A saurischian dinosaur braincase from the Middle Jurassic (Bathonian) near Oxford, England: from the theropod *Megalosaurus* or the sauropod *Cetiosaurus*?

P. M. GALTON*† & F. KNOLL‡§¶

*Professor Emeritus, College of Naturopathic Medicine, University of Bridgeport, Bridgeport, CT 06601, USA
‡Abteilung Paläontologie, Staatliches Museum für Naturkunde, 70191 Stuttgart, Germany
§CNRS UMR 5143, Muséum national d'Histoire naturelle, 75231 Paris cedex 05, France

Abstract – A dinosaur braincase from the Middle Jurassic (Bathonian) of Oxfordshire (England) is described. The specimen, which has historical significance, has been erratically attributed to either a sauropod or a theropod on the basis of vague phenetic resemblances. It is here re-interpreted in the light of recent cladistic analyses of dinosaurs, allowing the first proper character-based discussion of its affinities. It resembles those of ornithischian and prosauropod dinosaurs in the absence of a prominent, caudolaterally directed bony sheet from either the crista tuberalis (as in all theropods) or the crista prootica (as in all sauropods except juveniles of the eusauropod *Shunosaurus*). This braincase shows two synapomorphic characters of the Eusauropoda: the region of the cranium is rostrocaudally shortened and the long axis of the supratemporal fenestra is transversely oriented. For these characters, ornithischians, theropods, and prosauropods retain the plesiomorphic condition. It is concluded that the specimen is an important exemplar of a Middle Jurassic sauropod braincase and it is suggested that it could be from the eusauropod *Cetiosaurus*.

Keywords: systematics, phylogeny, sauropod, Jurassic, England.

1. Introduction

Huene (1906*a*) described an incomplete braincase (OUMNH J13596) as *Megalosaurus bucklandi*, from the Dogger (Bathonian, Middle Jurassic) of Stonesfield near Oxford, England (see sketch map showing Oxford and nearby villages in Upchurch & Martin, 2003, fig. 1). This paper was based on casts from the Oxford University Museum and notes Huene made when he located the braincase in 1901 in a drawer with bones of *Megalosaurus*. The Stonesfield Slate (or 'tilestones') of Stonesfield (part of Taunton Limestone Formation: Boneham & Wyatt, 1993) has yielded many remains referred to the theropod *Megalosaurus* Buckland, 1824, the first dinosaur to be described (Day & Barrett, 2004), but very few of *Cetiosaurus*, Owen, 1841 (Benton & Spencer, 1995, p. 142), the first genus of sauropod dinosaur to be described. The identifications of a few of the foramina were discussed by Huene (1906*b*,*c*) and Hay (1909). Huene (1907–08, fig. 328.2) correctly re-identified most of the nerves on a small figure of the endocranial cast. Woodward (1910, p. 111) noted that the braincase, which was found isolated, was more likely referable to the sauropod *Cetiosaurus*. This identification was accepted by Huene (1926, p. 46), who briefly described it as *C. oxoniensis* Phillips,

1871 (Huene, 1932, p. 221–2, fig. 21; horizon given as Great Oolite, Bathonian). Janensch (1935–36, p. 252) noted that the braincase of *Cetiosaurus*, with its steeply rising dorsal contour and a particularly strong upward bending of the floor of the cerebral cavity anterior to the abducens foramen, was more similar to *Brachiosaurus* than it was to *Barosaurus* and *Dicraeosaurus*, the other two genera of sauropods from the Tendaguru (Kimmeridgian, Upper Jurassic, Tanzania).

The braincase is regarded as *Megalosaurus* or theropod by Whetstone & Martin (1979, p. 234 as BMNH R1946, R3129; actually two casts of OUMNH J13596), Currie (1985, p. 1652) and Currie & Zhao (1993*a*, p. 2233). It is both a theropod and a sauropod in Lapparent & Lavocat (1955, pp. 808, 821, 913) and Benton & Spencer (1995, pp. 144, 160), who noted that the braincase of *Cetiosaurus* sp. (OUMNH J13596) from the Kirtlington Old Cement Works Quarry, Kirtlington, resembles that of the prosauropod dinosaur *Plateosaurus* (see Galton, 1984, 1985). The referral to *Cetiosaurus* was accepted by Swinton (1934, 1970), Steel (1970), Hopson (1979), and by Buffetaut, Pennetier & Pennetier (1991), who noted that it does not resemble the braincases of Middle Jurassic theropods (*Eustreptospondylus,* England; *Piveteausaurus,* France) and it bears unspecified resemblances to the braincases of Tendaguru sauropods. However, McIntosh (1990, p. 377) noted that *Cetiosaurus oxoniensis* is known from most parts

¶ Author for correspondence: knoll.smns@naturkundemuseum-bw.de, knoll@mnhn.fr
† 315 Southern Hills Drive, Rio Vista, CA 94571, USA.

of the skeleton except the skull that is largely unknown in the 'Cetiosaurinae'. This omission was not an oversight because, as specifically noted by McIntosh & Williams (1988, p. 23), the braincase 'referred by von Huene (1906(*a*), 1932) to *Cetiosaurus* OUM (NH J)13596 does not belong to a sauropod'. *Cetiosaurus* is not included in two detailed phylogenetic analyses of the Sauropoda (Wilson & Sereno, 1998; Wilson, 2002) but it is in those by Upchurch (1998, 1999; Upchurch & Martin, 2003; Upchurch, Barrett & Dodson, 2004), who included no braincase characters for *Cetiosaurus* in the data matrices.

Current cladistic analyses place *Megalosaurus* within the basal tetanuran theropods (Gauthier, 1986; Charig & Milner, 1997; Sereno, 1997; Holtz, 2000; Rauhut, 2003; Holtz, Molnar & Currie, 2004). Middle Jurassic braincases previously referred to *Megalosaurus* are more recent, being from the Upper Callovian rather than from the older Bathonian, and they are now referred to different genera of basal tetanurans, that is, *Eustreptospondylus* from England (Huene, 1932; Walker, 1964; Sadleir, Barrett & Powell, 2004; regarded as *Magnosaurus* by Rauhut, 2003) and *Piveteausaurus* from France (Taquet & Welles, 1977). The Middle Jurassic of Normandy, France, has recently yielded two basal tetanuran braincases. One was described but unnamed (Callovian: Knoll, Buffetaut & Bülow, 1999). The other is part of the holotype of '*Poekilopleuron*?' *valdesdunensis* Allain, 2002 (Bathonian), the type species of *Dubreuillosaurus* Allain, 2005, though this species may eventually prove to be based on a juvenile individual of *P. bucklandii* Eudes-Deslongchamps, 1837, as originally identified (Anonymous, 1999; Laurant, 1999). A partial braincase is also preserved in the basal tetanuran *Piatnitzkysaurus* (Callovian, Argentina: Bonaparte, 1986).

Cetiosaurus medius Owen, 1842, the generally accepted type species of the genus (McIntosh, 1990), is based on caudal vertebrae and a few other bones from near Chipping Norton, Oxfordshire. Upchurch & Martin (2003) redescribe the holotype and, after a review of the referred species, conclude that all except one are *nomina dubia* or *numina nuda*. *C. oxoniensis* Phillips, 1871 from the Forest Marble (Middle Jurassic, Bathonian) of Bletchingdon Station near Oxford, Oxfordshire, is the first sauropod to be represented by a large part of the skeleton (see Huene, 1927; Upchurch & Martin, 2003); it is the basis for our knowledge of the genus (McIntosh, 1990). Lydekker (1888) designated *Cetiosaurus oxoniensis* as the type species of the genus for which he erected the family Cetiosauridae. Upchurch & Martin (2002) describe a new specimen and restrict the genus to *C. oxoniensis* (details in Upchurch & Martin, 2003). However, no skull has been described for this genus, even though a variety of remains have been referred to it (see McIntosh, 1990) and subsequently removed (Upchurch & Martin, 2003; Upchurch, Barrett & Dodson, 2004). Recently, a partial

'cetiosaur' skeleton was discovered in the Middle Jurassic (Bathonian) of the Caen area, Normandy, France, but it lacks any skull bones (Jussiaume, 1998; L. & F. Dubrulle, pers. comm. 1999).

Basal sauropodomorph phylogeny is presently in a confused state and the skull of early sauropods is poorly known (see e.g. Barrett *et al.* 2003, Leal & Azevedo, 2003; Yates, 2003, 2004; Yates & Kitching, 2003; Upchurch, Barrett & Dodson, 2004; Barrett, Upchurch & Wang, 2005; Sereno, 2005; Upchurch, Barrett & Galton, 2005; Yates, 2005). Upchurch, Barrett & Dodson (2004) recovered a monophyletic Cetiosauridae, which is composed of *Cetiosaurus*, *Barapasaurus* and *Patagosaurus,* that nests basally within the Eusauropoda between *Shunosaurus* and (*Omeisaurus* + *Tehuelchesaurus*). Unfortunately, the braincase is known neither for cetiosaurids nor for *Tehuelchesaurus* (Middle to Upper Jurassic, Argentina: Rich *et al.* 1999), but it has been described for *Shunosaurus* and *Omeisaurus* (?Bajocian, Middle Jurassic, China: He, Li & Cai, 1988; Zhang, 1988; Zheng, 1991; Chatterjee & Zheng, 2002).

There are several reasons why there has been uncertainty regarding the systematic position of the Oxford braincase. (1) The Oxford braincase, until recently the only dinosaurian one known from the Bathonian of western Europe, is possibly the oldest described braincase for a basal sauropod or a basal tetanuran theropod. However, because of the absence of associated remains of related forms, it could equally well be referred to either *Megalosaurus bucklandi* or *Cetiosaurus oxoniensis*. The description of the skull and braincase of '*Poekilopleuron*?' from Normandy, France (Allain, 2002), finally provides data on a Bathonian braincase associated with diagnostic theropod material. Middle Jurassic braincases (and the adjacent part of the skull roof) of sauropods are also rare, with only two described to date; both are from the Lower Shaximiao Formation (?Bajocian) of China, namely, *Omeisaurus tianfuensis* (He, Li & Cai, 1988) and *Shunosaurus* (Zhang, 1988; Zheng, 1991; Chatterjee & Zheng, 2002). (2) The braincase lacks the ventral part, namely the occipital condyle, basal tubera, basipterygoid processes and parasphenoid rostrum, which bears phylogenetically significant characters that form the basis for synapomorphies in theropods (Tetanurae, Allosauroidea: see Sereno *et al.* 1994, p. 270) and especially in sauropods, in which many of the characters from the braincase and occiput are based on this region (Upchurch, 1998; Upchurch, Barrett & Dodson, 2004). (3) The lateral wall in the region of the foramina for the cranial nerves is plesiomorphic in lacking any sheet-like development of the crista that are developed in most theropods (crista tuberalis) and sauropods (crista prootica). In this respect, the braincase resembles those of prosauropods (Galton, 1984, 1985, 1990; Gow, 1990; Galton & Upchurch, 2004) and of many ornithischians, such

as *Lesothosaurus* (Sereno, 1991), stegosaurs (Galton, 1988) and ornithopods (Galton, 1989). (4) No derived characters of this braincase have been cited to identify it, mostly because of the absence until recently of cladistic analyses utilizing braincase characters for the higher categories of either the Theropoda or the Sauropoda. To some extent, this situation has been rectified for the Sauropoda by Wilson & Sereno (1998), Upchurch (1995, 1998, 1999), Wilson (2002) and Upchurch, Barrett & Dodson (2004). Unfortunately, the cladistic analysis of the Theropoda (Holtz, 2000; Holtz, Molnar & Currie, 2004) shows that, apart from the Neoceratosauria (and the Ceratosauria: Rauhut, 2003; Tetanurae, Allosauroidea: Sereno *et al.* 1994, p. 270), braincase characters serve essentially to diagnose lower categories within the Theropoda.

The purpose of this paper is to describe the Oxford braincase (Figs 1–3, 6) and, for the first time, to present a character-based discussion of its affinities. It is our contention that this braincase is referable to the Eusauropoda and that it might be part of the paralectotype of *Cetiosaurus oxoniensis* Phillips, 1871.

Institutional abbreviations. BMNH – The Natural History Museum, London (formerly British Museum (Natural History)); OUMNH – Oxford University Museum of Natural History, Oxford; UUVP – University of Utah Museum, Vertebrate Paleontology, Salt Lake City, USA.

2. Occurrence

There are no original records for the occurrence of this braincase and the following discussion is mostly based on information kindly provided by H. P. Powell (pers. comm.). In 1892, H. G. Seeley wrote to J. Parker that 'it would be most interesting to visit Kirtlington. I have been working at a *Megalosaurus* braincase from Kirtlington which Professor Green has lent me' (OUMNH archives; locality information presumably supplied by A. H. Green, long since deceased, of Oxford University). Although the braincase was not published on, casts of it were made. A label with one of these casts (BMNH R1946, made at BMNH in 1892) also indicates that it came from Kirtlington, the locality given in the OUMNH Register. However, the label with BMNH R3129 (by exchange from OUMNH) gives the locality as Enstone and the label with a plaster endocranial cast (BMNH, from Seeley Collection) gives it as Stonesfield.

Nowadays, 'Kirtlington' would signify the Kirtlington Old Cement Works Quarry beside the Oxford Canal, about 1.6 km (nearly a mile) northwest of the village (SP 494 199; Upchurch & Martin, 2003, fig. 1). This is the locality given for this specimen by Benton & Spencer (1995, pp. 159–60, as *Cetiosaurus* sp., but locality of OUMNH J13596 as *Megalosaurus* is Stonesfield on p. 144). Many *Cetiosaurus* bones were recovered from here, but probably not until after 1907 when the quarry started to be much more extensively worked. The dark red-brown wax used to repair this braincase matches that on the rest of the OUMNH *Cetiosaurus* collection of Phillips (1871), which led J. M. Edmonds (in OUMNH Register) to consider this braincase to be part of Phillips' material. However, this brown wax was used on many other specimens from different sources and collections in the OUM so that it does not tie the bone to the *Cetiosaurus* originals.

Although not definite, the Oxford braincase probably came from the old '*Cetiosaurus* quarries' of Phillips (1871, pp. 250–2). These are located 12.9 km (8 miles) north of Oxford, at the Bletchingdon (old Kirtlington) Station Quarry (which is 'now much overgrown with trees and undergrowth' (Arkell, 1947, p. 57)) along Lince Lane (the A4095) to the east of the station (SP 484 182: Benton & Spencer, 1995, fig. 6.10; see Phillips, 1860, p. 117; Woodward, 1894, p. 323; Richardson, Arkell & Dines, 1946, p. 70, layer 6 for bone bed). The bone bed is in the Forest Marble in the *fimbriatus–waltoni* Beds (base of the Bladon Member) of the White Limestone Formation (lower third of Upper Bathonian, *Procerites hodsoni* Zone: see Palmer, 1979; Cope *et al.* 1980, fig. 6a. B12). However, the occurrence of the ostracod *Glyptocythere penni* in the *fimbriatus–waltoni* Beds led Bate (1978) to suggest that this unit belongs to the *discus* unit (upper third of Upper Bathonian). Details on the lithostratigraphy, biostratigraphy and the terrestrial fauna of the *fimbriatus–waltoni* Beds of the nearby Kirtlington Old Cement Works Quarry are given by Benton & Spencer (1995, pp. 156–64).

3. Braincase

3.a. Description and comparisons of bones

The phylogenetic classification used in this paper is adapted from those of Gauthier (1986), Holtz (1994, 2000), Charig & Milner (1997), Sereno (1997), Rauhut (2003) and Holtz, Molnar & Currie (2004) for the Theropoda and Wilson & Sereno (1998), Upchurch (1998, 1999), Wilson (2002) and Upchurch, Barrett & Dodson (2004) for the Sauropoda. Unless stated to the contrary, comparisons with the braincases of other saurischians in Sections 3 and 4 are based on the following references: for prosauropods: in general (Galton & Upchurch, 2004), *Plateosaurus* (Norian, Germany: Galton, 1984, 1985, 1990) and *Massospondylus* (?Hettangian, southern Africa: Gow, 1990; Gow, Kitching & Raath, 1990; Sues *et al.* 2004); for sauropods: the basal eusauropods *Omeisaurus* (?Bajocian, China: He, Li & Cai, 1988) and *Shunosaurus* (?Bajocian, China: Zhang, 1988; Zheng, 1991; Chatterjee & Zheng, 2002), and the neosauropods *Camarasaurus* (Fig. 5, ?Kimmeridgian, USA: Madsen, McIntosh & Berman, 1995; Ostrom
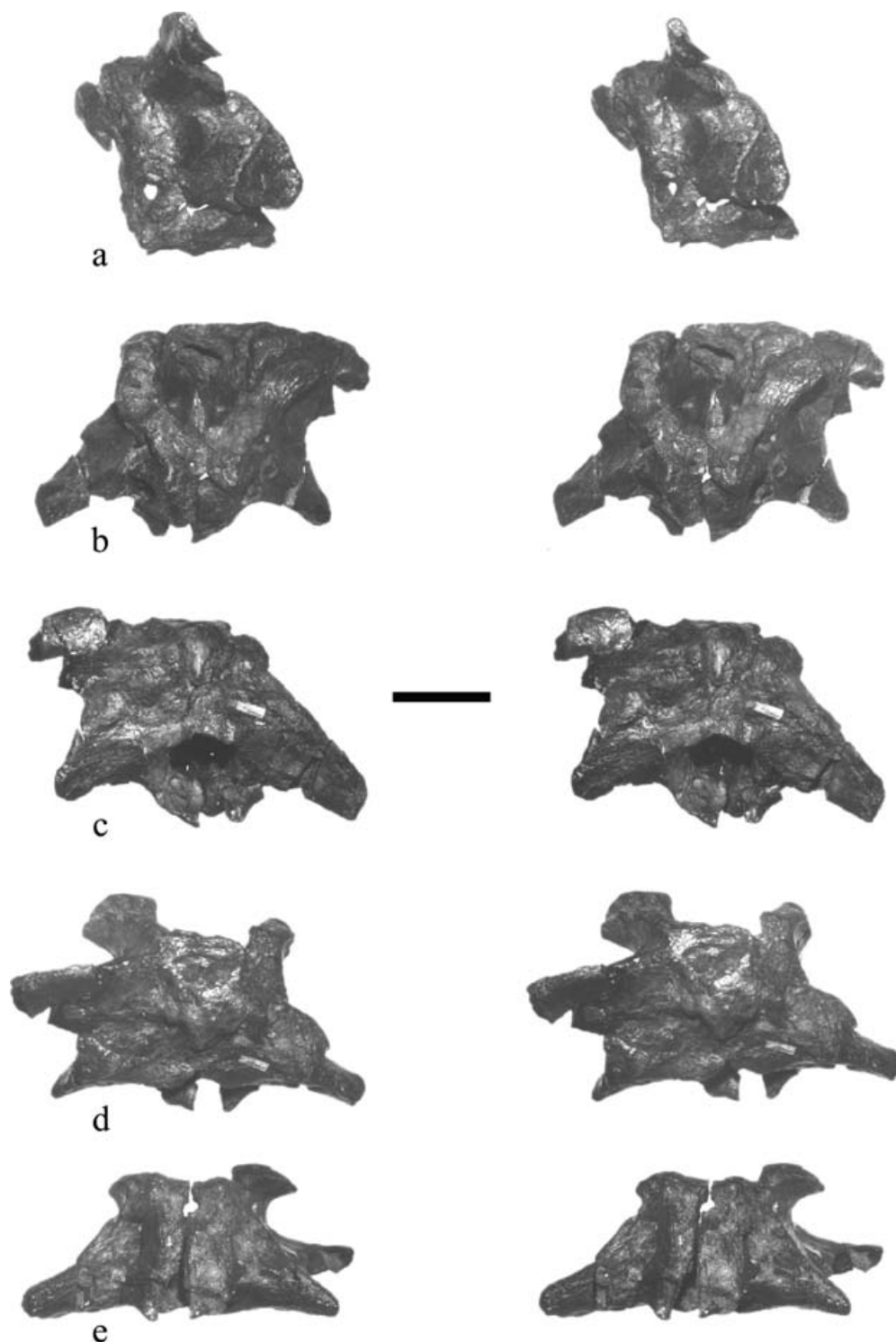
Figure 1. Eusauropod cf. *Cetiosaurus*, OUMNH J13596. Photographs of the assembled braincase, stereo photographs in (a) left lateral, (b) rostral, (c) caudal, (d) dorsal and (e) ventral views. Scale line represents 5 cm.

& McIntosh, 1966, p. 71 for disarticulated braincase), *Barosaurus, Brachiosaurus* and *Dicraeosaurus* (Kimmeridgian, Tanzania: Janensch, 1935–36), and *Diplodocus* (?Kimmeridgian, USA: Osborn, 1912); and for theropods: the basal theropod *Herrerasaurus* (Carnian, Argentina: Sereno & Novas, 1994), the ceratosaurians *Coelophysis* (as '*Syntarsus*':

?Sinemurian, Zimbabwe: Raath, 1985) and *Dilophosaurus* (?Sinemurian, USA: Welles, 1984), the basal tetanurans '*Poekilopleuron*?' (Bathonian, France: Allain, 2002), *Eustreptospondylus* (OUMNH J13558, Callovian, England: Huene, 1932, pl. 43, figs 2–5; Walker, 1964, fig. 17e; *Magnosaurus* of Rauhut, 2003), *Piveteausaurus* (Callovian, France: Taquet &
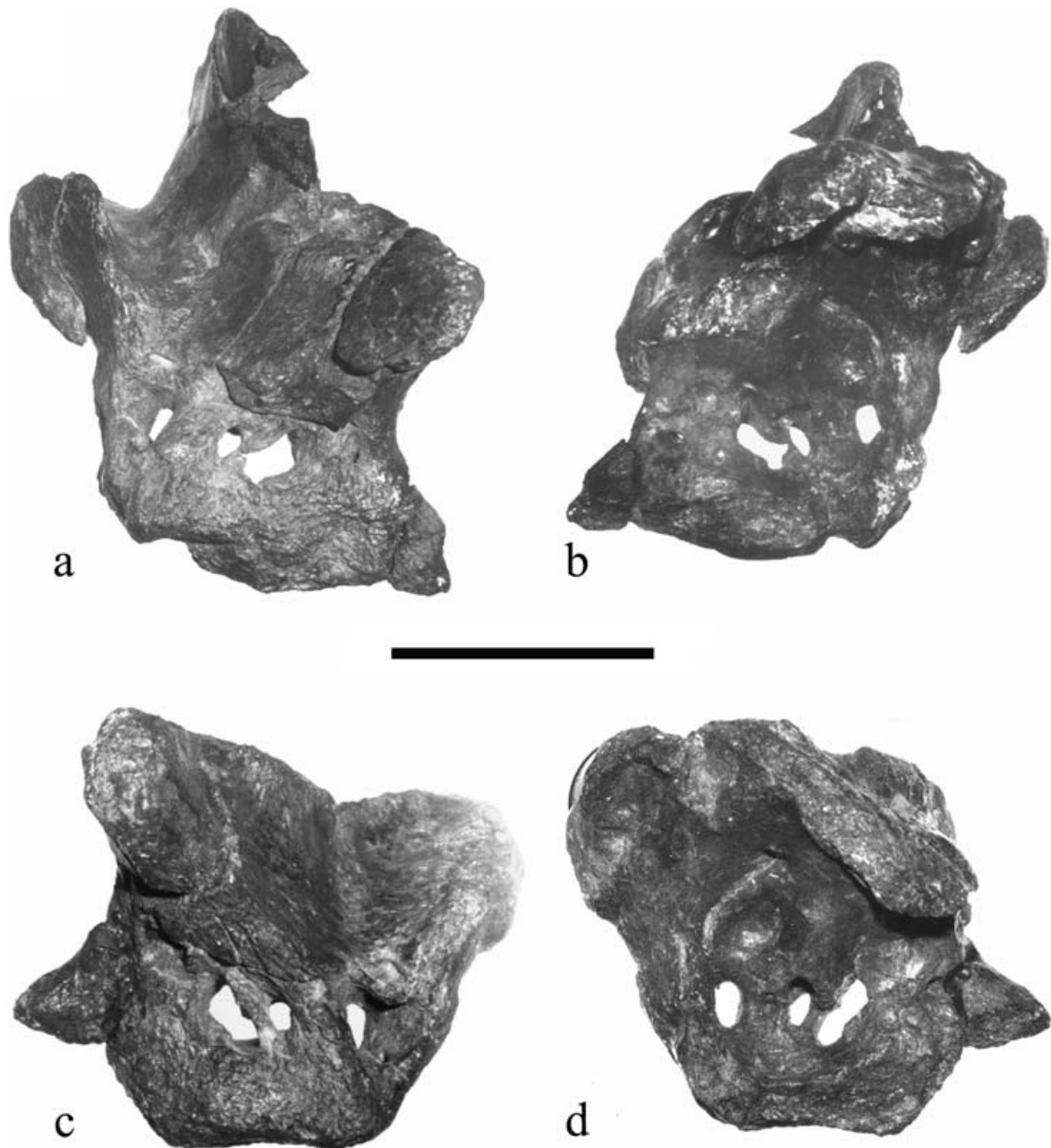
Figure 2. Eusauropod cf. *Cetiosaurus*, OUMNH J13596. Photographs of the disassembled braincase: left side in (a) lateral and (b) medial views; right side in (c) lateral and (d) medial views. Scale line represents 5 cm.

Welles, 1977), *Piatnitzkysaurus* (Callovian, Argentina: Bonaparte, 1986) and *Baryonyx* (Barremian, England, Charig & Milner, 1997), the allosauroids *Allosaurus* (Fig. 4, ?Kimmeridgian, USA: Osborn, 1912; Madsen, 1976) and *Acrocanthosaurus* (?Aptian, U.S.A: Stovall & Langston, 1950; Currie & Carpenter, 2000) and the coelurosaurians *Itemirus* (Turonian, Mongolia: Kurzanov, 1976), *Dromaeosaurus* (Campanian, USA: Currie, 1995) and *Tyrannosaurus* (Maastrichtian, USA: Osborn, 1912; Brochu, 2003).

The partial braincase is completely free of matrix and it is represented by two halves that still fit together very closely (Figs 1–3). The specimen has a maximum preserved width of 159 mm across the distally incomplete paroccipital processes. The most dorsal point of the foramen magnum is 31 mm from the tip of the supraoccipital that is 68 mm caudal to the level of the tip of the capitate process. The foramen magnum is 36 mm high and 38 mm wide. It is probably from an adult individual because there is no sign of any of the sutures between the individual bones, the boundaries of which must be recognized by comparisons with other saurischians in which the bones are separate or the sutures are not obliterated (e.g. *Plateosaurus*; *Allosaurus*, Fig. 4; *Camarasaurus*, Fig. 5). The braincase is preserved rostrally as far as
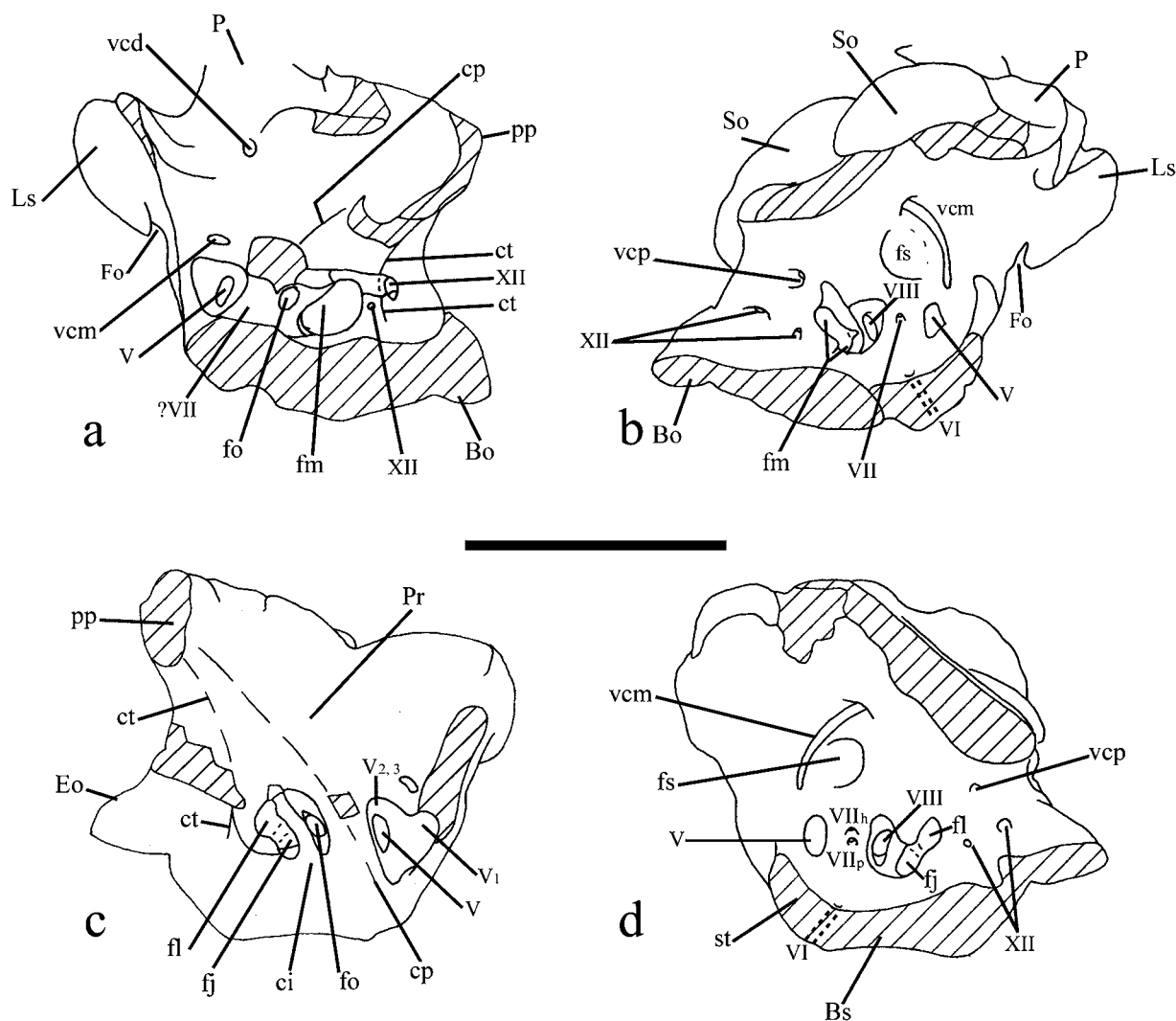
Figure 3. Eusauropod cf. *Cetiosaurus*, OUMNH J13596. Interpretative drawings of the disassembled braincase: left side in (a) lateral and (b) medial views; right side in (c) lateral and (d) medial views. Scale line represents 5 cm. Abbreviations: Bo – basioccipital; Bs – basisphenoid; ci – crista interfenestralis; cp – crista prootica; ct – crista tuberalis; Eo – exoccipital; fj – foramen jugulare; fl – foramen lacerum; fm – metotic fissure; Fo – orbital fissure; fo – fenestra ovalis; fs – fossa subarcuata; Ls – laterosphenoid; P – parietal; pp – paroccipital process; Pr – prootic; So – supraoccipital; st – sella turcica; vcd – vena capitis dorsalis; vcm – vena cerebralis medius; vcp – vena cerebralis posterior; V – trigeminal foramen; V_1 – notch for the ophthalmic ramus of the trigeminal nerve; $V_{2,3}$ – notch for the maxillo-mandibular ramus of the trigeminal nerve; VI – abducens foramen; VII – facial foramen; VIIh – fork for the hyomandibularis ramus of the facial nerve; VIIp – fork for the palatinus ramus of the facial nerve; VIII – internal auditory meatus; XII – hypoglossal foramen.

the sella turcica ventrally and the left laterosphenoid dorsally. The ventral margin of the foramen magnum is incomplete caudally due to breakage, and most of the basioccipital and basisphenoid are missing due to erosion and/or breakage. Consequently, the occipital condyle, basal tubera, basipterygoid processes and parasphenoid rostrum are not preserved.

The small subtriangular left laterosphenoid (Figs 2a, b, 3a, b), the alisphenoid of Huene (1906a), is closely applied to the parietal. A small lateral process (capitate process), which is eroded away on the right side, would have articulated with the postorbital. Ventrally, the laterosphenoid borders a notch, the 'Fissura orbitalis' of Huene (1906a). On the basis of this identification,

Hay (1909) re-identified the bone rostrodorsal to this notch as the orbitosphenoid. However, in saurischians the orbitosphenoids meet (prosauropods *Plateosaurus, Massospondylus*) or fuse (theropods, sauropods) to form a single median foramen for the optic nerve. This notch, which is too lateral to have bordered part of the optic foramen, probably formed part of the trochlear foramen (for IV), with the rest bordered rostrally by the missing orbitosphenoid. The relevant surfaces are eroded so it cannot be determined if the attachment of the orbitosphenoid was loose, as in prosauropods, or firm or fused, as in theropods and sauropods.

The parietal is damaged rostrally, where it may be slightly incomplete medially (Fig. 1a, b, d), but it
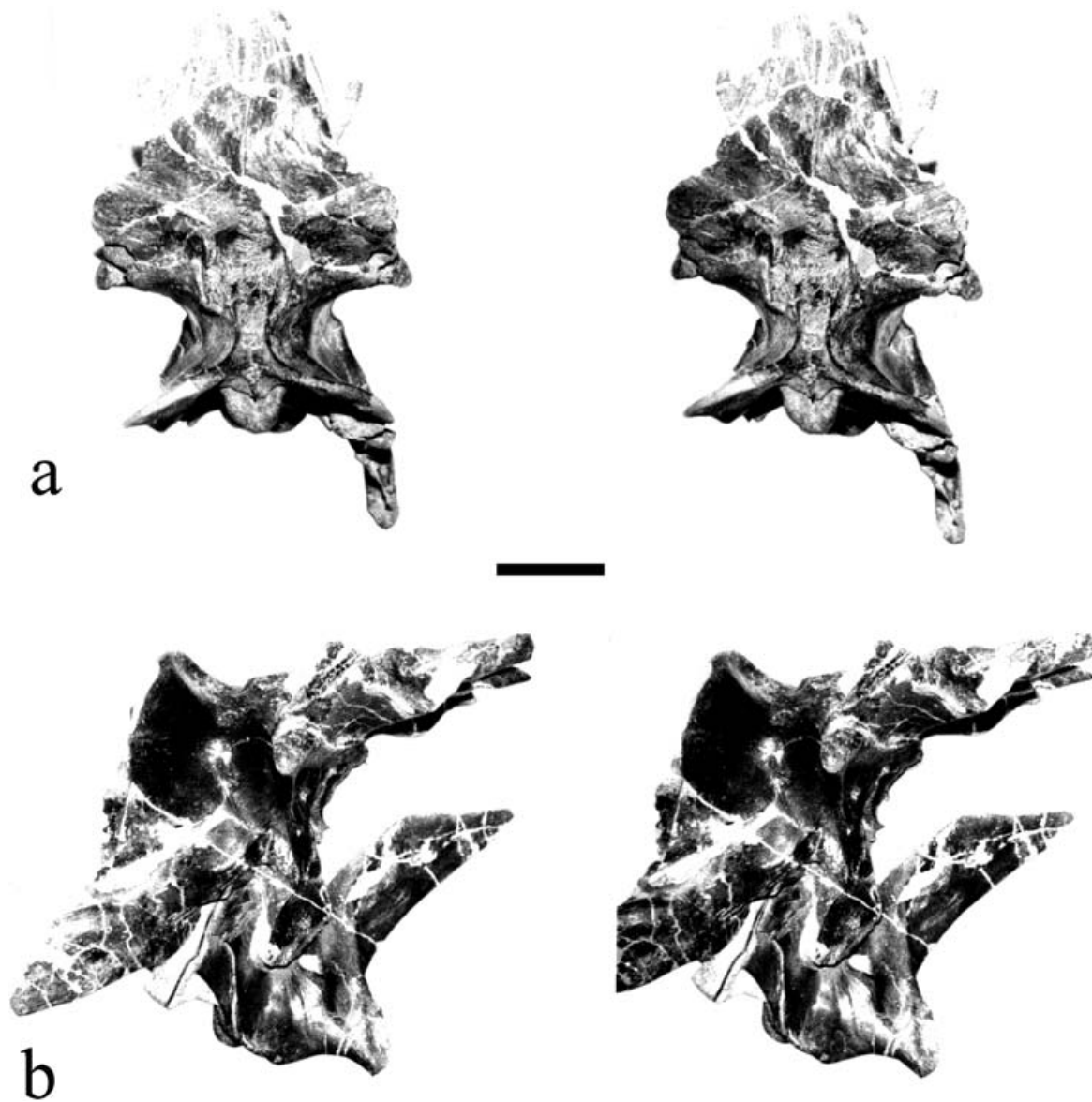
Figure 4. Tetanuran theropod *Allosaurus fragilis,* from Morrison Formation (Upper Jurassic) of Cleveland-Lloyd Quarry, Emery Co., Utah, braincase and adjacent part of skull roof of UUVP 5961 as stereo photographs in (a) dorsal and (b) right lateral views. Scale line represents 5 cm.

was obviously transversely wide, and rostrocaudally short as in sauropods (Fig. 5). In theropods (Fig. 4) and prosauropods the parietal is not shortened. In lateral view, the approximate ventral extent of the parietal is indicated by the foramen for the vena capitis dorsalis (Figs 1a, 2a, 3a). Rostrally, the braincase is broken, with the adjacent parts of the frontal and postorbital missing (Fig. 1d), so it cannot be determined if the parietal and postorbital met to exclude the frontal from the margin of the supratemporal fenestra, the rostromedial margin of which is indicated by a distinct edge on the parietal (Fig. 1d) as in *Omeisaurus* and neosauropods (Fig. 5). In theropods (Fig. 4), prosauropods and *Shunosaurus*, the supratemporal fenestra is bordered by the frontal, the

adjacent part of which has a shallow fossa, extending onto it from the parietal, that represents part of the attachment area for a jaw closing muscle, the m. pseudotemporalis. The small central roofing part of the parietal has a gently concave dorsal surface. Caudally, it sweeps out on each side to form a large, very deep and almost vertical caudolateral wing (Fig. 1a, b, d). Comparisons with the braincases of theropods and sauropods (Figs 4, 5) indicate that this element is the occipital wing of the parietal rather than a combination of the parietal and squamosal as described by Huene (1906*a*). The angle between the two lateral processes of the parietal, which formed the medial angle of the supratemporal fenestra (Fig. 1d), is acute, so this fenestra was probably rostrocaudally constricted,
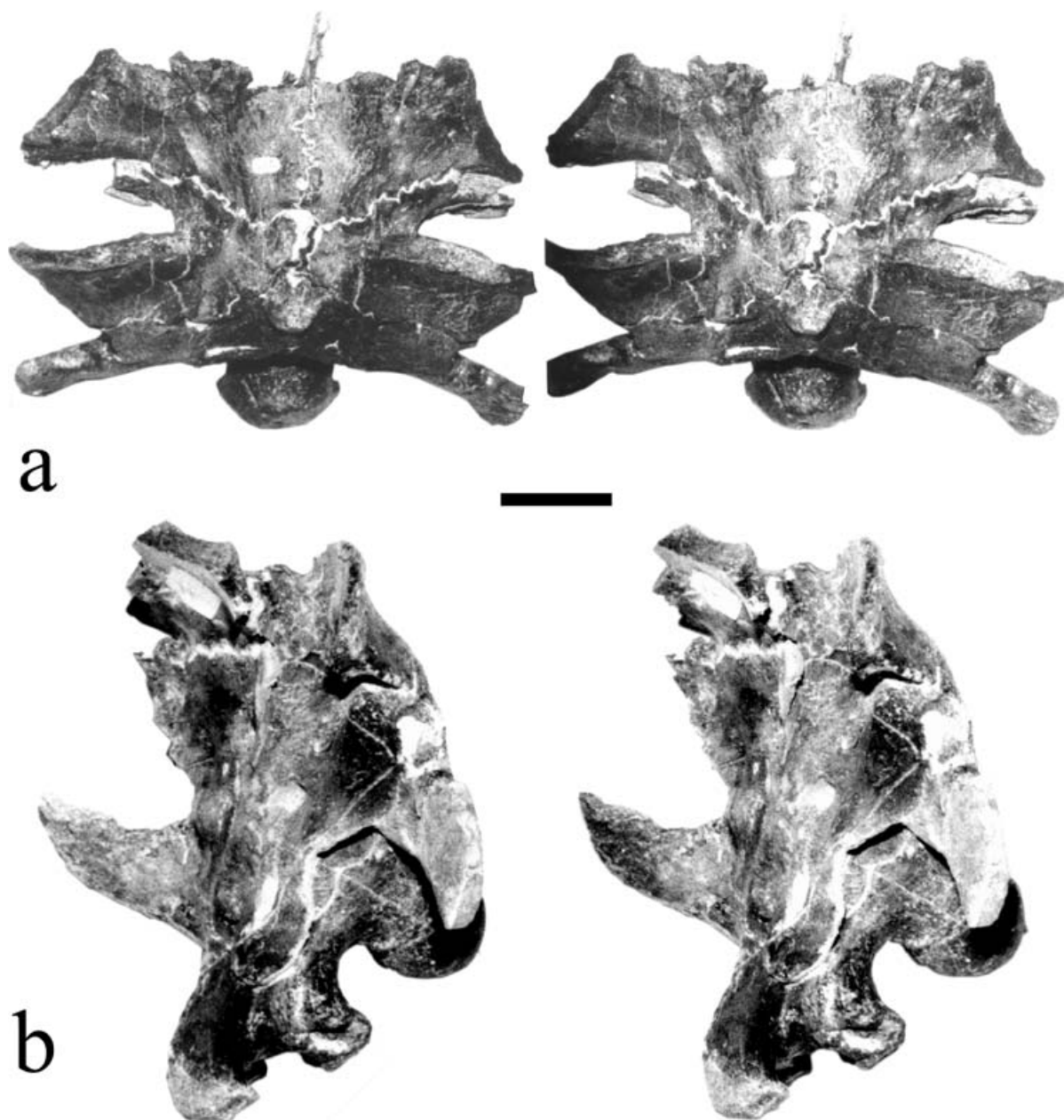
Figure 5. Neosauropod *Camarasaurus grandis,* from Morrison Formation (Upper Jurassic) Cleveland-Lloyd Quarry, Emery Co., Utah, braincase and adjacent part of skull roof of UUVP 10070 as stereo photographs in (a) dorsal and (b) left lateral views. Scale line represents 5 cm.

with the transverse width probably at least twice the rostrocaudal width as in *Omeisaurus* and neosauropods (Fig. 5a); in theropods (Fig. 4a), prosauropods and *Shunosaurus* this fenestra is longer rostrocaudally than it is wide.

Caudodorsally the parietal contacts a prominent medial convexity or boss that represents the apex of the supraoccipital (Fig. 1c, d). The supraoccipital usually makes at least a narrow contribution to the dorsal margin of the foramen magnum in theropods and sauropods, but it cannot be determined whether or not this was the case for the Oxford specimen (Fig. 1c).

The exoccipital and opisthotic are coosified as in most other saurischians and archosaurs (Figs 1–3). The paroccipital processes are downwardly directed at an angle of about 25° to the horizontal (Fig. 1c) and, originally, they probably became slightly more expanded vertically, with a straight distal margin, as in most other sauropods (Upchurch, 1998; plesiomorphic state for character C38). The exoccipitals presumably form the lateral and part of the dorsal rim of the foramen magnum. The distinct dorsolaterally situated angle on the rim (Fig. 1c) may have acted as a facet for the articulation of the proatlas, but distinct protuberances, as described for a neosauropod braincase by

Berman & Jain (1982), are not visible on the Oxford specimen or in most other sauropods. The exoccipital–opisthotic complex forms most of the caudal corner of the sidewall of the braincase, enclosing the hypoglossal foramina (XII) and forming the caudal boundary of the jugular foramen. The crista tuberalis, which starts as a slight ridge with a L-shaped cross-section at the base of the paroccipital process (Fig. 2a, c), is small, as in prosauropods, and more ventrally it does not expand laterally to form a thin, prominent sheet as occurs in theropods (Fig. 4b).

Huene (1906a) indicated an epiotic but, although this bone forms from its own centre of ossification in reptiles, it is completely fused with the supraoccipital in braincases of adult saurischians. The sutures in this region are completely obliterated, but the point labelled epiotic is probably part of the prootic rather than part of the supraoccipital. The prootic forms the rostral border of the jugular foramen, encloses the fenestra ovalis and facial foramen, and borders most of the trigeminal foramen (Figs 2, 3), the rostrodorsal part of which is bordered by the laterosphenoid. The crista prootica is thick and gently convex (Figs 2a, c, 3a, c), as in prosauropods, and it does not expand laterally into a thin, prominent large sheet as occurs in most sauropods (Fig. 5b).

Most of the basioccipital is missing, making the exact outline of the foramen magnum uncertain ventrally (Fig. 1c, d). The preserved part of the basisphenoid, which is rostrally limited by the dorsum sellae, encloses the foramina for the right and left abducens nerves rostrally (Figs 2b, d; 3b, d). In medial view, certain structures other than foramina (see below) are recognizable (Figs 2b, c, 3b, c; see Fig. 6, for casts of the medial parts of these structures and the foramina described in next section). Dorsally, a median excavation probably originated from an unossified zone that was originally filled with cartilage. This region corresponds to the parietal 'foramen' of Janensch (1936), which is more usually interpreted as a fontanel or unossified region (see Hopson, 1979). The prominent, more centrally located and gently rounded concavity rostrocaudal to this zone is the fossa subarcuata, an identification suggested for sauropods by Janensch (1935–36). In numerous mammals, the fossa subarcuata is a slot above and behind the internal auditory meatus that is occupied by the flocculus of the cerebellum. However, the homology between the dinosaurian structure and the mammalian fossa subarcuata is doubtful. The deeper caudoventral part of this fossa was misinterpreted by Huene (1906a) as the entrance into the inner ear for parts of the lagena, cochlea and the vestibular ramus of cranial nerve VIII. However, these structures would be much lower down relative to the semicircular canals (Hay, 1909), the position of which is indicated by the prominent, obliquely orientated convexity caudal to the fossa, the pyramid of Huene (1906a). The prominent groove bordering the rostrodorsal margin of the fossa subarcuata was for the vena cerebralis medius.

3.b. Identification of foramina

The caudal branches of each internal carotid artery unite to form a single basilar artery that passed from the pituitary space into the cranial cavity through a median notch in the caudodorsal wall of the sella turcica in *Shunosaurus* (Chatterjee & Zheng, 2002). However, the opening in this region in the Oxford braincase (Fig. 1b) appears to be the result of breakage rather than representing a foramen.

A centrally located hole filled with matrix on the lateral surface (Figs 2a, 3a, vcd) was identified by Huene (1906a) as the external auditory meatus. However, this identification is incorrect because, as noted by Hay (1909), penetration of the Eustachian canal into the vestibule is totally out of the question. In reptiles, the eardrum generally lies directly on the exterior surface, at the bottom of a shallow depression or, as in crocodilians, it may be covered by a flap of skin. The external auditory meatus is an acquisition of homeotherms that was developed independently in mammals and birds. In the latter, it is a relatively short tract without any particular osseous covering; it is limited in part by the occipital bones and the quadrate but its lining remains membranous (Portmann, 1950a). Hay (1909) suggested that the dorsolateral opening was the outlet from the internal depression but this is unlikely. As noted above, this zone was probably filled with cartilage in life. This opening was probably a foramen for the vena capitis dorsalis that, as in *Sphenodon* (Dendy, 1909, p. 418; O'Donoghue, 1920, pp. 215–16) and *Lacerta* (Bruner, 1907), drained the muscles of the spino-occipital region and then passed rostrally through the post-temporal foramina at the angle between the parietal and the paroccipital process (closed laterally by the squamosal that is not preserved; cf. He, Li & Cai, 1988, fig. 6 for *Omeisaurus*; Wilson & Sereno, 1998, figs 6C, 7B, 8B for Neosauropoda). There are indications of a shallow depression passing rostrally from this angle along the lateral surface to the lateral opening ventral to the parietal (Figs 1a, 2a). In *Lacerta*, the vena capitis dorsalis passes through the rostral end of the great parietal fissure (between parietal and prootic: Bruner, 1907). In lower vertebrates, the vena capitis dorsalis enters the transverse sinus lying within the sidewall of the braincase (Romer, 1956).

Huene (1906a) identified a centrally located medial opening, and the associated prominent groove, as the region occupied by the aquaeductus vestibuli and the saccus endolymphaticus. However, this opening (Figs 2b, d, 3b, d) represents the exit from the cranial cavity of the vena cerebralis medius as interpreted by Janensch (1935–36) for sauropods. This vein, which drained blood from the transverse sinus, then ran in the groove until its ventral end re-entered the wall of the

braincase (Figs 2b, d, 3b, d, 6). In *Plateosaurus*, the vena cerebralis medius leaves the cranial cavity by a canal within the prootic–laterosphenoid suture to exit into the dorsal part of the trigeminal foramen. This exit corresponds to the separate foramen laterally above the trigeminal foramen (Figs 2a, 3a), which was misidentified by Huene (1906*a*) as the possible exit for the trochlear nerve (IV) and blood vessels of the eye.

The braincase is not preserved far enough rostrally to show the olfactory or optic foramina. In fact, the notch identified by Huene (1906*a*) as the fissura orbitalis possibly represents part of the trochlear foramen (IV), while the slight depression a few millimetres more ventrally may have bordered part of the occulomotor foramen (for III), with the rest of these foramina being bordered by the missing orbitosphenoid (Figs 2a, b, 3a, b).

The trigeminal foramen (V) is one of the largest lateral nervous foramina of the braincase. This opening was incorrectly identified by Huene (1906*a*) as the foramen ovale for $V_{2,3}$. This foramen is internally egg-shaped (Figs 1b, d, 2b, d) but externally heart-shaped (Figs 2a, c, 3a, c). This last character is related to the division of this nerve into a rostral (ophthalmic, V_1) and a caudal (maxillo-mandibular, $V_{2,3}$) ramus. Part of the large foramen prooticum may have been occupied by the large sensory trigeminal or Gasserian ganglion, which is close to the root of the trigeminal nerve. However, this ganglion is absent in most reptiles, in which the ophthalmic and maxillo-mandibular ganglia remain unfused (Starck, 1979, p. 11). In all sauropods, the ophthalmic branch of the trigeminal exits the braincase from a single opening (Currie, 1997), but the separation is more pronounced in birds in which the trigeminal leaves the cerebral cavity by two (rarely three) openings (Portmann, 1950*b*).

The small abducens foramen is ventral to that of the trigeminal (VI; Figs 2b, d, 3b, d). It passes rostroventrally through the sella turcica into the caudal part of the pituitary fossa (Fig. 1b), as in most dinosaurs (Currie, 1997) except coelurosaurians (Currie & Zhao, 1993*a*). The small facial foramen passes through the crista prootica and it is about the same size as the abducens foramen. The facial foramen is barely recognizable in lateral view (Figs 2a, c, 3a, c), but medially it is represented by a small depression caudal to the middle of the trigeminal foramen (Figs 2b, d, 3b, d). The main, laterally directed path was probably for the ramus palatinus, whereas a smaller, dorsolaterally directed one may have been for the ramus hyomandibularis (Figs 3d, 6), but a separate opening is not visible laterally on the crista prootica.

As remarked by Hay (1909), the foramen jugulare of Huene (1906*a*) represents the lateral and medial passages into the inner ear. The external oval-shaped aperture, the fenestra ovalis (Figs 2a, c, 3a, c), would have been closed by the footplate of the stapes. The inner aperture (Figs 2b, d, 3b, d), subtriangular in outline, is that of the internal auditory meatus for the vestibulocochlear nerve (VIII). It is bordered caudally by a bony bar, the crista interfenestralis, part of which is missing laterally on the left side so it appears to have a bend in it (Figs 2a, 3a), but the right one is complete and straight (Figs 2c, 3c). Adjacent to this crista is a much larger foramen, the foramen lacerum (posterius) of Huene (1906*a*) that actually combines with the foramen jugulare (anterius) to form the fissura metotica more laterally (Figs 2, 3), through which exited the glossopharyngeal, vagus and accessory nerves (IX, X, XI). The jugular foramen is of particular importance, as it formed the exit for the internal jugular vein. In *Shunosaurus* the exit for cranial nerves IX to XI is assumed to be separated internally from that of the internal jugular vein before merging outside into a metotic fissure (Zheng, 1991; Chatterjee & Zheng, 2002). In the Oxford braincase the obliquely inclined medial aperture is constricted in its middle part; before the bony surfaces on either side were broken (Fig. 2c), a bony bar divided it in two so it looked like an obliquely inclined figure 8 (Fig. 3c). In *Brachiosaurus* the jugular and lacerum foramina are fused to form one sigmoid-shaped aperture.

The most caudal foramina (Figs 3, 4) were identified as the hypoglossal foramina by Huene (1906*a*). However, the internal depression he marked XII'' is probably the remnant of the opening through which the vena cerebralis posterior originally passed (Figs 3b, d), and the external 'opening' is a slight break in the bone (Figs 2a, 3a). The large external opening that Huene (1906*a*) believed was for the internal carotid artery is one end of a matrix-free canal, the medial opening of which he correctly assigned to the hypoglossal nerve (Figs 2a, b, 3a, b). Hay (1909), who correctly referred the medial opening to the venous circulation, noted that it is improbable that the internal carotid artery entered the cranial cavity so far posteriorly. In fact, the internal carotid arteries would have entered the pituitary fossa through the Vidian canal that is not preserved in the Oxford braincase. The small medial opening that Huene (1906*a*) attributed to the internal carotid artery is a different foramen that he later correctly identified (Huene, 1907–08) as the opening for the smaller ramus of the hypoglossal nerve (Figs 1b, 2b). Laterally there is a corresponding small foramen (Figs 2a, 3a), not shown by Huene (1906*a*), with the opening for the larger ramus caudodorsal to it.

4. Endocranial cast

4.a. Brain

The following study is based on latex casts made from the original two pieces of the braincase (OUMNH J13596a, b) and a silicone endocast made from plaster casts of the originals (OUMNH J13596a,b/pl). The description of the endocranial cast (Fig. 6) will follow
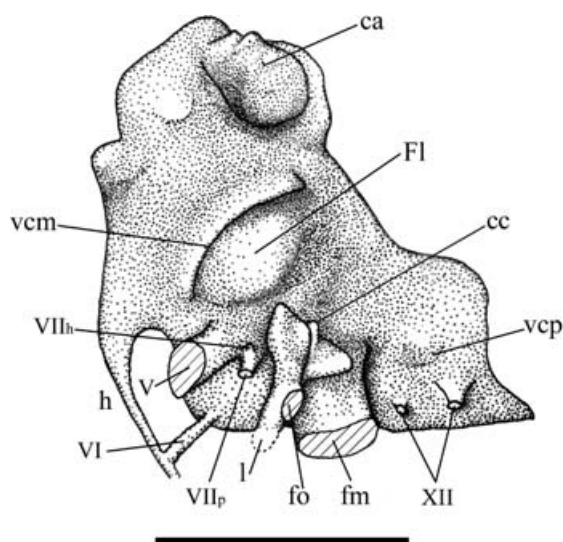
Figure 6. Eusauropod cf. *Cetiosaurus*, OUMNH J13596. Interpretative drawing of the endocranial cast in left lateral view. Scale line represents 5 cm. Abbreviations: ca – cartilaginous zone; cc – base of the crus commune of the anterior and posterior semicircular canals; Fl – flocullar lobe of the cerebellum; h – location of the hypophysis; l – lagena; others see Figure 3.

the usual practice of assuming that it approximately represents the form of the brain because, as Hopson (1979, p. 78) noted, the brains of dinosaurs 'appear to have molded the cranial cavity to a greater extent than is usual in reptiles'. The contracted appearance of the brain of sauropods was remarked on by Hopson (1979, p. 54). Thus in *Diplodocus* the extreme shortness of the temporal region of the skull, the sharply downward-turned facial region, and the very large posterodorsally placed orbit have combined to crowd the braincase far back in the skull. Hence, the brain is shaped to fill the available space most economically, to such an extent that the volume of the endocast might not be very different from the actual volume of the encephalon. The Oxford endocast is relatively short and deep, with strong cerebral and pontine flexures (about 55°), and a steeply inclined caudal edge (Fig. 6). The general shape is quite similar to the most complete one of *Brachiosaurus* (Kimmeridgian, Tanzania: Janensch, 1935–36), in which there is a dorsal projection, reminiscent of the probable cartilaginous zone, and there is a thin curved convexity on the mid-endocast with a caudal bulge.

Because of the prominent flexures, many of the regions of the brain can only be recognized by the structures that they bear (Fig. 6):

Telencephalon. The cerebral hemispheres form the widest part of the brain.

Diencephalon. The endocast has a small dorsal projection that represents an unossified space that in life was probably occupied with cartilage. The optic nerve (II) arose laterally from this region that, more ventrally, occupied part of the incompletely preserved hypophyseal fossa or pituitary space.

Mesencephalon. The extent of this region is uncertain because there are no dorsal optic lobes and the exact points of origin of the oculomotor and trochlear nerves (III, IV) cannot be determined.

Metencephalon. There is no cerebellar expansion in the dorsal region of the metencephalon. The flocullar lobe of the cerebellum is interpreted from a slight concavity, the 'fossa subarcuata', in the medial wall of the prootic and supraoccipital. The trigeminal nerve originates from this region of the brainstem, the posterior part of which has transversely constricted sidewalls to accommodate the inner ear. With the adjacent part of the myelencephalic walls, this area is the narrowest part of the brain.

Myelencephalon. Cranial nerves VI to XII and the inner ear originate from the ventral part of the myelencephalon, the widest part of which is slightly posterior to the vena cerebralis posterior.

4.b. Inner ear

Casts of the inner ear (Fig. 6) include most of the bony labyrinth except for the semicircular canals, the more central parts of which are still filled with matrix. Swellings at the base of each canal, the ampullae, are visible. By analogy with lizards, the utriculus was a roughly V-shaped system of tubes, the ends of which connected with the semicircular canals. Only the base of the crus commune, from which the medial ends of the vertical canals originate, is preserved. The sacculus is poorly developed, whereas in lizards it is much enlarged. The lagena is straight and short. The fenestra ovalis is delimited from the fissura metotica by the crista interfenestralis. This crista is more complete on the right side (Figs 2c, d, 3c, d), in which it funnels into an oval-shaped fenestra ovalis, the complete margin of which is preserved on both sides.

5. Systematic position of Oxford braincase

5.a. Theropod affinities of braincase

Until recently, no synapomorphies were discussed for the braincase of the Theropoda or for the major constituent groups (Gauthier, 1986; Benton, 1990; Holtz, 1994; Novas, 1994, 1996; Sereno & Novas, 1994; Sereno *et al.* 1994). Holtz (2000, characters 83.1, 84.1) gives the presence of a pronounced nuchal crest and a prominent median ridge on the supraoccipital, two structures not present on the Oxford braincase, as synapomorphies of the Neoceratosauria. However, most of the other relevant characters of the bones and foramina are synapomorphies for more terminal nodes and are not relevant because the Oxford braincase has the plesiomorphic condition.

Rowe & Gauthier (1990, p. 156) noted for the Ceratosauria that the paired parietals abut without interdigitation or fusion to the underlying bones of the neurocranium so, on this character, the Oxford

braincase (Figs 1–3) is not that of a ceratosaurian theropod (but this character was not used by Holtz, 2000). The loose union of the parietal to the rest of the neurocranium is also the case in *Herrerasaurus,* basal ornithischians (Sereno, 1991) and prosauropods (Galton & Upchurch, 2004), so the extensive fusion of the parietal with the adjacent bones in sauropods (Fig. 5b) represents the derived condition that was acquired independently within the Tetanurae (Fig. 4b).

The crista tuberalis of theropods (Fig. 4b) is a prominent caudolaterally expanded sheet of bone that continues the ventral edge of the paroccipital process across the lateral wall of the braincase ventrally to the basal tubera. This sheet forms the caudal (posterior) tympanic recess of Raath (1985), which backs the fenestra ovalis and the adjacent jugular foramen, with the hypoglossal foramina caudal to this sheet. This arrangement appears to be present in all theropods in which this region is preserved, namely, the basal theropod *Herrerasaurus* (Sereno & Novas, 1994, figs 7C, E, 8C, E), the ceratosaurians '*Syntarsus*' (Raath, 1985, fig. 1) and *Dilophosaurus* (Welles, 1984, fig. 6A, C), the basal tetanurans *Piveteausaurus* (Taquet & Welles, 1977, figs 1–5), *Piatnitzkysaurus* (Bonaparte, 1986, figs 3, 4), *Eustreptospondylus* (Huene, 1932, pl. 43, fig. 2a, e), *Baryonyx* (Charig & Milner, 1997, fig. 9A, B) and *Allosaurus* (Fig. 4b; Osborn, 1912, figs 9–11; Madsen, 1976, figs 13, 15), and the coelurosaurs *sensu* Holtz (1994, 2000) *Sinraptor* (Currie & Zhao 1993*b*, fig. 7), *Itemirus* (Kurzanov, 1976, figs 1–3), *Tyrannosaurus* (Osborn, 1912, figs 4, 6–8), *Dromaeosaurus* (Currie, 1995, fig. 6), *Troodon* (Currie & Zhao, 1993*a*, fig. 1d) and *Stenonychosaurus* (Currie, 1985, figs 4–6). The absence of a sheet-like crista tuberalis suggests that the Oxford braincase is not referable to the Theropoda.

Recent cladistic analyses of the Sauropoda reveal a few synapomorphies based on the braincase region (Upchurch, 1998, 1999; Wilson & Sereno, 1998; Wilson, 2002). For these characters, the Oxford braincase has the derived condition (see below), whereas the braincases of theropods (along with those of prosauropods and ornithischians) retain the plesiomorphic condition, so the Oxford braincase does not appear to belong to a theropod dinosaur.

5.b. Sauropod affinities of braincase

The Oxford braincase possesses several derived characters, the result of the change in cranial proportions during sauropod evolution, that were used in recent cladistic analyses of the Sauropoda (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002).

5.b.1. Membership of the Eusauropoda

(1) Supratemporal region of cranium shortened rostrocaudally (Wilson & Sereno, 1998, p. 36, character 27). It is certainly true for the Oxford braincase that the 'upper portion of the laterotemporal fenestra is narrow' (Wilson & Sereno, 1998, p. 36). Upchurch (1998, p. 98,

character 11 for node C, Eusauropoda, but not discussed or plotted as a data-matrix character) listed the character 'frontals and parietal short rostrocaudally' and the parietal is short in the Oxford braincase (Figs 1d, 2a, 3a), as is also the case in the Eusauropoda and Neosauropoda (Fig. 5a). Theropods (Fig. 4a), including the braincase of '*Poekilopleuron*?' (Allain, 2002) and prosauropods (Galton & Upchurch, 2004), retain the plesiomorphic state with a parietal that is not shortened rostrocaudally. Although not considered in either analysis, the rostrocaudal shortening of the supratemporal region is clearly reflected in the form of the endocranial cast with this region being more elongate in theropods and prosauropods (the plesiomorphic state) and short in sauropods and the Oxford specimen (Fig. 6).

(2) Supratemporal fossa broadly exposed laterally. Wilson & Sereno (1998, p. 36, character 26; Wilson, 2002) noted that 'in prosauropods and theropods, the supratemporal fossa faces dorsally and is largely obscured in lateral view by the postorbital–squamosal bar'. Given the ventral position of the apex of the paroccipital process and the flared and deep form of the lateral process of the parietal (Fig. 1a, b), it is apparent that the temporal fenestra was probably broadly exposed in lateral view, as in the eusauropods *Shunosaurus* and *Omeisaurus*.

(3) Loss of excavated area around dorsal margin of the supratemporal fenestra (Upchurch, 1998, p. 98, character 12 for Eusauropoda, data-matrix character C31). The excavation, part of the supratemporal fossa, on the dorsal part of the parietal and frontal for the attachment areas for the M. adductor mandibulae externus medialis and the M. adductor mandibulae internus (m. pseudotemporalis), was originally suggested as a synapomorphic character for Saurischia (Gauthier, 1986; Benton, 1990). However, it is present in an assumed basal ornithischian (Sereno, 1991; Knoll, 2002*a*, *b*), so it is probably a synapomorphy of Dinosauria (Novas, 1994). This plesiomorphic condition is retained in theropods (Fig. 4a; '*Poekilopleuron*?': Allain, 2002), and prosauropods (Galton, 1990). However, it is lost in the eusauropods *Shunosaurus* and *Omeisaurus*, and in neosauropods but present in *Camarasaurus* (Fig. 5b; Madsen, McIntosh & Berman, 1995). The parietal of the Oxford braincase does not have an excavated area on the parietal (Fig. 1d).

*5.b.2. Membership of (*Omeisaurus*, Neosauropoda)*

(1) Supratemporal fenestra, long axis oriented transversely (Wilson & Sereno, 1998, character 66; Wilson, 2002). In prosauropods (Galton & Upchurch, 2004) and theropods (Fig. 4a), the fenestra is longer rostrocaudally than broad transversely as also occurs in *Shunosaurus*. However, in *Omeisaurus*, the Oxford braincase (as indicated by the medial boundary formed by the parietal; Fig. 1d), and neosauropods (Fig. 5a), the long axis of the supratemporal fenestra is oriented transversely, not longitudinally.

(2) Occipital region of skull, shape: anteroposteriorly flat, paroccipital processes oriented transversely; the plesiomorphic condition is a deep occipital region and posterolaterally directed paroccipital processes (Wilson, 2002, p. 266). This character is not discussed further but it is present in the Oxford braincase, in which the occiput is rather flat (Fig. 1c, d) except for the boss formed by the top of the supraoccipital (as also occurs in many sauropods) and the paroccipital processes are transversely oriented (Fig. 1), with the plesiomorphic condition in theropods and prosauropods.

5.b.3. *Non-membership in Neosauropoda*

In the cladistic analyses of Upchurch (1998), Wilson & Sereno (1998), Wilson (2002) and Upchurch, Barrett & Dodson (2004), the Neosauropoda and higher nodes are characterized by postcranial synapomorphies, the polarity of which cannot be determined for the Oxford braincase.

Laterally the sidewall of the Oxford braincase (Figs 2a, c, 3a, c) is very similar to that of prosauropods (Galton, 1984, 1985; Gow, 1990; Galton & Upchurch, 2004), with the crista prootica forming a low, rounded ridge rather than a prominent laterally directed sheet. In neosauropods this crista forms a large sheet that, as noted for *Camarasaurus* (Fig. 5b) by Madsen, McIntosh & Berman (1995, p. 17) is 'angled so strongly posteriorly as to make openings in the lateral wall posterior to it difficult to see'. A braincase of a titanosauriform (?Albian, USA: Tidwell & Carpenter, 2003) appears to have a low crista prootica, but this is the result of breakage and erosion (V. Tidwell, pers. comm.). The braincase of *Omeisaurus* is only figured as part of the palatal view of the complete skull (He, Li & Cai, 1988, fig. 7) and the crista prootica is very well developed (He, pers. comm.). In adult individuals of *Shunosaurus* the crista prootica is prominent, but not nearly as extensive, being robust and elongated posteriorly to the base of the paroccipital process (He X., pers. comm.; see Zhang, 1988, fig. 13 for ventral view of specimen with braincase *in situ*). However, in an immature individual (with a skull length 43 % of that in adult: Zhang, 1988, figs 3–5 for skull, fig. 6 for braincase), the crista prootica is rounded in cross-section without any sheet-like part (He X., pers. comm.). Unfortunately, the braincase is not described for any basal Lower Jurassic or Upper Triassic sauropod. However, the plesiomorphic condition of the crista prootica makes it non-parsimonious that the Oxford braincase is from a neosauropod.

6. Conclusions

The characters of the Oxford braincase (Figs 1–2, 6) place it in the Eusauropoda and possibly within the clade (*Omeisaurus*, Neosauropoda) of Wilson & Sereno (1998). The cladistic analysis of Upchurch (1998) placed the postcrania of *Cetiosaurus* (restricted

to English material from Oxford and Rutland: Upchurch & Martin, 2002, 2003) between the Euhelopodidae (including *Omeisaurus*) and the Neosauropoda. Upchurch, Barrett & Dodson (2004) have the Cetiosauridae (including *Cetiosaurus*) as basal eusauropods between *Shunosaurus* and *Omeisaurus*. However, it should be noted that they recognize no synapomorphies of the braincase for the Eusauropoda. Given the possible occurrence of the Oxford braincase, namely, from the old '*Cetiosaurus* quarries' of Phillips (1871, pp. 250–2), the Bletchingdon (old Kirtlington) Station Quarry near Oxford (see Section 2), Huene (1932) may have been finally correct in referring this braincase to *Cetiosaurus oxoniensis*

The OUMNH Phillips Collection from the '*Cetiosaurus*' quarries consists of a few bones and a tooth of '*Megalosaurus*' (Phillips, 1871, p. 251; see fig. 84 for quarry plan; Upchurch & Martin, 2003, for history of discovery) plus associated bones representing three different sized individuals, the syntypes of *Cetiosaurus oxoniensis* Phillips, 1871 (see Huene, 1927; Upchurch & Martin, 2003). Phillips (1871, p. 251) noted that there was no sign of 'a head or any very intelligible part of one, as far as we have yet ascertained . . . . There remains, however, a small portion of unmoved ground yet to be examined'. In addition, he tabulated under 'head' for the large individual of *Cetiosaurus*, 'Unascertained bones, and part of one tooth' (Phillips, 1871, p. 252; tooth fig. 85; Upchurch & Martin, 2003, fig. 4). Admittedly, the 'unascertained bones' are unlikely to have included a well-preserved braincase that would have been easily recognized and there are no records to indicate whether or not the 'unmoved ground' was ever excavated. Yet it is possible that the OUM braincase could have come from the large individual (the lectotype), which represents most of the bones from this excavation (Upchurch & Martin, 2003; see Glut, 1997, p. 274 for photograph of limb bones and vertebrae) versus four other bones each for the medium and small sized individuals (Upchurch & Martin, 2003). In fact, the extensive fusion of the bones of the braincase, with no sutures discernable, indicates that it is from an adult animal. Consequently, this braincase is definitely not from the small individual (whose humerus length of about 610 mm obviously points to a juvenile individual because large ones are at 1260 and 1236 mm: Upchurch & Martin, 2003, p. 224; Phillips, 1871, p. 273, figs 100, 101). The large femur is 1615 mm. Neither Phillips (1871) nor Upchurch & Martin (2003) give the length of the medium sized humerus or femur but the latter (OUMNH J13617) is 1290 mm (H. P. Powell, pers. comm.). Because of the high degree of fusion of the bones, the braincase would have rather come from the large lectotype individual. However, given the difficulty of making accurate proportional data of braincase size to long bone lengths for the Oxford material, the lack of this data for other cetiosaurids, and the lack of

any written records to support the assumption that this braincase was found at the type locality after the main excavation, this braincase is best regarded as Eusauropoda indet., cf. *Cetiosaurus*. On the basis of an earlier version of this paper, Upchurch & Martin (2003, p. 216) listed it as one of the paralectotypes of *Cetiosaurus oxoniensis* Phillips, 1871. Be that as it may, this braincase is important because it is the earliest described to date for a sauropod, it will possibly prove to enhance our knowledge of *Cetiosaurus*, a basal eusauropod for which the skull was previously unknown, and it is quite plesiomorphic for a sauropod in lacking a sheet-like crista prootica in the adult.

References

ALLAIN, R. 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology* **22**, 548–63.

ALLAIN, R. 2005. The postcranial anatomy of the megalosaur *Dubreuillosaurus valesdunensis* (Dinosauria Theropoda) from the Middle Jurassic of Normandy, France. *Journal of Vertebrate Paleontology* **25**, 850–8.

ANONYMOUS. 1999. Un dinosaure carnivore en Normandie: le retour du *Poecilopleuron*. Paris: Muséum national d'Histoire naturelle, unpaginated press material.

ARKELL, W. J. 1947. *The Geology of Oxford*. Oxford: Clarendon Press, 267 pp.

BARRETT, P. M., UPCHURCH, P. & WANG, X.-L. 2005. Cranial osteology of *Lufengosaurus huenei* Young (Dinosauria: Prosauropoda) from the Lower Jurassic of Yunnan, People's Repubic of China. *Journal of Vertebrate Paleontology* **25**, 806–22.

BARRETT, P., UPCHURCH, P., ZHOU, X.-D & WANG, X.-L. 2003. Prosauropod dinosaur from the Lower Lufeng Formation (Lower Jurassic) of China. *Journal of Vertebrate Paleontology* **23** (suppl. to no. 3), 32A.

BATE, R. H. 1978. The Jurassic. Part II. Aalenian to Bathonian. In *A Stratigraphical Index of British Ostracoda* (eds R. H. Bate and E. Robinson), pp. 213–58. *Geological Journal, Special Issue* **8**. Liverpool: Steel House Press.

BENTON, M. B. 1990. Origin and interrelationships of dinosaurs. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 11–30. Berkeley: University of California Press.

BENTON, M. B. & SPENCER, P. S. 1995. *Fossil Reptiles of Great Britain*. London: Chapman & Hall, 386 pp.

BERMAN, D. S. & JAIN, S. L. 1982. The braincase of a small sauropod dinosaur (Reptilia: Saurischia) from the Upper Cretaceous Lameta Group, Central India, with a review of Lameta group localities. *Annals of the Carnegie Museum of Natural History* **51**, 405–22.

BONAPARTE, J. F. 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie* **72**, 247–89, 325–86.

BONEHAM, B. F. W. & WYATT, R. J. 1993. The stratigraphical position of the Middle Jurassic (Bathonian) Stonesfield Slate of Stonesfield, Oxfordshire, UK. *Proceedings of the Geologists' Association* **104**, 123–36.

BROCHU, C. A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Memoir of the Society of Vertebrate Paleontology* **7**, 1–138.

BRUNER, H. L. 1907. On the cephalic veins and sinuses of reptiles, with description of a mechanism for raising the venous pressure in head. *American Journal of Anatomy* **7**, 1–117.

BUCKLAND, W. 1824. Notice on the *Megalosaurus* or great fossil lizard of Stonesfield. *Transactions of the Geological Society of London* **2**, 390–96.

BUFFETAUT, E., PENNETIER, G. & PENNETIER, E. 1991. Un fragment de mâchoire de *Megalosaurus* dans le Callovien supérieur des Vaches Noires (Calvados, France). *Revue de Paléobiologie* **10**, 379–87.

CHARIG, A. J. & MILNER, A. C. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum, Geology Series* **53**, 11–70.

CHATTERJEE, S. & ZHENG, Z. 2002. Cranial anatomy of *Shunosaurus*, a basal sauropod dinosaur from the Middle Jurassic of China. *Zoological Journal of the Linnean Society* **136**, 145–69.

COPE, J. C. W., DUFF, K. L., PARSONS, C. F., TORRENS, H. S., WIMBLEDON, W. A. & WRIGHT, J. K. 1980. A correlation of Jurassic rocks in the British Isles. Part Two: Middle and Upper Jurassic. *Special Report of the Geological Society of London* **15**, 1–109.

CURRIE, P. J. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds. *Canadian Journal of Earth Sciences* **2**, 1643–58.

CURRIE, P. J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology* **5**, 576–91.

CURRIE, P. J. 1997. Braincase anatomy. In *The Encyclopedia of Dinosaurs* (eds P. J. Currie and K. Padian), pp. 81–5. New York: Academic Press.

CURRIE, P. J. & CARPENTER, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* **22**, 207–46.

CURRIE, P. J. & ZHAO, X.-J. 1993*a*. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences* **30**, 2231–47.

CURRIE, P. J. & ZHAO, X.-J. 1993*b*. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinijiang, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2037–81.

DAY, J. J. & BARRETT, P. M. 2004. Material referred to *Megalosaurus* (Dinosauria: Theropoda) from the Middle Jurassic of Stonesfield, Oxfordshire, England: one taxon or two? *Proceedings of the Geologists' Association* **115**, 359–66.

DENDY, A. 1909. The intracranial vascular system of *Sphenodon*. *Philosophical Transactions of the Royal Society of London* **B 200**, 403–26.

EUDES-DESLONGCHAMPS, E. 1837. Mémoire sur le *Poekilopleuron bucklandii*, grand saurien fossile, intermédiaire entre les crocodiles et les lézards, découvert dans les carrières de la Maladrerie, près Caen, au mois de juillet 1835. Caen: A. Hardel, 112 pp.

GALTON, P. M. 1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. I. Two complete skulls from Trossingen/Württ. with comments on the diet. *Geologica et Palaeontologica* **18**, 139–71.

GALTON, P. M. 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. II. All the cranial material and details of soft-part anatomy. *Geologica et Palaeontologica* **19**, 119–59.

GALTON, P. M. 1988. Skull bones and endocranial casts of stegosaurian dinosaur *Kentrosaurus* Hennig, 1915 from Upper Jurassic of Tanzania, East Africa. *Geologica et Palaeontologica* **22**, 123–43.

GALTON, P. M. 1989. Crania and endocranial casts from ornithopod dinosaurs of the families Dryosauridae and Hypsilophodontidae (Reptilia: Ornithischia). *Geologica et Palaeontologica* **23**, 217–39.

GALTON, P. M. 1990. Basal Sauropodomorpha – Prosauropoda. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 320–44. Berkeley: University of California Press.

GALTON, P. M. & UPCHURCH, P. 2004. Prosauropoda. In *The Dinosauria. Second Edition* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 232–58. Berkeley: University of California Press.

GAUTHIER, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Science* **8**, 1–55.

GLUT, D. F. 1997. *Dinosaurs. The Encyclopedia.* London: McFarland & Co., Ltd., 1076 pp.

GOW, C. E. 1990. Morphology and growth of the *Massospondylus* braincase (Dinosauria, Prosauropoda). *Palaeontologia Africana* **27**, 59–75.

GOW, C. E., KITCHING, J. W. & RAATH, M. A. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for Palaeontological Research. *Palaeontologia Africana* **27**, 45–58.

HAY, O. P. 1909. On the skull and the brain of *Triceratops*, with notes on the brain-cases of *Iguanodon* and *Megalosaurus*. *Proceedings of the United States National Museum* **36**, 95–108.

HE, X., LI, K. & CAI, K. 1988. [Sauropod dinosaur (2) *Omeisaurus tianfuensis*]. In *The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan*, vol. 4, pp. 1–143. Chengdu: Sichuan Publishing House of Science and Technology.

HOLTZ, T. R. JR. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* **68**, 1100–17.

HOLTZ, T. R. JR. 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia* **15**, 5–61.

HOLTZ, T. R. JR., MOLNAR, R. E. & CURRIE, P. J. 2004. Basal Tetanurae. In *The Dinosauria. Second Edition* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 71–110. Berkeley: University of California Press.

HOPSON, J. A. 1979. Paleoneurology. In *Biology of the Reptilia, vol. 9A* (eds C. Gans, R. G. Northcutt and P. Ulinsky), pp. 39–146. London: Academic Press.

HUENE, F. VON. 1906*a*. Ueber das Hinterhaupt von *Megalosaurus bucklandi* aus Stonesfield. *Neues Jahrbuch fuer Mineralogie, Geologie und Palaeontologie* **1906**, 1–12.

HUENE, F. VON. 1906*b*. Ueber die Foramina der Carotis interna und des Hypoglossus bei einigen Reptilien. *Centralblatt fuer Mineralogie, Geologie und Palaeontologie* **1906**, 336–8.

HUENE, F. VON. 1906*c*. Ueber die Dinosaurier der Aussereuropaeischen Trias. *Geologische und Palaeontologische Abhandlungen* (n. s.) **8**, 97–156.

HUENE, F. VON. 1907–08. Die Dinosaurier der europaeischen Triasformation mit Berucksichtigung der ausereuropaeischen Vorkommnisse. *Geologische und palaeontologische Abhhandlungen, Supplement* **1**, i–xii, 1–419.

HUENE, F. VON. 1926. The carnivorous Saurischia in the Jura and Cretaceous formations principally in Europe. *Revista del Museo de la Plata* **29**, 35–114.

HUENE, F. VON. 1927. Sichtung der Grundlagen der Jetzigen Kenntnis der Sauropoden. *Eclogae Geologicae Helvetiae* **20**, 444–70.

HUENE, F. VON. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* **4**, 1–361.

JANENSCH, W. 1935–36. Die Schaedel der Sauropoden *Brachiosaurus, Barosaurus* und *Dicraeosaurus* aus den Tendaguruschichten Deutsch-Ostafrikas. *Palaeontographica Supplementband* **7**(2), 145–298.

JANENSCH, W. 1936. Ueber Bahnen von Hirnvenen bei Saurischiern und Ornithischiern, sowie einigen anderen fossilen und rezenten Reptilien. *Palaeontologische Zeitschrift* **18**, 181–98.

JUSSIAUME, C. 1998. Depuis 165 millions d'années… le dinosaure dormait dans la pierre de Caen. *Liberté de Normandie – Le Bonhomme libre* **8853**, 22.

KNOLL, F., BUFFETAUT, E. & BÜLOW, M. 1999. A theropod braincase from the Jurassic of the Vaches Noires cliffs (Normandy, France): osteology and palaeoneurology. *Bulletin de la Société géologique de France* **170**, 103–9.

KNOLL, F. 2002*a*. Nearly complete skull of *Lesothosaurus* (Dinosauria: Ornithischia) from the Upper Elliot Formation (Lower Jurassic: Hettangian) of Lesotho. *Journal of Vertebrate Paleontology* **22**, 238–43.

KNOLL, F. 2002*b*. New skull of *Lesothosaurus* (Dinosauria: Ornithischia) from the Upper Elliot Formation (Lower Jurassic) of southern Africa. *Geobios* **35**, 595–603.

KURZANOV, S. M. 1976. Brain case structure in the carnosaur *Itemirus* n. gen. and some aspects of the cranial anatomy of dinosaurs. *Paleontological Journal* **10**, 361–9.

LAPPARENT, A. F. DE & LAVOCAT, R. 1955. Dinosauriens. In *Traité de Paléontologie, vol. 5* (ed. J. Piveteau), pp. 785–962. Paris: Masson et Cie.

LAURANT, S. 1999. Le dinosaure "*Poekilopleuron*" resurgit de l'histoire. *La Croix* **35324**, 8.

LEAL, L. A. & AZEVEDO, S. A. K. 2003. A preliminary Prosauropoda phylogeny with comments on Brazilian basal Sauropodomorpha. *Journal of Vertebrate Paleontology* **23** (suppl. to no. 3), 32A.

LYDEKKER, R. 1888. *Catalogue of the Fossil Reptilia and Amphibians in the British Museum. Pt. I. Containing the Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria.* London: British Museum (Natural History), 309 pp.

MADSEN, J. H. JR. 1976. *Allosaurus fragilis*: a revised osteology. *Bulletin of the Utah Geological and Mineral Survey* **109**, 1–163.

MADSEN, J. H. JR., MCINTOSH, J. S. & BERMAN, D. S. 1995. Skull and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia: Saurischia). *Bulletin of the Carnegie Museum of Natural History* **31**, 1–115.

MCINTOSH, J. S. 1990. Sauropoda. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 345–401. Berkeley: University of California Press.

MCINTOSH, J. S. & WILLIAMS, M. E. 1988. A new species of sauropod dinosaur, *Haplocanthosaurus delfsi* sp. nov., from the Upper Jurassic Morrison Fm. of Colorado. *Kirtlandia* **43**, 3–26.

NOVAS, F. E. 1994. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology* **13**, 400–23.

NOVAS, F. E. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**, 723–41.

O'DONOGHUE, C. H. 1920. The blood vascular system of the tuatara, *Sphenodon punctatus*. *Philosophical Transactions of the Royal Society of London* **B 210**, 175–252.

OSBORN, H. F. 1912. Crania of *Tyrannosaurus* and *Allosaurus*. *Memoirs of the American Museum of Natural History* **1**, 1–30.

OSTROM, J. H. & MCINTOSH, J. S. 1966. *Marsh's Dinosaurs. The Collections from Como Bluff.* New Haven: Yale University Press, 388 pp.

OWEN, R. 1841. A description of a portion of the skeleton of *Cetiosaurus*, a gigantic extinct saurian occuring in the Oolitic Formation of different parts of England. *Proceedings of the Geological Society of London* **3**, 457–62.

OWEN, R. 1842. Report on British fossil reptiles. Pt. II. *Report of the British Association for the Advancement of Science* **11**, 60–204.

PALMER, T. J. 1979. The Hampen Marly and White Limestone formations: Florida type carbonate lagoons in the Jurassic of central England. *Palaeontology* **22**, 189–228.

PHILLIPS, T. J. 1860. Notice of some sections of the strata near Oxford. No. 1. The Great Oolite in the valley of the Cherwell. *Quarterly Journal of the Geological Society of London* **16**, 115–19.

PHILLIPS, J. 1871. *Geology of Oxford and the Valley of the Thames.* Oxford: Clarendon Press, 529 pp.

PORTMANN, A. 1950*a*. Les organes des sens. In *Traîté de Zoologie* (ed. P.-P. Grassé), Tome **15**, pp. 204–20. Paris: Masson et Cie.

PORTMANN, A. 1950*b*. Système nerveux. In *Traîté de Zoologie* (ed. P.-P. Grassé), Tome **15**, pp. 185–203. Paris: Masson et Cie.

RAATH, M. A. 1985. The theropod *Syntarsus* and its bearing on the origin of birds. In *The Beginning of Birds* (eds M. K. Hecht, J. H. Ostrom, G. Viohl and P. Wellnhofer), pp. 219–27. Eichstätt: Freunde des Jura-Museums.

RAUHUT, O. W. M. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* **69**, 1–213.

RICH, T. H., VICKERS-RICH, P., GIMENEZ, O., CUNEO, R., PUERTA, P. & VACCA, R. 1999. A new sauropod dinosaur from the Chubut Province, Argentina. *National Science Museum Monograph* **15**, 61–84.

RICHARDSON, L., ARKELL, W. J. & DINES, H. G. 1946. Geology of the country around Witney. *Memoirs of the Geological Survey of Great Britain, explanation of sheet* **236**, 1–150.

ROMER, A. S. 1956. *Osteology of the Reptiles.* Chicago: University of Chicago Press, 772 pp.

ROWE, T. & GAUTHIER, J. 1990. Ceratosauria. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 151–68. Berkeley: University of California Press.

SADLEIR, R., BARRETT, P. & POWELL, P. 2004. Anatomy and systematics of *Eustreptospondylus oxoniensis* (Dinosauria: Theropoda): evolutionary implications. *Journal of Vertebrate Paleontology* **24** (suppl. to no. 3), 107A.

SERENO, P. C. 1991. *Lesothosaurus*, "fabrosaurs," and the early evolution of Ornithischia. *Journal of Vertebrate Paleontology* **11**, 168–97.

SERENO, P. C. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* **25**, 435–89.

SERENO, P. C. 2005. Basal sauropodomorph phylogeny: a comparative analysis. *Journal of Vertebrate Paleontology* **25** (suppl. to no. 3), 114A.

SERENO, P. C. & NOVAS, F. E. 1994. The skull and neck of the basal theropod *Herrerasaurus ischigualensis*. *Journal of Vertebrate Paleontology* **13**, 451–76.

SERENO, P. C., WILSON, J. A., LARSSON, H. C. E., DUTHEIL, D. B. & SUES, H.-D. 1994. Early Cretaceous dinosaurs from the Sahara. *Science* **265**, 267–71.

STARCK, D. 1979. Cranio-cerebral relations in recent reptiles. In *Biology of the Reptilia, vol. 9A* (eds C. Gans, R. G. Northcutt and P. Ulinsky), pp. 1–38. London: Academic Press.

STEEL, R. 1970. Saurischia. In *Handbuch der Palaeoherpetologie* (ed. O. Kuhn), part 14, pp. 1–87. Stuttgart: G. Fischer.

STOVALL, J. W. & LANGSTON, W. JR. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *The American Midland Naturalist* **43**, 696–728.

SUES, H.-D., REISZ, R. R., HINIC, S. & RAATH, M. A. 2004. On the skull of *Massospondylus carinatus* Owen, 1854 (Dinosauria, Sauropodomorpha) from the Elliot and Clarens formations (Lower Jurassic) of South Africa. *Annals of Carnegie Museum* **73**, 239–57.

SWINTON, W. E. 1934. *The Dinosaurs: a short History of a great Group of extinct Reptiles.* London: Thomas Murby & Co., 233 pp.

SWINTON, W. E. 1970. *The Dinosaurs.* London: George Allen & Unwin Ltd, 331 pp.

TAQUET, P. & WELLES, S. P. 1977. Redescription du crâne de théropode de Dives (Normandie). *Annales de Paléontologie (Vertébrés)* **63**, 191–206.

TIDWELL, V. & CARPENTER, K. 2003. Braincase of an Early Cretaceous titanosauriform sauropod from Texas. *Journal of Vertebrate Paleontology* **23**, 176–80.

UPCHURCH, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London* **B 349**, 365–90.

UPCHURCH, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society of London* **124**, 43–103.

UPCHURCH, P. 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* **19**, 106–25.

UPCHURCH, P., BARRETT, P. M. & DODSON, P. 2004. *Sauropoda.* In *The Dinosauria. Second Edition* (eds D. B. Weishampel, P. Dodson and H. Osmólska), pp. 259–324. Berkeley: University of California Press.

UPCHURCH, P., BARRETT, P. M. & GALTON, P. M. 2005. The phylogenetic relationships of basal sauropodomorphs: implications for the origin of sauropods. *Journal of Vertebrate Paleontology* **23** (suppl. to no. 3), 126A.

UPCHURCH, P. & MARTIN, J. 2002. The Rutland *Cetiosaurus*: the anatomy and relationships of a Middle Jurassic British sauropod dinosaur. *Palaeontology* **45**, 1049–74.

UPCHURCH, P. & MARTIN, J. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* **23**, 208–31.

WALKER, A. D. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London* **B 248**, 53–134.

WELLES, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica, Abteilung A, Palaeozoologie, Stratigraphie* **185**, 85–180.

WHETSTONE, K. N. & MARTIN, L. D. 1979. New look at the origin of birds and crocodiles. *Nature* **279**, 234–6.

WILSON, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society of London* **136**, 217–76.

WILSON, J. A. & SERENO, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology* **5**, 1–68.

WOODWARD, A. S. 1910. On a skull of *Megalosaurus* from the Great Oolite of Minchinhampton (Gloucestershire). *Quarterly Journal of the Geological Society of London* **66**, 111–15.

WOODWARD, H. B. 1894. The Lower Oolitic rocks of England (Yorkshire excepted). In *The Jurassic Rocks of Britain*, vol. 4, pp. i–xiv, 1–628. London: Geological Survey of the United Kingdom.

YATES, A. M. 2003. A new species of the primitive dinosaur *Thecodontosaurus* (Saurischia: Sauropodomorpha) and its implications for the systematics of early dinosaurs. *Journal of Systematic Palaeontology* **1**, 1–42.

YATES, A. M. 2004. *Anchisaurus polyzelus* (Hitchcock): the smallest known sauropod dinosaur and the evolution of gigantism among sauropodomorph dinosaurs. *Postilla* **230**, 1–57.

YATES, A. M. 2005. The skull of the Triassic sauropodomorph, *Melanorosaurus readi*, from South Africa and the definition of Sauropoda. *Journal of Vertebrate Paleontology* **23** (suppl. to no. 3), 132A.

YATES, A. M. & KITCHING, J. W. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proceedings of the Royal Society of London, Biological Sciences* **270**, 1753–58.

ZHANG, Y. 1988. Sauropod dinosaur (1) *Shunosaurus*. In *The Middle Jurassic Dinosaur Fauna from Dashanpu, Zigong, Sichuan*, vol. 1, pp. 1–89. Chengdu: Sichuan Publishing House of Science and Technology.

ZHENG, Z. 1991. [Morphology of the braincase of *Shunosaurus*]. *Vertebrata PalAsiatica* **29**, 108–18.