Naish 2000; Naish *et al*. 2001): most seem consistent with a compsognathid identity. Wessex Formation teeth were identified as belonging to velociraptorine dromaeosaurids by Sweetman (2004). These belonged to animals perhaps on par with *Utahraptor* and *Achillobator*, and thus far larger than the approximate 1.5 m estimated for *O. cluniculus* (Naish *et al*. 2001). The identification of these teeth as velociraptorine might be correct, but there are indications that the tooth morphology previously regarded as unique to velociraptorines was in fact present in several maniraptoran clades (Senter *et al*. 2004). A vertebra tentatively identified as dromaeosaurid has been reported from the Hastings Beds Group of Bexhill (Brooks 2001).

Whereas *C. foxi* and other Wessex Formation coelurosaurs are based on fragmentary remains, *Eotyrannus lengi* Hutt *et al*., 2001 is more complete, being known from a partial skull and incomplete postcranium (Naish *et al*. 2001) (Fig. 8). Premaxillary teeth that are U-shaped in cross-section, elongate, dorsoventrally thickened, fused nasals, and other characters, indicate that *E. lengi* is a basal member of Tyrannosauroidea (Holtz 2004). Although the holotype would have been approximately 4.5 m long, its unfused neurocentral sutures and sacrum indicate that it was a subadult, and adult individuals were presumably large animals. Another Wessex Formation theropod traditionally dismissed as indeterminate is *Thecocoelurus daviesi* (Seeley, 1888), based on half a cervical vertebra. Naish & Martill (2002) argued that the similarity seen between this specimen and caenagnathid oviraptorosaurs indicates that *T. daviesi* is the first reported European oviraptorosaur. *T. daviesi* also resembles the cervical vertebrae of the basal therizinosauroid *Falcarius utahensis* Kirkland *et al*., 2005 and consequently has been suggested to be a close relative of this taxon. However, *T. daviesi* shares more characters with caenagnathids than it does with *Falcarius*. Lacking autapomorphies, *T. daviesi* should not be regarded as a valid taxon, but it does indicate the presence of caenagnathid-like oviraptorosaurs in the English Lower Cretaceous. Non-avian theropods have yet to be reported from British rocks younger than those of the Barremian. Three sacral vertebrae from the Cenomanian Cambridge Greensand, referred by Seeley (1876*b*) to *Enaliornis*, were suggested by Galton & Martin (2002*a*) to be those of a small non-avian theropod, and if this is valid then this is Britain's youngest non-avian theropod. A theropod identity is

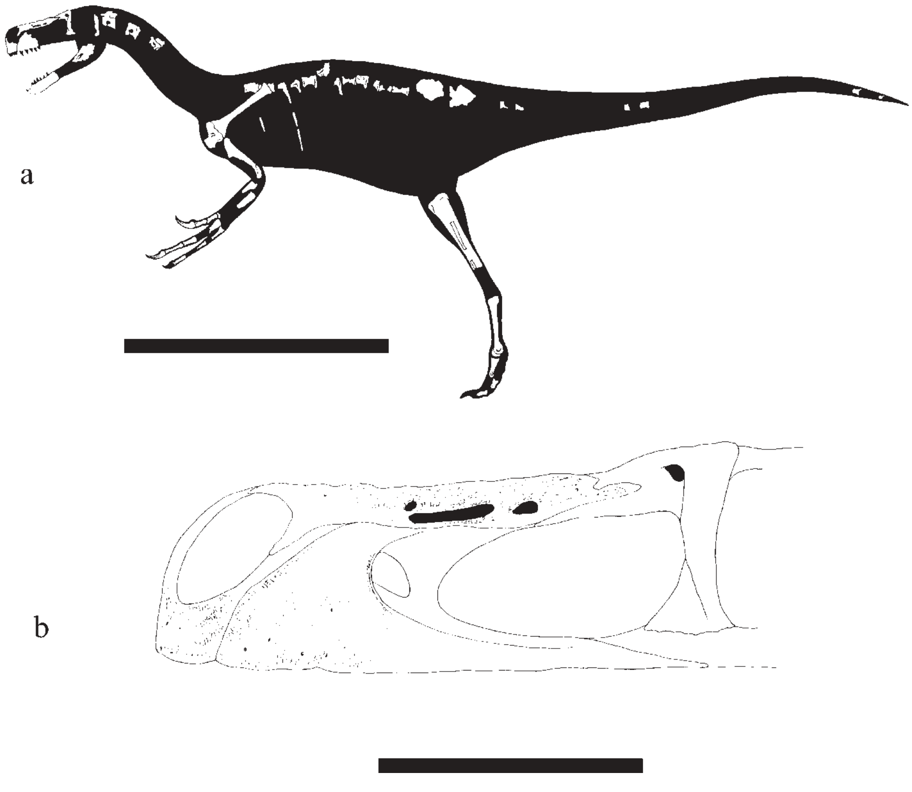

Fig. 8. (**a**) Skeletal reconstruction of the basal tyrannosauroid *Eotyrannus lengi* Hutt *et al*., 2001 from the Wessex Formation of the Isle of Wight. Scale bar 100 cm. (**b**) Reconstructed anterior part of skull of *E. lengi*. Scale bar 20 cm.

possible for the specimen but cannot be confirmed, and indeed Galton & Martin (2002*b*) had earlier regarded the specimen as a probable portion of pterosaur notarium.

Avian fossils have been known from the Cenomanian Cambridge Greensand since the 1850s (Seeley 1876*b*; Galton & Martin 2002*a*, *b*). A few apneumatic, amphicoelous avian vertebrae and the proximal end of a femur from the Cambridge Greensand represent an as-yet-unidentified taxon (Seeley 1876*b*; Galton & Martin 2002*b*). However, most of the bird bones from the unit have been referred to *Enaliornis* Seeley, 1876, a basal member of Hesperornithes (*sensu* Clarke 2004). Whereas *Enaliornis* was clearly a foot-propelled diver, it was not as specialized as later members of Hesperornithes and it remains uncertain whether it was capable of flight, although its thick bone walls suggested flightlessness to Galton & Martin (2002*b*). Three species of *Enaliornis* are recognized: *E. barretti* Seeley, 1876, *E. sedgwicki* Seeley, 1876 and *E. seeleyi* Galton & Martin, 2002. They differ in size and details of hindlimb morphology.

Discussion

The study of British taxa has made a significant contribution to our understanding of dinosaur morphology, diversity and phylogeny. How does the British dinosaur record compare with what we know of dinosaur diversity overall? Although several major clades are almost or entirely absent from the British record (see below), in general the British dinosaur record matches global patterns of dinosaur diversity (Fig. 9). Of the 50 British taxa (excluding *nomina dubia* and *nomina nuda*), sauropodomorphs account for a quarter of the total (compared with a similar percentage for global diversity), and ornithopods are similarly represented in both datasets (20% of British taxa compared with 19% of total taxa). Theropods were less well represented in the British sample than in the global count (26% compared with 38% of total taxa) whereas, intriguingly, thyreophorans appear particularly speciose in the British record compared with the global one (24% compared with 11%). These data suggest that the diversity reported for British dinosaurs conveys a valid signal of true diversity.

A surprisingly high number of British dinosaurs represent the earliest reported occurrences of their respective clades. Among these are the oldest neosauropod (the indeterminate Aalenian specimen described by Reid (1984)), oldest diplodocoid ('*Cetiosaurus*' *glymptonensis* from the Bathonian), oldest rebbachisaurid (*Nigersaurus*-like teeth from the Barremian), oldest titanosaur tracks (Bathonian of Ardley), oldest spinosaurid (*Baryonyx* from the Barremian, and with cf. *Baryonyx* from the Valanginian), oldest carcharodontosaurid (*Neovenator* from the Barremian), oldest coelurosaur (*Proceratosaurus* from the Bathonian), oldest hesperornithine (*Enaliornis* from the Cenomanian, but reworked from the Albian or earlier), and oldest iguanodontian (the *nomen dubium Callovosaurus leedsi* from the Callovian).

Whether Britain really does have an unusually high number of such records is deserving of further study: is it an artefact resulting from over-zealous attempts to classify Britain's often poorly preserved dinosaurs, or is it because virtually every British dinosaur bone is interpreted and written about? Or is it a true reflection of Britain's importance in terms of dinosaur diversification and palaeobiogeography? Some palaeobiogeographical studies provide support for this last possibility. Strong similarities between the Lower Cretaceous faunas of England, mainland Europe, western North America and Niger led Holtz *et al*. (2004*b*) to recognize a Laurasian 'Greater Wealden' fauna. The early appearance within this fauna of spinosaurids, carcharodontosaurids and rebbachisaurids in Britain suggests that they originated here. Noting that the isolation of the Alaskan microterrane prevented Laurasian dinosaurs migrating from Asia to North America prior to the Albian, Kirkland *et al*. (2004) proposed that England was 'at the crossroads' and that dinosaur groups common to Cretaceous Asia and North America must have crossed via the North Atlantic.

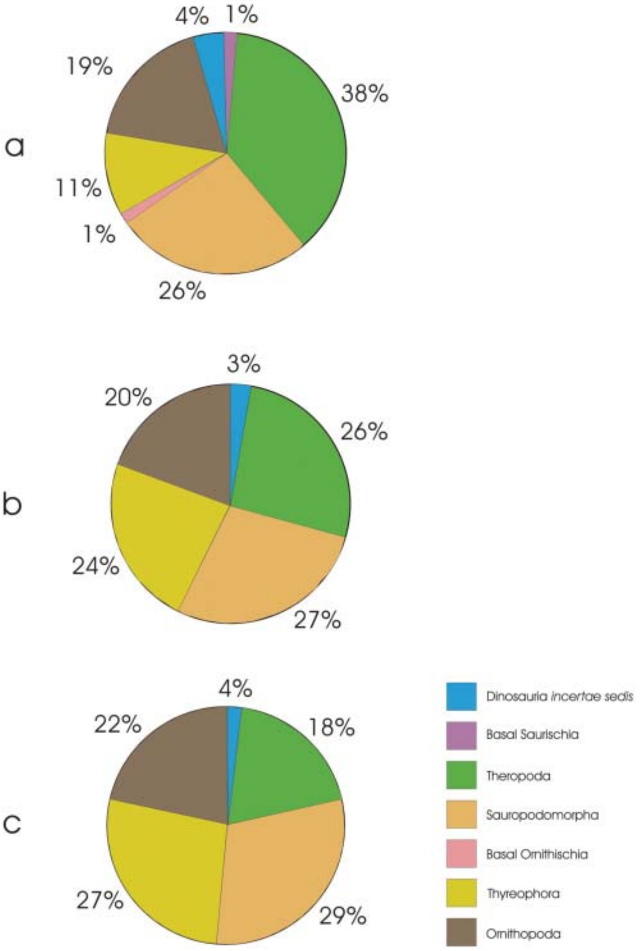

Fig. 9. Pie charts illustrating the relative abundances of British dinosaur groups of varying taxonomic validity with dinosaur groups worldwide. (**a**) British dinosaur groups considered to be valid taxa; (**b**) British groups considered as *nomina dubia*; (**c**) worldwide dinosaur groups including both valid taxa and *nomina dubia*.

However, several clades are either absent from Britain or known only from controversial fragments. If *Yaverlandia* is not a marginocephalian, then this predominantly Cretaceous clade is absent from Britain. Similarly, the presence of hadrosaurids is based only on fragments from open marine strata. Their alleged absence may have been palaeogeographically controlled, as by the late Albian Britain was isolated relative to the rest of Europe (e.g. Head 1998; Holtz *et al*. 2004*b*).

Many British dinosaurs are regarded as *nomina dubia* (a taxonomic breakdown of British dinosaur taxa is given in the Supplementary Publication; see p. 000). This has implications for two areas: taxonomic diversity, and the quality of Britain's dinosaur record. On the issue of taxonomic diversity, it has become *de rigeur* within vertebrate palaeontology to think of taxa based on poor remains (and this includes *nomina dubia*, as well as taxa that have never been named) as labels for indeterminate objects that do not really refer to biological entities. Although there is good evidence for taxonomic inflation across animal groups (Alroy 2002), and although the recognition of taxa erected without autapomorphies should not be advocated, a proportion of *nomina dubia*, and specimens that appear distinct but remain unnamed, probably do represent good taxa; it is simply that better data are absent. This is particularly relevant to Britain, where approximately 54% of named taxa are *nomina dubia* (see the Supplementary Publication; see p. 000): the fact that Britain has so many of these is a consequence of the fact that dinosaur science arose in Britain. Britain has far more than its fair share of taxa based on obsolete characters.

At least some taxa regarded as *nomina dubia* could be regarded as metataxa: entities that probably represent valid taxa, although lacking unique characters as a consequence of incomplete preservation. Examples of this in the British record include '*Zanclodon*' *cambrensis*, *Sarcosaurus woodi*, *Iuticosaurus valdensis*, *Callovosaurus leedsi* and *Regnosaurus northamptoni*. As soon as *nomina dubia* come to be regarded as metataxa, the number of 'acceptable' taxa increases (although it should be noted that we have not done this, and have retained these taxa as *nomina dubia*). Also potentially increasing this count are specimens representing taxa that have never been named. As an example, in the case of the Northampton Sands Formation 'brachiosaurid' reported by Reid (1984), even though no autapomorphies have been identified, there still remains no other taxon that this specimen can be referred to, and thus it could be regarded as a provisionally valid taxon. Other examples are the Wessex Formation rebbachisaurid, Bexhill diplodocid, Taynton Limestone Formation large basal theropod and Sharp's Hill stegosaur. While 'the practise of naming genera on such a slim basis is a highly undesirable one, greatly to be discouraged' (Dodson 1996, p. 240), naming taxa, even those based on fragmentary remains, can be a useful exercise simply because named taxa are incorporated into large-scale studies of systematics and diversity. Unnamed taxa, even those thought to represent new species, generally are not.

If those taxa presently regarded as 'valid' are assumed to be the only real taxa, an unrealistically low view of diversity is obtained. Indeed, despite various studies of Mesozoic dinosaur diversity (e.g. Holmes & Dodson 1997; Fastovsky *et al*. 2004; Wang & Dodson 2006), and cognizant of the evidence indicating that diversity has increased over geological time (Benton *et al*. 2000), it is unlikely that dinosaur clades were as paucispecific as is to be assumed, if current lists are regarded as accurate.

On the implications that *nomina dubia* have for the quality of Britain's dinosaur record, it might appear that Britain's dinosaur record is poor. However, as shown by many taxa represented by substantially complete remains, this is not accurate. Furthermore, the record of 'good' British dinosaur specimens is better than suggested by the literature, as we know of several exceptionally complete specimens that are in private collections and are as yet unreported in the literature (e.g. Fig. 2).

Although much British dinosaur material is fragmentary, superbly preserved specimens have been recovered, including near-complete specimens and examples with soft-tissue preservation. Considering the small size of Great Britain and the limited outcrop of Mesozoic strata (relative to the dinosaur hunting gounds of Mongolia, North America and north Africa), British dinosaurs are both abundant and diverse.

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