A REVIEW OF THE TERRESTRIAL VERTEBRATE FOSSILS OF THE OXFORD CLAY (CALLOVIAN-OXFORDIAN) OF ENGLAND

by

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Summary

Dinosaurians form a rare but important part of the allochthonous fauna of the Oxford Clay of Central England. Their stratigraphic and geographical distribution is assessed. Comparisons of the English Oxford Clay dinosaur fauna are made between slightly younger faunas from Africa and North America. English Callovian dinosaur faunas are shown to have affinities with North America and African faunas, but it is assumed that local "islands" in North West Europe were populated by dinosaurs and that the Oxford Clay dinosaur fauna was locally derived. The history of dinosaur palaeontology in the Oxford Clay is reviewed. This paper is the first attempt to discuss the various Oxford Clay dinosaurs as a composite assemblage.

Introduction

The Oxford Clay of Southern and Eastern England has yielded a few incomplete skeletons of dinosaurs and pterosaurs, including the presence of a varied terrestrial vertebrate fauna on nearby land during the Callovian and Lower Oxfordian. The remains include representatives of most of the major dinosaur orders known to occur in the Jurassic. Sauropods, theropods, ornithopods, anklyosaurs and stegosaurs have all been reported. Rhamphorhynchoid pterosaurs are represented by fragmentary material only, which is nevertheless important for palaeobiogeographical and palaeoecological interpretations.

The distribution of dinosaur skeletons within the Oxford Clay does not appear to be restricted geographically or stratigraphically. Initially it would seem that dinosaurs are more abundant in the Peterborough district where they are restricted to the Lower Oxford Clay, but this is most likely an effect of collector bias, as the early collectors concentrated their efforts in the local brick pits. There is also more exposure of the Lower Oxford Clay than the Middle and Upper Oxford Clays and this too will have biased the data set.

Most of the dinosaurian material held in museums was collected during the latter half of the last century and the early part of this century, almost certainly reflecting the non-mechanical methods used for winning the clay from the pits where the discoveries were made. The widespread introduction of mechanical excavators at the turn of the century led to the destruction of many of the large Oxford Clay vertebrate fossils. The reduction in the size of the labour force in the pits also meant that fewer people were available to collect the fossils. Recent discoveries have been made of Callovian and Oxfordian marine reptiles and fishes (Charig & Horell 1971, Martill 1985, 1987), but vertebrate fossils, though still abundant in the brick pits, are usually very fragmentary. The only dinosaurian specimen to come to light in recent years is a small ornithopod phalanx of uncertain provenance (Martil 1984).

Material examined for this review is held in the following institutions:

SMC, Sedgwick Museum, Cambridge; BMNH, British Museum (Natural History); PCM, Peterborough City Museum, Peterborough, Cambridgeshire; OUM, Oxford University Museum, Oxford.

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History of Discovery of Oxford Clay Dinosauria

A number of early discoveries of fragmentary dinosaur material from the Oxford Clay of Weymouth, Dorset, and the coeval Arigle de Dives, of Normandy, France, were made in the 1850's, although this material was not noticed until 1888 (Lydekker 1888, p. 163, 180). None of this material can be identified satisfactorily to a generic level, and must remain indeterminate. The earliest written account of an English dinosaur referred to the Oxford Clay was by Seeley, who drew attention to a fragment of a femur named *Cryptosaurus eumerus* in a footnote (Seeley 1869, p. 93). The femur was more fully described in 1875 (Seeley 1875, p. 149) and was considered to have affinities with the iguanodonts of the Lower Cretaceous. There is some doubt about the stratigraphic origin of this specimen and Galton (1980) has demonstrated that it probably came from the Ampthill Clay (Upper Oxfordian). It is thought to belong to the ankylosaur family *Nodosauridae*. This specimen need not be considered further here as it clearly does not belong in the Oxford Clay biota.

During 1874, Seeley visited the now famous, but at that time almost unknown, collection of Mr. Alfred Leeds of Eyebury, Peterborough. A detailed account of the visit is given by Leeds (1956, p. 6), and briefly by Seeley himself (1889). The collection, which consisted chiefly of marine reptiles and fishes, also included a few dinosaur bones.

Seeley notified J.W. Hulke at the British Museum (Natural History) of the presence of dinosaurian remains in the collection, but it was not until May 1886 that Hulke visited Alfred Leeds to view the material for himself. Hulke was accompanied by Arthur Smith Woodward, who became a regular visitor to the collection at Eyebury and a good friend of Alred Leeds and his family. The following year Hulke paid a repeat visit to Eyebury to describe the contained dinosaur material (Hulke 1887), but it is interesting to note that Hulke believed the Leeds specimens were collected from the Kimmeridge Clay, despite it being well known that most of the Leeds collection was obtained from the Oxford Clay. There are no local exposures of the Kimmeridge Clay in the Peterborough area. It is possible that Hulke confused the name Kimmeridge with Kellaways, as the Kellaways beds are frequently exposed in the bottoms of the brick pits, and that the confusion found its way into the literature. Woodward described many of the fish from the collection, and one of the more spectacular dinosaur discoveries (Woodward 1905).

Hulke's 1887 paper described the first sauropod remains found in the Callovian of Britain, *Ornithopsis leedsi*. The specimen consisted of parts of an incomplete pelvic girdle, ribs and vertebrae, and was found during the sinking of a well on the east side of Peterborough on the site of the old gas works. Seeley (1889) gave a detailed account of the discovery and described the succession in the well, which if compared with present knowledge of the stratigraphy of this area indicates that the specimen was discovered at the junction between the Kellaways clay and Kellaways sand. The specimen is therefore of Lower Callovian age, probably from the *M. macrocephalus Zone.*

A second dinosaur from the Oxford Clay in Hulke's paper of 1887 was assigned to *Omosaurus*, (= *Dacentrurus*), an armourless stegosaur known from the Kimmeridge Clay of Swindon, Wiltshire. This assignation was probably made because of the confusion of formation names as outlined above. This was the most complete skeleton of a dinosaur to come from the Oxford Clay at that date. The specimen consists of a pelvic girdle, limb bones and parts of the axial skeleton. Described with the specimen were large plate-like bones, then thought to be part of the dermal armour, but which are now known to be from the giant fish *Leedsichthys problematicus* Woodward. However, later discoveries of this dinosaur by Leeds, did indicate the presence of dermal armour including large spines. It was unfortunate that the first specimen did not possess dermal armour including large spines (presumably lost due to taphonomic processes), and even more unfortunate that the specimen was mixed up with *Leedsichthys* bones. This might have been a result of indiscriminate collecting by pit workers rather than by Alfred Leeds, who was almost certainly a meticulous collector.

Alfred Leeds' second stegosaur from Fletton, was undoubtedly a true stegosaur. Described by Nopsca (1911) as *Stegosaurus priscus*, this specimen possessed dermal armour distinct from the material assinged to *Leedsichthys*, and also distinct from the dermal armour of the well known North American *Stegosaurus* from the slightly younger Morrison Formation.

The historical confusion over the Oxford Clay stegosaurs, although complex is less confusing than that of a single limb bone (BMNH R1933) of an ornithopod dinosaur, also from the Leeds collection. A full account of the synonymy of the specimen is given by Galton (1980), but it is interesting to note that after being first described by Lydekker (1889) as *Camptosaurus leedsi*, this specimen has been placed in two different genera and three different families in six papers by three authors. It is now known as *Callovosaurus leedsi*.

Since much of the early material collected by Leeds and other collectors in the Peterborough area was described without comparative material being available for study, it is hardly surprising that the relationships of the specimens has been difficult to establish. The following list indicates all of the valid dinosaur taxa from the English Oxford Clay (see appendix for systematics):

Dinosauria
Saurischia
Cetiosauriscus stewarti Charig
"Ornithopsis" leedsi Hulke
Metriacanthosaurus parkeri (von Huene)
Eustreptospondylus oxoniensis Walker

Ornithischia
Sarcolestes leedsi Lydekker
Lexovisaurus durobrivensis (Hulke)
Callovosaurus leedsi (Lydekker)
Dryosaurus sp.

Origin of the Oxford Clay dinosaur remains

Throughout its outcrop in England, the Oxford Clay is a fully marine deposit as indicated by a super-abundance of marine bivalves and cephalopods. Although some dinosaurs are known to have occasionally entered freshwater, and some forms may have lived much of their lives in or near water, most were terrestrial (Bakker 1971). Moreover the Oxford Clay sea was too deep to allow wading to take place, and land was probably in excess of 50 km from the present outcrop (Ziegler 1982). The dinosaur fossils are therefore allochthonous and their derivation requires explanation.

Terrestrial vertebrate fossils are unusual in marine deposits; most dinosaur remains being found in fluviatile or lacustrine deposits. Dinosaur remains found in the English Oxford Clay probably did not enter the sea directly from land, but were transported into the sea *via* large river systems. Evidence for this is indicted by vast quantities of fossil wood in the Lower and Middle Oxford Clays. The wood was either washed down rivers or drifted from "mangrove" type swamps bordering the sea. Some of the wood is worn indicating prolonged transport with abrasion.

Dinosaurs may have entered rivers to drink and been drowned accidentally, or more likely, became the prey of large crocodiles. Crocodiles are abundant in the Lower Oxford Clay and although adapted for a marine environment (Tresman, 1987), it is quite likely that they also inhabited local river systems (Martill 1984). Two forms of crocodile were abundant in the English Callovian and Oxfordian, *Steneosaurus* which had a long narrow snout typical of many fish eaters, and *Metriorhynchus* which was more massive, and was a cephalopod feeder, but may have been able to take large prey (Martill 1986).

On becoming the prey of a crocodile the dinosaur would be mutilated. Limbs and neck may have been removed from the carcase, and in most cases it is likely that very little of the kill would remain, but it is known that some crocodiles store caches of foód under roots in river banks (Taylor 1987). Occasionally portions of the kill may drift downstream, especially during periods of flood, and may have avoided being scavanged until they reached the sea. Bloated carcases may drift for many days (Schafer, 1972), and many kilometres out to sea. The drifting carcases would be subjected to intense scavenging by marine animals and, as a consequence, only very incomplete skeletons would arrive on the sea floor. During transport scavenging may take place and isolated bones would fall to the sea floor; for this reason terrestrial animals in marine deposits are usually represented by isolated bones or incomplete skeletons.

Only very rarely has a complete articulated dinosaur been found in the Oxford Clay. An almost complete skeleton of *Eustreptospondylus oxoniensis*, a slender carnosaur, was discovered in the Middle Oxford Clay at Wolvercote, Oxfordshire. This specimen clearly entered the sea as a complete, presumably bloated carcase. It is difficult to see how it avoided attack by scavengers, but possibly fewer scavengers were available since marine reptile bones are significantly less abundant in the Middle Oxford Clay than in the Lower Oxford Clay (Martill 1985). If the abundance of bones is representative of the fauna, then the chances of arrival on the sea floor undamaged may have been greater during this period, but the abundance may also have been controlled by the flow regimes of the source rivers.

The drifting process can cause wide dispersal of carcases and the introduction of endemic fauna to foreign areas. The time taken from entering the sea to arrival on the sea floor is dependent on a variety of factors including the size of the carcase and the degree of post-mortem attack. Schafer (1972) has shown seal carcases can drift for more than fifty days. A larger animal may well drift for longer.. During the drifting period a carcase is broken down by bacterial processes, by its own gastric juices and by scavengers, but provided the body wall is not punctured, the build up of decomposition gasses will keep it afloat. In a strong current a carcase may drift for hundreds of kilometres, perhaps even thousands. The English Callovian dinosaur fauna may therefore not be derived from a local land mass, but may be a composite fauna derived from a variety of sources.

Table 1 shows the stratigraphic distribution of Callovian and Lower Oxfordian dinosaurs from England and France. The map in Fig. 1 shows that dinosaurs have been found over most of the outcrop of the Lower Oxford Clay.

Comparisons with other Callovian dinosaur faunas

Although there are no records of European Callovian dinosaur species being found outside Europe, at the generic level there are taxa in common with younger faunas (Late Upper Jurassic) from North America and Africa. Bonaparte (1979) has announced the discovery of Callovian dinosaur faunas in South America, but these are not fully described, and their relationship to the European faunas is as yet unknown.

The stegosaur *Lexovisaurus* from England and France is similar to, and regarded by some authors as a subgenus of *Kentrosaurus* from the Tendaguru Shale (Kimmeridgian) of East Africa (Lavocat 1955; Steel 1969). The ornithopod *Dryosaurus*, well known from both the Morrison Formation (Kimmeridgian) of North America and the Tendagaru Shales (probably Kimmeridgian), has also been reported from the Oxford Clay of Peterborough (Galton 1977a and b). Since the English Callovian specimen is an isolated limb bone the generic assignation may be in doubt. The faunas which contain taxa in common with the Peterborough fauna have been dated as Kimmeridgian, and are hence some thirteen million years younger.

The presence of inter-continental dinosaur genera shows that land links between major continents existed during the Jurassic (Charig 1973; Colbert 1973; Galton 1977a), even during major transgressive episodes such as the Kimmeridgian, and also in the Cretaceous (Suess 1979; Anderton et al. 1980) when the two super continents of Laurasia and Gondwana were undergoing rifting. Even before plate tectonics and continental drift was accepted, the world wide distribution of sauropod dinosaurs prompted Osborn (1931) to discuss the existence of land-bridges between the major continents.

It is possible to examine the similarities between faunas at different taxonomic levels using similarity coefficients. Theoretically there should be a correlation between the level of similarity and the difference in age of the faunas, or if both faunas are of the same age there should be a decrease in similarity with effective distance as evolution takes a different direction in each fauna. If a succession of faunas on different continents is examined there should be a decrease in similarity with time. This approach has been used by a number of authors using Simpson's coefficient of similarity:

$$\frac{c}{n^1} \times 100$$

where c = number of taxa common to both faunas, and n^1 = number of taxa in the smaller of the two faunas.

This simple approach has been used by Charig (1973) and Cox (1973), but Galton (1977a) has further considered the coefficient of difference:

$$1 - \frac{c}{n^2} \times 100$$

where n^2 = number of taxa in larger of two faunas.

Charig (1980) suggests that with the present state of the science and the limited amount of material available comparisons at anything higher than the familiar level are unreliable. The results may also be affected by the classification system used.

I have followed the classification used by Galton (1977b) to compare the English fauna with the Tendaguru and Morrison faunas, but I must stress that the English fauna is very poorly known compared to the two continental faunas. The results can only be used in the most general terms. The Tendaguru and Morrison faunas are taken from Galton (1977b).

Table 1.

AGE	STAGE	BIOZONE	LITHOSTRATIGRAPHY	DINOSAUR SPECIES
UPPER JURASSSIC	LOWER OXFORDIAN	*Cardioceras cordatum*	Upper Oxford Clay	*Eustreptospondylus divesensis* *Metriacanthosaurus parkeri*
		Quenstedtoceras mariae		
MIDDLE JURASSIC	UPPER CALLOVIAN	*Q. Lamberti*	Middle Oxford Clay	*Eustreptospondylus oxoniensis*
		Peltoceras athleta		
	MIDDLE CALLOVIAN	*Erymnoceras coronatum*	Lower Oxford Clay	
		Kosmoceras jason		*Callovosaurus leedsi* *Dryosaurus sp.* *Lexovisaurus durobrivensis* *Sarcolestes leedsi* *Cetiosauriscus stewarti*
	LOWER CALLOVIAN	*Sigaloceras calloviense*	Kellaways Sand	*Ornithopsis leedsi*
		Macrocephalites macrocephalus	Kellaways Clay	
			Upper Cornbrash	

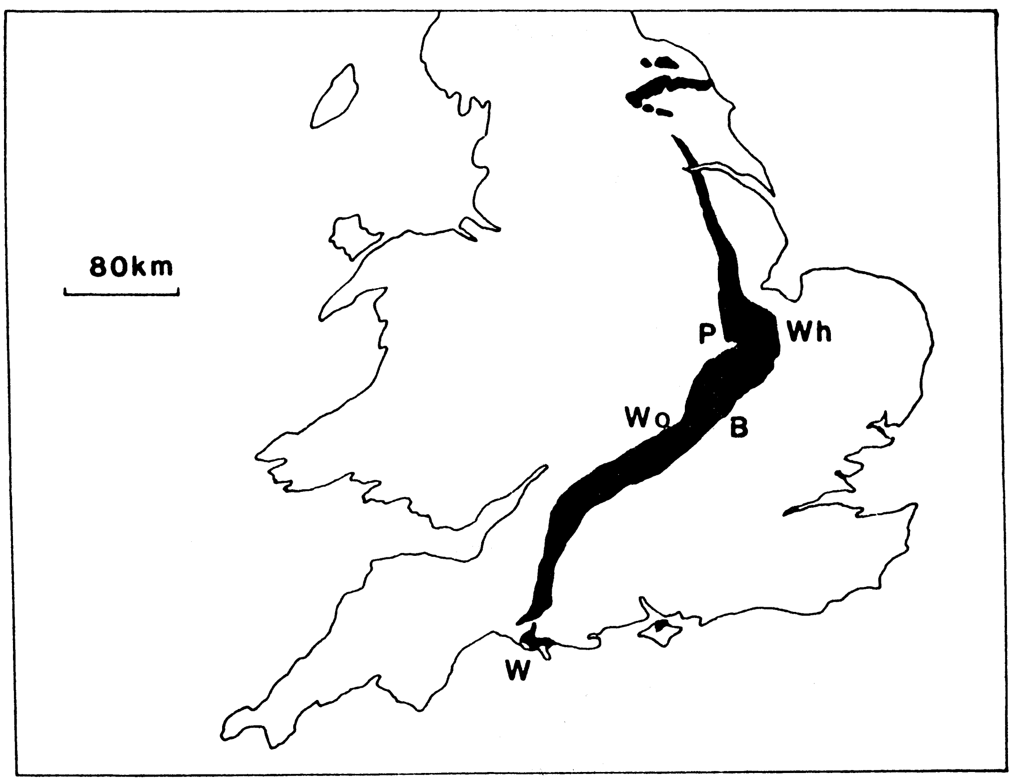

Fig. 1. Outcrop of the Oxford Clay with dinosaur sites indicated. P. Peterborough, B. Bedford, W. Weymouth, Wo. Wolvercote, Wh. Whittlesey.

Morrison Fauna (after Galton 1977b)

Cetiosauridae	*Haplocanthosaurus sp.*
Brachiosauridae	*Brachiosaurus altithorax*
Camarosauridae	*Camarosaurus sp.*
Apatosauridae	*Apatosaurus ajax*
Diplodocidae	*Barosaurus lentus*
	Diplodocus carnegei
Coeluridae	*Coelurus sp.*
	Ornitholestes sp.
Megalosauridae	*Ceratosaurus nasicornis*
	+ a new genus and species
Allosauridae	*Allosaurus fragilis*
Incertae sedis	*Iliosuchus sp.*
	Marshosaurus sp.
Stegosauridae	*Stegosaurus sp.*
Fabrosauridae	*Nanosaurus sp.*
Hypsilophodontidae	*Dryosaurus altus*
	Othnielia
Camptosauridae	*Camptosaurus sp.*

Tendaguru Fauna (after Galton 1977b)

Brachiosauridae	*Brachiosaurus brancas*
Diplodocidea	*Barosaurus africanus*
Dicraeosauridae	*Dicraeosurus*
Titanosauridae	*Torniera*
Coeluridae	*Elaphrosaurus*
Megalaosuridae	*Ceratosaurus (?) roechlingi*
	Megalosaurus (?)
Stegosauridae	*Kentrosaurus*
Hypsilophodontidae	*Dryosaurus lettow-vorbecki*

European Callovian Fauna (after various authors)

Cetiosauridae	*Ornithopsis (?) leedsi*
Diplodocidae	*Cetiosaursicus stewarti*
Megalosauridae	*Eustreptospondylus oxoniensis*
	Metriacanthosaurus parkeri
Stegosauridae	*Lexovisaurus (Kentrosaurus) durobrivensis*
Nodosauridae	*Sarcolestes leedsi*
Hypsilophodontidae	*? Dryosaurus sp.*
Camptosauridae	*Callovosaurus leedsi*

Morrison/European

	Families	*Genera*
European Fauna N_1	7	8
Morrison Fauna, N. America N_2	12	18
Taxa in common C	6	1
Coefficient of similarity	85.7%	12.5%
Coefficient of difference	57.1%	94.4%

Tendaguru/European

	Families	*Genera*
European Fauna N_1	7	8
Tendaguru Fauna, E. Africa N_2	8	9
Taxa in common C	4	2
Coefficient of similarity	57.1%	25%
Coefficient of difference	55.5%	81.1%

Similarity coefficients at the family level between the continental dinosaur faunas of the Morrison Formation and the Tendaguru Shales with the European Oxford Clay allochthonous fauna show that there are stronger affinities between the North America Morrison fauna (app. 85%) than with the African Tendaguru fauna (app. 57%). Galton (1980) has suggested that the strong similarity between Morrison and Tendaguru faunas indicates that the African and North American continents were connected during the Middle and Upper Jurassic, but that the connection was probably through South America. Palaeogeographic reconstructions of the continental positions during the Middle and Upper Jurassic show the Oxford Clay epicontinental sea to be approximately mid-way between the two continents. It is likely that dinosaur carcases could have drifted from rivers draining either continent, but the greater similarity between the Oxford Clay fauna and the North American fauna favours derivation from North America. European massifs were presumably populated by dinosaurs, so it is not unlikely that the Oxford Clay fauna may be locally derived, (figure 2). If European massifs were populated with dinosaur faunas then connections must have existed with either Africa or North America at times of world wide marine regression.

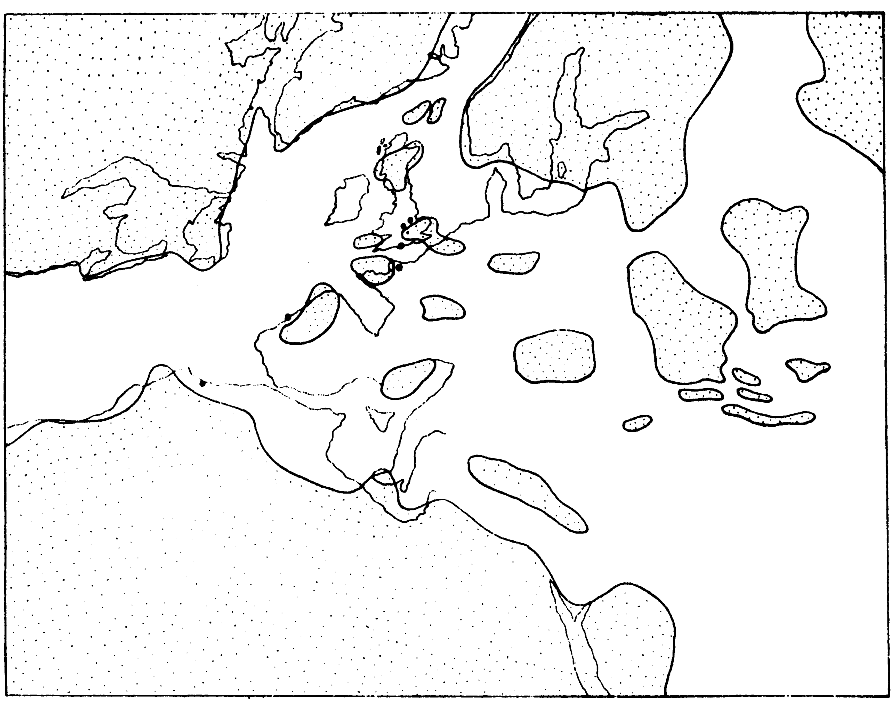

Fig. 2. Palaeogeographic reconstruction of North Africa and Europe during Callovian times. Dots indicate dinosaur localities.

Callovian dinosaur faunas world-wide

Several isolated dinosaur discoveries have been made in Normandy, France, from beds coeval with and in similar facies to the Oxford Clay. The marine reptile fauna of these beds does not differ from that recorded from the Lower Oxford Clay of England (Hoffstetter & Brun 1958, p. 70), and the dinosaur fauna contains some similar elements, including the stegosaur *Lexovisaurus durobrivensis*. But there are differences; no sauropods have been recorded, and a theropod, although closely related, belongs to distinct genus and species, *Piveteausaurus divesensis*.

Worldwide there are very few dinosaur sites that can be definitely dated as Callovian. Thulborn (1972) indicated the presence of a small ornithischian dinosaur *Alcodon kuehnei*, in the Upper Callovian of Pedrogoa, Portugal. But this animal is only known by its teeth, and its relationship with other Callovian dinosaurs is uncertain.

Isolated sauropod vertebrae from the North of Morocco have been dated as Middle Callovian (Lapparent & Lucas 1957). The poorly dated dinosaur faunas from the High and Middle Atlas mountains of central Morocco may also be of Callovian age, in contradiction to recent workers (Monbaron 1980, Monbaron & Taquet 1981) who used the dinosaurs as evidence for a Bathonian age for these beds. The great thickness of fluvio-deltaic red beds in the High Atlas, especially in the Tilouguit basin (600–700 m) may indicate that the Callovian is also included within the sequence.

Dinosaurs have also been reported from the Callovian of Patagonia, Argentina (Bonaparte 1981). There are no genera common to the European Callovian dinosaur faunas, but Bonaparte (1981) has suggested some similarities between the Argentinian sauropod *Patagosaurus fariasi* and *Cetiosaurus leedsi* (= *Cetiosauriscus leedsi*, Bonaparte *pers. com.*)

The Xiaoshaximiao Formation of the Sichuan basin, China, is dated as Bathonian to Callovian, and has yielded a rich fauna of sauropods, *Datousaurus* and *Shunosaurus*, and the stegosaur *Huayangosaurus*. Benton (1985) has indicated that there are similarities between the Chinese sauropods and the English *Cetiosaurus*, but *Cetiosaurus* is not well known. A small ornithopod, *Xiaosaurus*, and a carnosaur, *Xuanhanosaurus*, have also been reported.

Pterosauria

Pterosaur remains are extremely rare in the Oxford Clay and have been reported on only three occasions. The earliest record is that of Phillips who figures a phalanx and a femur of *Rhamphorhynchus bucklandi* (Phillips 1871, plate 12, Figs. 29–33). These specimens, OUM J28533 and J28534 were found at St. Clements, Oxford, probably in the Middle Oxford clay.

Lydekker (1890) recorded the second occurrence of a pterosaur from the Oxford Clay of St. Ives, Huntingdonshire, now Cambridgeshire, which he assigned to the genus *Rhamphorhynchus* under the new name of *R. Jessoni*. This specimen, BMNH R.4759 (Wellnhofer 1978), is almost certainly from the Middle Oxford Clay. Lydekker believed this represented the first pterosaur to be discovered in the Oxford Clay, but he was evidently unaware of Phillips (1871) earlier discovery. The material includes two cervical vertebrae, a dorsal vertebrae, left innominate and left femur. Lydekker's figure of the femur (Lydekker 1890, p. 430, Fig. 3) appears to be very similar to that figured by Phillips (1871, plate 12, Fig. 32), and the two are probably conspecific.

In an address to the Ealing Naturalist and Microscopists Society, Andrews (1911) notes the presence of *Rhamphorhynchus* in the Oxford Clay of Peterborough. He was referring to specimens later mentioned by Leeds (1956, p. 76), which were described as being "some insignificant wing-bones". Two individuals are represented; BMNH R.1995 comprising a complete right ulna 10 cm long and broken left and right humeri; and R.4759 a single complete wing bone 14 cm long.

Discussion

Although the Oxford Clay is a fully marine deposit, yielding an abundant fauna of belemnites, ammonities and comparatively abundant marine reptiles, it is clear from the occasional discovery of dinosaur bones and the superabundance of fossil wood that nearby land was populated by abundant and diverse dinosaur faunas.

The dinosaur remains so far discovered in the Oxford Clay are likely to be the remains of prey of large crocodiles or carnivorous dinosaurs. Large crocodiles drag their prey into water to drown and such a process would introduce terrestrial elements into the aquatic environment enabling at least a few mutilated carcases to reach the Oxford Clay basin. Crocodiles are an abundant element of the Peterborough fauna, although the forms *Steneosaurus* and *Metriorhynchus* were fully adapted to the marine environment (Tresman 1987a & b) more terrestrially adapted crocodiles may have inhabited local rivers and estuaries.

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Appendix

Systematics of valid dinosaur taxa from the English Oxford Clay

Class DINOSAURIA Bakker & Galton 1974
Subclass ORNITHISCHIA (Seeley 1888)
Order STEGOSAURIA (Marsh 1877)
Family STEGOSAURIDAE Marsh 1880
Subfamily STEGOSAURINAE Nopsca 1917
Genus *LEXOVISAURUS* Hoffstetter 1957
Lexovisaurus durobrivensis (Hulke 1887)

1887	*Omosaurus durobrivensis* Hulke, p. 699, Fig. 2
1901	*Omosaurus leedsi* Seeley, Huene, *nomen nudem* p. 718
1911	*Stegosaurus priscus* Nopcsa, p. 109–114, 145–153 Figs. 1–9
1911	*Stegosaurus durobrivensis* (Hulke), Nopcsa, p. 148, 153
1933	*Omosaurus durobrivensis* Hulke, Arkell, p. 358
1956	*Omosaurus durobrivensis* Hulke, Leeds, p. 104
1957	*Lexovisaurus durobrivensis* (Hulke), Hoffstetter, p. 537–547
1958	*Lexovisaurus durobrivensis* (Hulke), Hoffstetter & Brun, p. 76
1969	*Lexovisaurus durobrivensis* (Hulke), Steel, p. 49
1973	*Lexovisaurus durobrivensis* (Hulke), White, p. 138
1980	*Lexovisaurus durobrivensis* (Hulke), Galton, p. 825 Fig. 1Q–U
1980	*Lexovisaurus durobrivensis* (Hulke), Galton, et. al. p. 39, Plate 1 Figs. 1–5
1981	*Lexovisaurus* (Nopcsa, 1911 as *Stegosaurus priscus*) Galton, p. 40
1983	*Lexovisaurus durobrivensis* (Hulke), Galton, p. 142
1983	*Lexovisaurus durobrivensis* (Hulke), Galton & Powell, p. 221, Plate 1, Figs. 22–24

Holotype BMNH R. 1989

Other material. BMNH R. 584, R. 1989–92, R, 3167; PCM R. 177; SMC J. 46875, J. 46879.

Diagnosis Armoured stegosaur in which the dorsal armour consists of alternating plates along the back and spines towards the tail. There is a pair of parasacral spines. The femur exceeds the ilium in length. The skull is not known.

Discussion Stegosaurs known only by fragmentary skeletons and isolated spines. The genus has close affinities with the East African *kentrosaurus* Hennig, and possibly with the Chinese *Huayangosaurus*.

Early confusion over the name *Omosaurus*, and the referring of British stegosaurs to both *Omosaurus, Dacentrurus* and *Stegosaurus* has resulted in a long synonymy. Marsh (1889) showed that *Omosaurus* was almost indestinguishable from *Stegosaurus*, and pointing out that *Omosaurus* was pre-occupied by a phytosaur (Leidy 1856), suggested that all British *Omosaurus* material be referred temporarily to *Stegosaurus*.

A second "Stegosaur" obtained by Henry Keeping was described as *Stegosaurus sp.* by Huene (1901), but in his discussion he suggests that material had been referred to *Omosaurus leedsi* by Seeley. In the Sedgwick Museum catalogue (unpublished) it is pointed out that Huene made this assumption on a museum label in Seeley's handwriting. *O. leedsi* is therefore a *nomen nudum*.

The problem of the name *Omosaurus* occurred again, when Lucas (1902) considered the type material of *Omosaurus* from the Kimmeridge Clay of Swindon to be distinct from the North American *Stegosaurus* because it lacked dermal armour. Lucas proposed the new name of *Dacentrurus* for stegosaurs without dermal armour. This new name was never used for Oxford Clay stegosaurs as the third specimen was found with dermal armour. Had this specimen not been found, the first specimen may well have been referred to *Dacentrurus*. The first specimen, although its so called dermal armour was shown to be from a fish, was considered to be conspecific with the third specimen. Later however, Hoffstetter (1957), considered the dermal armour described by Huene (1901) in the second specimen also to be from the giant fish *Leedsichthys*. I have examined this material and agree with Hoffstetter, but it is not possible with present knowledge of *Leedsichthys* to positively identify the bones.

The differences in the structure of the dermal armour mentioned above were not used to separate Oxford Clay stegosaurs from their North American cousins until 1957. Hoffstetter reviewed both English and French Callovian stegosaur material and synonymised *S. priscus* Nopsca with O. *durobrivensis* Hulke. He erected for their inclusion the new genus *Lexovisaurus* (Hoffstetter, 1957), (*Figs. 3 + 4 this paper*).

Locality Peterborough, Cambridgeshire, Bedford, Bedfordshire, doubtfully from Weymouth, Dorset. Aslo known from Argence, France.

Horizon Lower Oxford Clay, Middle Callovian, of England. Most likely Jason zone. Lower Callovian of France, Calloviense zone.

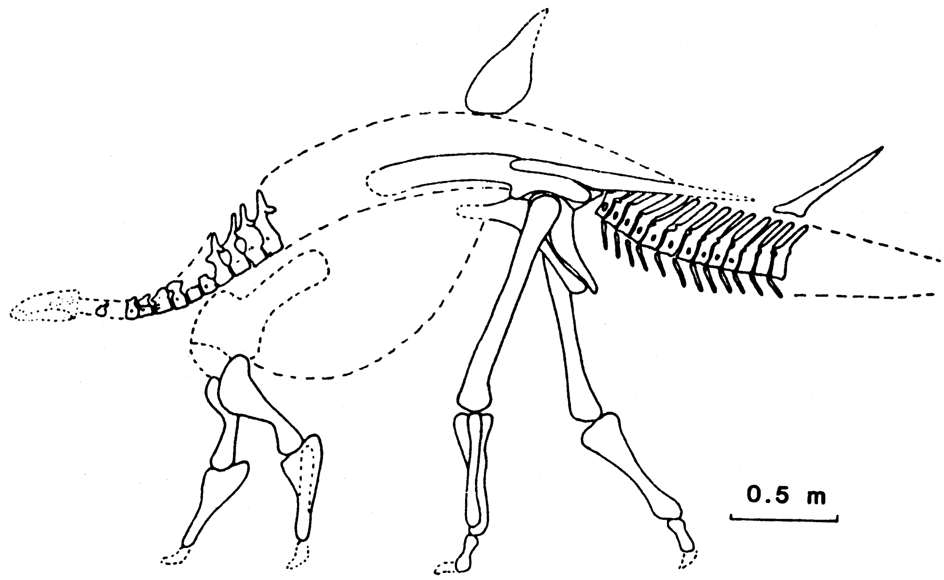

Fig. 3. *Lexovisaurus durobrivensis*. After Galton 1983.

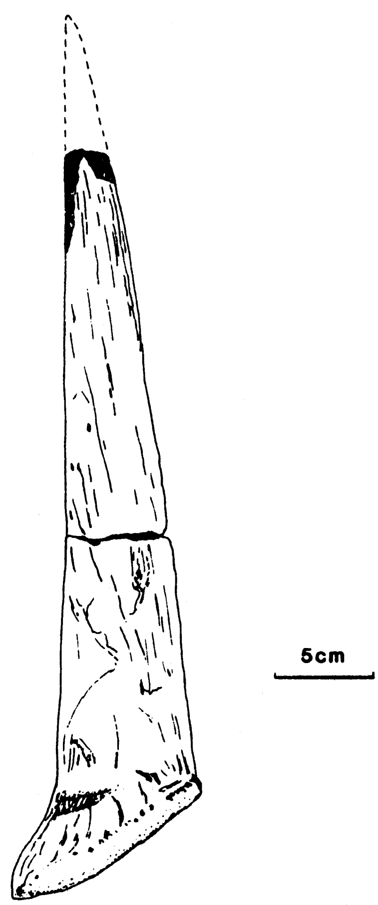

Fig. 4. ?Caudel spine of *Lesovisaurus cf. durobrivensis* drawn from a photograph of PCM R177.

Order ANKYLOSAURIA (Osborn 1923)
Family NODOSAURIDAE Marsh 1980
Genus *Sarcolestes* Lydekker 1893

Sarcolestes leedsi Lydekker 1893

1893	*Sarcolestes leedsi*	Lydekker, p. 286
1933	*Sarcolestes leedsi*	Lydekker, Arkell, p. 358
1955	*Sarcolestes leedsi*	Lydekker, Lapparent & Lavocat, p. 785–962
1956	*Sarcolestes leedsi*	Lydekker, Leeds, p. 35
1969	*Sarcolestes leedsi*	Lydekker, Steel, p. 44, Figs. 15, 4
1973	*Sarcolestes leedsi*	Lydekker, White, p. 148
1980	*Sarcolestes leedsi*	Lydekker, Galton, p. 825, Figs. 1a, b
1980a	*Sarcolestes leedsi*	Lydekker, Galton, p. 486
1983	*Sarcolestes leedsi*	Lydekker, Galton, p. 141, Figs. 1, 2

Holotype BMNH R. 2682. An incomplete left mandible with replacement teeth is the only known specimen of this taxon.

Diagnosis Small teeth extend to anterior end of dentary, short medially projecting process bears symphysis, mechelian canal open, coronoid eminence low. Crown of first dentary tooth laterally compressed with fine denticles on anterior edge, other teeth simple with regular marginal denticles, crowns smooth labially and lingually. There is a dermal plate fused to the lateral surface of the mandible.

Discussion Galton also refers to *Sarcolestes* ? a dermal scute SMC J. 46884, but this specimen was not found associated with the type material and cannot be satisfactorily referred to *Sarcolestes*.

Horizon Lower Oxford Clay, Middle Callovian, probably Jason zone.

Locality Fletton, near Peterborough, Cambridgeshire. White (1973, p. 148) lists Oxford as a locality but this is incorrect.

Order ORNITHOPODA Marsh (1871)
Family CAMPTOSAURIDAE Marsh 1885
Genus *Callovosaurus* Galton 1980

Callovosaurus leedsi (Lydekker 1889)

1889	*Camptosaurus leedsi*	Lydekker, p. 47
1890	*Camptosaurus leedsi*	Lydekker, p. 258, Fig. 61
1901	*Camptosaurus leedsi*	Lydekker, Huene, p. 716
1909	*Camptosaurus leedsi*	Lydekker, Gilmore
1933	*Camptosaurus leedsi*	Lydekker, Arkell, p. 358
1956	*Camptosaurus leedsi*	Lydekker, Leeds, p. 35
1969	*Camptosaurus leedsi*	Lydekker, Steel, p. 16, Figs. 8, 12
1972	*Camptosaurus leedsi*	Lydekker, Galton, p. 466
1975	*Camptosaurus (?) leedsi*	Lydekker, Galton, p. 741, Fig. 2
1980	*Camptosaurus leedsi*	Lydekker, Galton & Powell, p. 418, Fig. 2g
1980	*Callovosaurus leedsi*	Lydekker, Galton, p. 73, Figs. 2, 3
1983	*Callovosaurus leedsi*	(Lydekker), Galton, p. 142

Holotype BMNH R. 1993 A right femur. This is the only known specimen referable to this taxon.

Diagnosis Femur in which the greater trochanter is proportionally narrow, lesser trochanter expanded antero-posteriorly and flattened transversely, distal and unexpanded with shallow anterior intercondylar groove.

Discussion A full summary of the synonymy of *C. leedsi* is given by Galton (1980). Lydekker in referring this specimen to *Camptosaurus* noted that the assignation may be temporary, and pointed out that it was difficult to distinguish from *Camptosaurus* or *Iguanodon prestwichii*, a Kimmeridgian dinosaur which Lydekker placed in the genus *Camptosaurus* later that year (Lydekker 1889, p. 259). Gilmore (1909) considered that *C. leedsi* might be closely allied to the Hypsilophodontidae, and in particular to the genus *Dryosaurus*, a dinosaur which has been tentatively recorded from the Oxford Clay (see below). Galton (1972, 1973) also considered *C. leedsi* to be allied to the Hypsilophodontidae, and also questioned its inclusion in the genus *Camptosaurus*. Galton (1975) and Galton & Powell (1980) referred *C. leedsi* to the ornithopod family Iguanodontidae, but one month later *C. leedsi* was referred to the re-erected family Camptosauridae in the new genus *Callovosaurus* (Galton, 1980).

Horizon Known only from the Lower Oxford Clay, Middle Callovian, probably Jason zone.

Locality Recorded as Peterborough, Cambridgeshire.

Family HYPSILOPHODONTIDAE Dollo 1882
Genus *Dryosaurus* Marsh 1894

Discussion A slender tibia from the Oxford Clay of Fletton, SMC J. 46889, was referred by Galton (1977a) to *Dryosaurus sp.* but later (Galton 1977b, 1980) referred to the same specimen as hypsilophodontid *incertae sedis*. It is clear that a slender built ornithopod dinosaur is represented in the Oxford Clay dinosaur fauna, but the material is inadequate for positive generic assignation.

Subclass SAURISCHIA (Seeley 1888)
Order SAUROPODOMORPHA (Huene 1932)
Infraorder SAUROPODA Marsh 1878
Family DIPLODOCIDAE Marsh 1884
Genus *Cetiosauriscus* Huene 1927

Cetiosauriscus stewarti Charig 1980

1905	*Cetiosaurus leedsi* (Hulke), Woodward, p. 232, Figs. 39–49
1922	*Cetiosaurus leedsi* (Hulke), Huene, p. 86
1922	*Cetiosaurus leedsi* (Hulke), Anon, Plate III
1927	*Cetiosauriscus leedsi* (Hulke), Huene, p. 444
1927	*Cetiosauriscus leedsi* (Hulke), Huene, p. 122
1933	*Cetiosaur[isc]us leedsi* (Hulke), Arkell, p. 358
1956	*Cetiosaurus leedsi* (Hulke), Leeds, p. 36–8, 104
1973	*Cetiosaurus leedsi* (Hulke), White, p. 125
1979	*Cetiosaurus leedsi* (Hulke), Bonaparte, p. 1378
1979	*Cetiosauriscus stewarti* Charig, p. 231, Figs. 13.1, 13.3
1981	*Cetiosauriscus leedsi* (Hulke), Monbaron & Taquet, p. 244

Holotype BMNH R. 3078. A partial skeleton including portions of four dorsal vertebrae, neural spines of the sacrum, four anterior caudal vertebrae, a continuous series of twenty seven middle caudal vertebrae, numerous chevrons, a right scapulo-coracoid, right humerus, right radius and ulna, portions of left and right ilia, left femur, left tibia and fibula, left pes. Three sauropod teeth BMNH R. 3377, may also belong to this individual (see Leeds 1959, p. 38). Woodward (1905) also assigns a series of proximal caudal vertebrae BMNH R. 1967, to this specimen.

Diagnosis Sauropod dinosaur in which the dorsal centra are antero-posteriorly compressed. Caudal vertebrae with straight chevrons anteriorly, becoming boat shaped posteriorly. Humerus relatively short, with thick deltoid crest. Femur long and slender. Teeth spatulate. (*See figures 5 + 6 in this paper*).

Discussion BMNH R. 3078 is perhaps the most important dinosaur discovery to have been made in the Peterborough district. Until 1968 this was the most complete sauropod skeleton known in the British Isles, and contributed much to our knowledge of Middle Jurassic sauropod anatomy. It was erronously assigned to

Cetiosaurus leedsi by Woodward (1905), when it was considered to be conspecific with material described by Hulke (1887) as *Ornithopsis leedsi*. Charig (1981) has demonstrated that R. 3078 cannot be compared with *O. leedsi* as there are no elements common to both specimens. Unfortunately, this point was not recognised by Huene (1927) when he made R. 3078 the type of a new genus *Cetiosauriscus*. This meant that the type specimen of *Cetiosauriscus* was misidentified and was in need of a new specific name. Charig (1981) proposed the name of *C. stewarti*, after the former chairman of the London Brick Company, from whose pits many of the Oxford Clay vertebrates have come.

Berman & McIntosh (1978) and Charig (1981) show that *Cetiosauriscus* is allied to the North American *Diplodocus*, for which they re-erect the family Diplodocidae Marsh 1884 to contain these two and five other sauropod genera. Of the genera within the family Diplodocidae-*Apatosaurus, Barosaurus, Cetiosauriscus, Dicraeosaurus, Diplodocus, Mamenchisaurus* and *Nemegtosaurus:– Cetiosauriscus* is the oldest and considered to be a rather primitive member.

Locality Discovered in 1898 at the New Peterborough Brick Company, No. 1 yard, (Leeds 1956), near Peterborough, Cambridgeshire.

Horizon Lower Oxford Clay, Middle Callovian, Jason or Coronatum zone.

Family CAMARASAURIDAE Cope 1877
Genus *ornithopsis* Seeley 1870

Ornithopsis leedsi Hulke 1877

1887	*Ornithopsis leedsi* Hulke, p. 695, Fig. 1
1888	*Ornithopsis leedsi* Hulke, Lydekker, p. 57
1888	*Pelerosaurus leedsi* (Hulke), Lydekker, p. 242
1888	*Ornithopsis leedsi* Lydekker, Mansel-Pleydell, p. 39
1889	*(Ornithopsis) leedsi* Hulke, Seeley, p. 391–397, Fig. 3
1905	*Cetiosaurus leedsi* (Hulke), Woodward, p. 323
1956	*Ornithopsis leedsi* Hulke, Leeds, p. 35
1980	*Ornithopsis leedsi* Hulke, Charig, p. 242

Holotype BMNH R. 1985–8. Associated pelvic bones and vertebrae. A plaster cast believed to be of one of the type vertebrae is BMNH R. 1716.

Diagnosis Ischium long and slender with long antero-ventral projection. Pubis massive, becoming thickened towards distal end, foramen present proximally.

Locality Site of old gas works, East of Peterborough, Cambridgeshire.

Horizon Almost certainly at the junction of the Kellaways Clay with the overlying Kellaways sand. See Seeley (1889) and Woodward & Thompson (1909).

Discussion There has been much confusion over the nomenclautre of Oxford Clay sauropods. It appears that there are two taxa, based on two specimens, with a number of other isolated bones being referred to one or other of these taxa. If a complete specimen were ever found it may show the two to be congeneric and even conspecific. The following list indicates the whereabouts of all known Oxford Clay sauropod specimens.

Specimen	**Source**	**Institute**
4 caudal vertebrae	Lower Oxford Clay	BMNH R. 1984
Partial skeleton	Lower Oxford Clay	BMNH R. 3078
Pelvic girdle & vertebrae	Base of Kellaways Sand	BMNH R. 1988
Distal caudal vertebrae	Lower Oxford Clay	BMNH R. 1967
3 sauropod teeth	Lower Oxford Clay	BMNH R. 3377
2 dorsal vertebrae (probably pliosaurian)	Lower Oxford Clay	PCM R. 85
worn dorsal centrum	Kellaways Sand	PCM R. 242

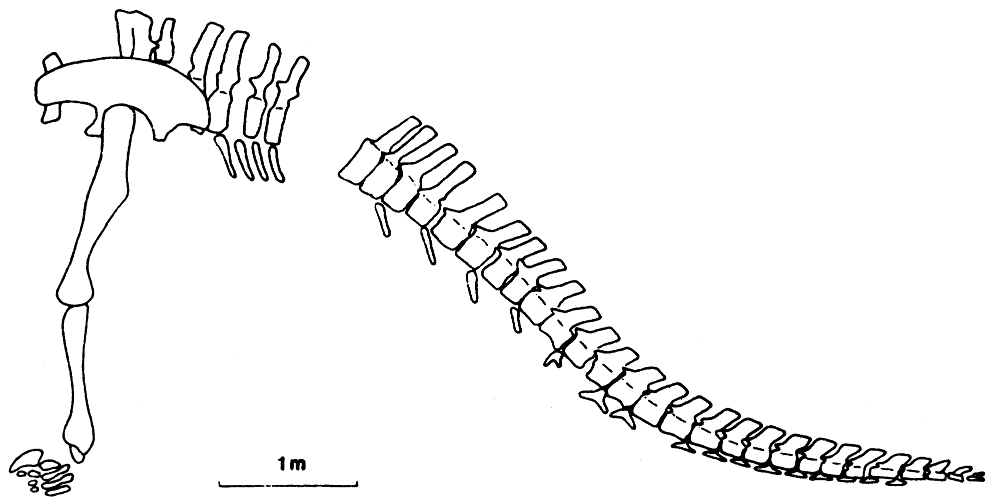

Fig. 5. Rear portion of skeleton of *Cetiosauriscus stewarti*. Based on Woodward (1905).

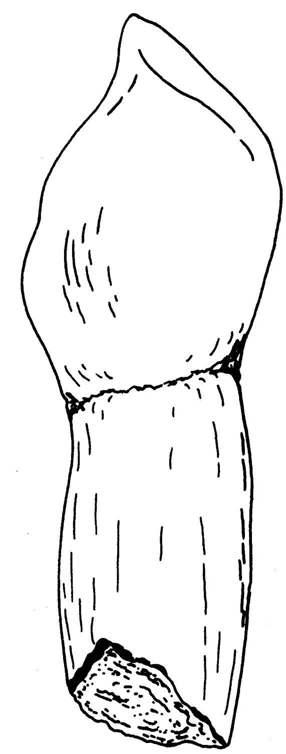

Fig. 6. Spatulate tooth of sauropod dinosaur. Probably referrable to *Cetiosauriscus stewarti* Charig. Lower Oxford Clay, Peterborough. Specimen BMNH R3377. Lingual view. X 2.5.

Order THEROPODA (Marsh 1881)
Infraorder CARNOSAURIA Huene 1920
Superfamily MEGALOSAUROIDEA Walker
Family MEGALOSAURIDAE Huxley 1869
Genus *Eustreptospondylus* Walker 1964

Eustreptospondylus oxoniensis Walker 1964

1871	*Streptopondylus cuvieri* Owen, Phillips, p. 319, Fig. 74
1905	*Streptopondylus cuvieri* Owen, Nopcsa
1905	*Streptopondylus cuvieri* H.V. Meyer, Nopcsa, p. 81
1923	*Streptopondylus cuvieri* Pivetaeu, p. 114
1926	*Megalosaurus cuvieri* (Owen), Huene, p. 35
1932	*Megalosaurus cuvieri* (Owen), Huene, p. ??
1952	*Streptopondylus cuvieri* Owen, Swinton, p. 130
1964	*Eustreptospondylus oxoniensis* Walker, p. 120, Fig. 17e
1970	*Eustreptospondylus oxoniensis* Walker, Steel, p. 32, Fig. 10
1977	*Eustreptospondylus oxoniensis* Walker, Taquet & Welles, p. 191

Holotype OUM J. 13558. An almost complete skeleton, with imperfect skull and teeth.

Diagnosis A large (up to seven metres long), but lightly built carnivorous dinosaur. Vertebrae elongate, cervicals and anterior dorsals strongly opisthocoelus, scapula small, humerus slender, pubis straight and rod-like with terminal expansion. Teeth laterally compressed, keeled with small serrations. See figure 7.

Discussion Confusion over the use of the generic name *Streptospondylus*, and the general fragmentary nature and rarity of megalosaur material, has led to a complicated synonymy for Callovian carnosaurian dinosaurs. A detailed account of the synonymy of *Eustreptospondylus*, and the background to the confusion is given by Walker (1964) and more concisely by Steel (1970).

Locality Summertown Brick Pit, near Oxford, Oxfordshire.

Horizon Middle Oxford Clay, Upper Callovian, Athleta Zone.

Genus *Metriacanthosaurus Walker 1964*

Metriacanthosaurus parkeri (von Huene 1926)

1922	*Megalosaurus parkeri* von Huene, p. 453
1926	*Megalosaurus parkeri* von Huene, p. 477
1926	*Megalosaurus parkeri* von Huene, p. 35–167, Figs. 51–53
1959	*Megalosaurus parkeri* von Huene, Delair, p. 78
1964	*Metriacanthosaurus parkeri* (von Huene), Walker, p. 109, Fig. 16
1970	*Metriacanthosaurus parkeri* (von Huene), Steel, p. 36
1973	*Metriacanthosaurus parkeri* (von Huene), White, p. 150

Holotype OUM J. 12144. Three dorsal vertebrae, four proximal caudal vertebrae, right ilium, portions of left and right ischia, left and right pubes, right femur and proximal part of left femur. The holotype is the only known specimen.

Diagnosis Megalosauridae with neural spines elongate, femur slender with lesser trochanter placed proximally, pubes with expanded foot, cnemial process of tibia with strong upward projection.

Discussion The relationship of *Metriacanthosaurus* is in some doubt. Whilst most workers (Walker 1964, Steel 1970) assign it to the Megalosauridae, the height of the neural spines indicated to von Huene (1926) that it could be an early member of the Spinosauridae. This has not been entirely ruled out by Walker (1964).

Locality Weymouth, Dorset.

Horizon There is doubt as to the exact stratigraphic position of this specimen. It is certainly from the Oxford Clay. An oyster, *Gryphaea dilatata* found adhering to one of the vertebrae has been taken to indicate an Upper Oxford Clay (Lower Oxfordian) age for the specimen.

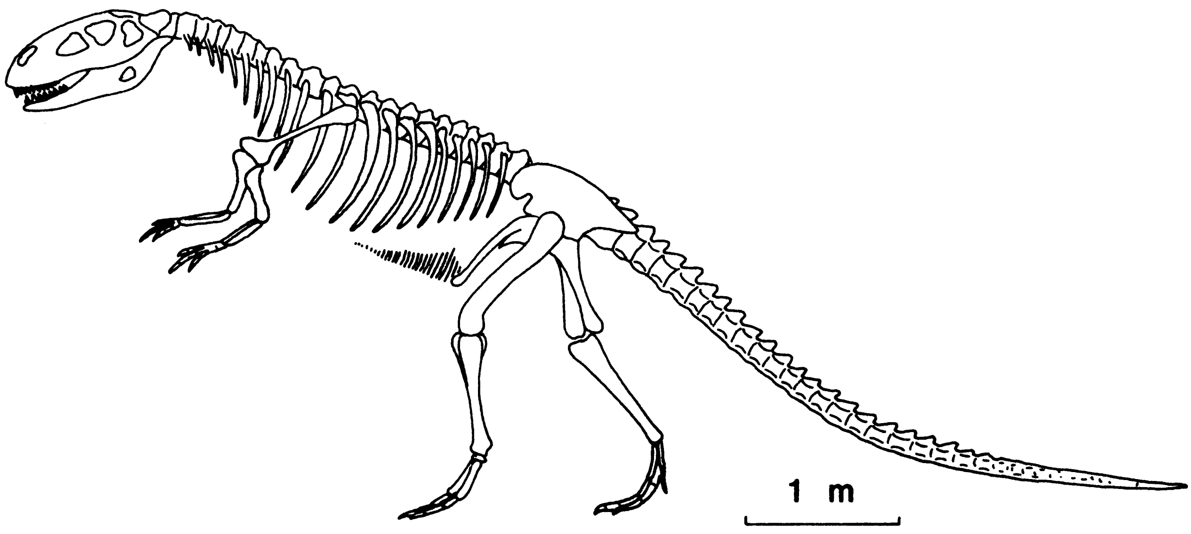

Fig. 7. Skeleton reconstruction of *Eustreptospondylus oxoniensis*. After Steel (1970).

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