THE ANATOMY AND TAXONOMY OF *CETIOSAURUS* (SAURISCHIA, SAUROPODA) FROM THE MIDDLE JURASSIC OF ENGLAND

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ABSTRACT—The Middle Jurassic sauropod *Cetiosaurus* is significant both historically and in terms of its potential phylogenetic relationships. The anatomy and taxonomy of this form are poorly understood because inadequate diagnoses have allowed the proliferation of species names and the referral of very fragmentary specimens. A review of *Cetiosaurus* species indicates that all, except *C. oxoniensis*, are unavailable or nomina dubia. The current type species, *C. medius*, can no longer be regarded as a valid taxon. Previous suggestions that *Cardiodon* is a senior subjective synonym of *Cetiosaurus* cannot be sustained because the two forms do not share any autapomorphies. It is proposed that the generic name *Cetiosaurus* be retained, with *C. oxoniensis* as the new type species. The most complete specimen of *C. oxoniensis* (a partial skeleton from Bletchingdon Station, Oxfordshire) is redescribed and compared with other sauropods. *Cetiosaurus* is rediagnosed on the basis of autapomorphies, including: (1) 'pyramid'-shaped neural spines in posterior cervical and anterior dorsal vertebrae; (2) loss of the spinodiapophyseal lamina on all dorsal vertebrae; (3) anterior chevrons with anteroposteriorly compressed distal shafts; (4) distal caudal centra have a 'tongue'-like projection at the dorsal midline of their articular ends; and (5) a distinct triangular hollow on the lateral surface of the ilium at the base of the pubic process.

INTRODUCTION

Cetiosaurus Owen represents one of the first sauropod genera to be named (McIntosh, 1990; contra Bakker, 1987:42), and has consequently played an important role in the study of sauropods. Although originally considered to be a marine crocodile (Owen, 1841a), the discovery of more complete material in Oxfordshire in 1868 enabled Phillips (1871) to identify this animal as a gigantic, terrestrial, herbivorous dinosaur. The well preserved sauropod material from the Morrison Formation of the U.S.A. (Marsh, 1877, 1878, 1879; Cope, 1877) prompted Marsh (1884, 1888) and Lydekker (1888, 1890) to reinterpret fragmentary European taxa. Both workers concluded that *Cetiosaurus* was a relatively primitive form similar to '*Morosaurus*' (=*Camarasaurus*). Lydekker (1888) created the family Cetiosauridae, and virtually all subsequent systematic classifications of the Sauropoda have utilized this term or the equivalent 'Cetiosaurinae' (Huene, 1927a, b; Romer, 1956, 1966; Steel, 1970; McIntosh, 1989, 1990; Upchurch, 1993, 1994, 1995, 1998). The importance of *Cetiosaurus*, however, is not merely due to its role in the history of sauropod classification. Recent phylogenetic studies have suggested that *Cetiosaurus* is closely related to, but lies outside, the advanced neosauropod clade (Upchurch, 1995, 1998). Thus, this Middle Jurassic British genus may provide insights into the origins of familiar sauropod clades that dominated the Late Jurassic and Cretaceous.

Given the taxonomic and phylogenetic importance of *Cetiosaurus*, it is remarkable that this genus has not been studied in detail since Phillips (1871) and Owen (1875). As a result of this neglect, relatively little useful data are currently available concerning several aspects of *Cetiosaurus* anatomy. For example, Bonaparte (1986a:252) noted that no adequate illustration of the dorsal vertebrae of this genus has ever been published. There are also errors in Phillips (1871) and Owen (1875), relating to the interpretation of *Cetiosaurus* anatomy, that have not been corrected. Finally, the 20th century has witnessed a tremendous influx of information on new sauropods, invalidating the original generic and species diagnoses of *Cetiosaurus*. The goals of this paper, therefore, are to: (1) review

the species-level taxonomy of *Cetiosaurus*; and (2) provide a detailed description of one of the best preserved specimens (a partial skeleton from Bletchingdon Station, Oxfordshire). The phylogenetic relationships of *Cetiosaurus* will be examined in detail in a subsequent publication.

ABBREVIATIONS

Anatomy—**Cd**, caudal vertebra; **Cv**, cervical vertebra; **D**, dorsal vertebra; **Mc**, metacarpal; **Mt**, metatarsal; **S**, sacral vertebra.

Institutions—**BMNH**, The Natural History Museum, London; **CIT**, Geology Museum, Chengdu Institute of Technology, Chengdu; **CMNH**, Carnegie Museum of Natural History, Pittsburgh; **GMNH**, Gunma Museum of Natural History, Gunma, Japan; **HMN**, Humboldt Museum für Naturkunde, Berlin; **LCM**, Leicester City Museum, Leicester; **OUMNH**, Oxford University Museum of Natural History, Oxford; **SCAWM**, Scarborough Woodend Museum, Scarborough; **SMG**, Sedgwick Museum of Geology, Cambridge; **USNM**, United States National Museum of Natural History, Washington D.C.; **ZDM**, Zigong Dinosaur Museum, Zigong.

MATERIAL

Cetiosaurus represents a classic 'wastebasket' taxon that has provided a convenient repository for a large quantity of sauropod remains from Britain and elsewhere. At present, '*Cetiosaurus*' specimens are known from Oxfordshire, Buckinghamshire, Northamptonshire, Rutland, Gloucestershire, Sussex, Yorkshire, the Isle of Wight, Skye, and Morocco (Owen, 1842a, b; Phillips, 1871; Lydekker, 1888; Huene, 1927a, b; Reynolds, 1939; Jones, 1970; Steel, 1970; Monbaron and Taquet, 1981; McIntosh, 1990; Upchurch, 1993, 1995). If all of these specimens genuinely belong to *Cetiosaurus*, the stratigraphic range of this genus would extend from the Bajocian to the Barremian; in reality, however, most of this material is fragmentary and indeterminate. In order to simplify the task of revising the confused taxonomy of *Cetiosaurus*, this paper focuses on the earliest discoveries (mainly from Oxfordshire and Northampton-

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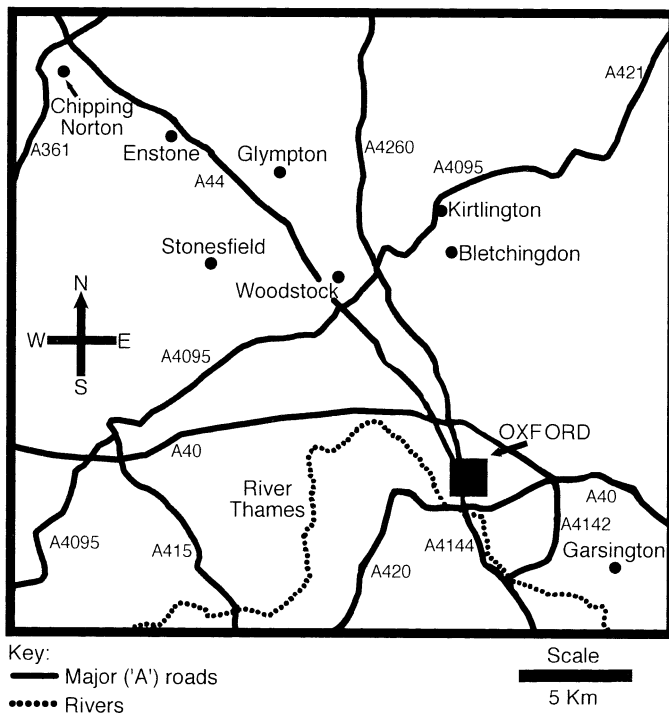— Major ('A') roads
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FIGURE 1. Sketch map showing Oxford and nearby villages.

shire) that encompass the type specimens of the various British species. The remaining material, largely referred to *Cetiosaurus* sp., will be evaluated in subsequent publications.

THE SPECIES-LEVEL TAXONOMY AND NOMENCLATURE OF *CETIOSAURUS*

The complex taxonomy of *Cetiosaurus* is revised in two stages: (1) brief description and identification of the material assigned to each species; and (2) application of the International Commission on Zoological Nomenclature (ICZN) rules to determine which species names should be retained. The species are discussed in the chronological order in which they were published.

Description and Identification

C. hypoolithicus **Owen, 1842a**—This species name was published in an anonymous report of Richard Owen's lecture at the 1841 meeting of the British Association for the Advancement of Science, Plymouth. The type series consists of an unspecified number of vertebrae and limb elements from the 'Inferior Oolite' of Chipping Norton, Oxfordshire (Oxon.) (Fig. 1). These specimens probably represent the Kingdon collection (see below) upon which Owen (1841a) based his original description of *Cetiosaurus*. The only anatomical characters mentioned in the anonymous report are the presence of biconcave vertebral centra and the absence of a central cavity in the limb bones. These features are listed as characteristics of the genus *Cetiosaurus* (Owen, 1841a, 1842a, b) and therefore cannot serve to distinguish *C. hypoolithicus* from *C. epioolithicus* (the latter being a second species named in the anonymous report). Thus, *C. hypoolithicus* was effectively published without adequate description or illustration and is therefore a nomen nudum.

C. epioolithicus **Owen, 1842a**—The type series of this species consists of an unspecified number of vertebrae and meta-

tarsals from White Nab, West Yorkshire, which Owen (1842b) incorporated into the type series of *C. longus* (see below). *C. epioolithicus* was published without any illustration or description (except width and height measurements for one centrum) and is therefore a nomen nudum.

C. brevis **Owen, 1842b**—Owen based *C. brevis* on several vertebrae (BMNH R10390?) from Sandown Bay and Culver Cliff (Barremian; Rawson et al., 1978), Isle of Wight (I.O.W.), and several specimens (BMNH R2133, R2115, R2544–2550) from the Hastings Beds (Valanginian; Rawson et al., 1978) of Cuckfield, Sussex. This species was diagnosed on the basis of a low centrum length:height ratio (e.g., ~0.54 in a dorsal from Culver Cliff). Although this low ratio represents a derived condition present in the anterior caudal centra of eusauropods (Upchurch, 1998), it also occurs in the posterior dorsals of *Iguanodon* (Norman, 1980, 1986). Melville (1849:293), Steel (1970) and Norman (pers. comm., 1999) have demonstrated that all the material assigned to *C. brevis* by Owen (1842b) belongs to *Iguanodon*, with the exception of BMNH R2544–2550 which represent a sauropod. The latter remains were therefore assigned to a new species, *C. conybeari*, by Melville (1849:297). This change of name is not justifiable under ICZN rules since part of the type series of *C. brevis* (i.e., BMNH R2544–2550) remains even after *Iguanodon* specimens are removed. Thus, *C. conybeari* is effectively a junior objective synonym of *C. brevis*.

Owen (1859) referred several vertebrae (BMNH R1010, R28635) to *C. brevis*, but once again these specimens probably belong to *Iguanodon* (Norman, pers. comm., 1999). Lydekker (1888:139–143) assigned other specimens (BMNH R28640, R36559, R36559a–e, and others) to *C. brevis*. This material consists largely of very fragmentary vertebrae and limb elements from the Wessex Formation of Brook, I.O.W., and the Hastings Beds of Cuckfield, Sussex. Most of these specimens are too poorly preserved to be identified precisely and may not even be confidently assigned to the Sauropoda.

BMNH R2544–2550 were found 'a few yards' from a right humerus (BMNH R28626) which is the holotype of *Pelorosaurus* Mantell, 1850. Mantell (1850) believed that the vertebrae and humerus belonged to the same individual and therefore adopted Melville's species name, creating *Pelorosaurus conybearei* (N.B. Mantell corrected Melville's spelling of 'Conybeare', but the former's misspelling remains the correct name under ICZN, Arts. 31a, 33). The humerus (Mantell, 1850:pl. 21) is a relatively slender element like that in several brachiosaurids. For example, the ratio of transverse width of the proximal end to humerus length is ~0.28 in *Pelorosaurus* (Upchurch, pers. obs.), 0.28–0.33 in *Brachiosaurus* (Janensch, 1961:table 3) and 0.32 in *Lapparentosaurus*, whereas this ratio is higher in other sauropods (e.g., 0.39 in *Omeisaurus*, He et al., 1988; 0.52 in *Opisthocoelicaudia*, Borsuk-Bialynicka, 1977). The deltopectoral crest is prominent, a possible synapomorphy of the Brachiosauridae according to Wilson and Sereno (1998), and extends down the proximal third of the lateral margin. The most distinctive feature of BMNH R28626 is that the anconeal fossa (the concave area at the distal end of the posterior surface) is extremely shallow. This concavity is considerably more prominent in all other sauropods except *Lapparentosaurus*. The four anterior caudal vertebrae (BMNH R2544–2547, Mantell, 1850:pls. 24, 25) have short centra (length:height ratios ranging from 0.55–0.74). The articular faces of the centra are subcircular, although they become slightly dorsoventrally compressed in the most distal specimen (BMNH R2547). The centra are amphicoelous, with the anterior face markedly more concave than the posterior one. The lateral surfaces of the centra curve downwards and a little medially, but meet the broad and shallowly concave ventral surface at a distinct angle. On the lateral surface, just below each rib, there is

a small, moderately deep pit, but these do not resemble the 'pleurocoels' present in *Barosaurus* and *Diplodocus* (Hatcher, 1901; Lull, 1919). The chevron facets are axially short and transversely wide, but are not prominent ventrally. The caudal ribs are essentially simple, dorsoventrally flattened, processes that project laterally and a little backwards. At the base of each rib the anterior surface gives rise to two ridges, one extending ventromedially to the top of the centrum, while the other runs strongly upwards to join the lateral face of the arch close to the prezygapophysis. The latter ridge extends along the anterodorsal margin of the rib to its distal end and expands forwards to form an overhanging 'shelf,' as also occurs in *Camarasaurus* (GMNH 101, McIntosh et al., 1996) and *Brachiosaurus* (Riggs, 1904). Between the upper and lower ridges, on the anterior face of the rib base, there is a shallow triangular concavity. The neural arch is fairly low and situated on the anterior half of the centrum. The neural canal is subcircular in the most anterior specimens (BMNH R2544–5), but becomes more vertically elongate in the remaining two caudals. The prezygapophyses are prominent, blunt, anterodorsally directed processes. The neural spines are simple, laterally compressed, plates that project posterodorsally at right-angles to the prezygapophyses. These spines appear to have been very short, but their tops are not preserved. The postzygapophyses are represented by distinct areas at the base of each spine where there is a marked 'in-pinching.' These articular areas join each other ventrally at the top of the neural canal, so that there is no space for the 'hyposphenal' ridge usually found in sauropod anterior caudals (Upchurch, 1995, 1998). This hyposphenal ridge is absent in some titanosauriform sauropods, including *Alamosaurus* (Gilmore, 1946), *Saltasaurus* (Powell, 1992) and *Titanosaurus colberti* (Jain and Bandyopadhyay, 1997), and probably represents a reversal. The chevrons (BMNH R2548–2550) are represented by one large element and two separate proximal rami, all from the anterior end of the tail. The proximal articular surfaces are divided into two facets, one facing dorsally (i.e., perpendicular to the long-axis of the bone) and one directed backwards. As in *Haplocanthosaurus*, *Rayososaurus* and camarasauromorph sauropods, the hemal canal is not 'roofed' dorsally by a bridge of bone connecting the proximal rami (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998). The region immediately below the hemal canal is moderately compressed anteroposteriorly (transverse width divided by axial width = 1.42). The lateral surfaces of the distal shaft are mildly convex anteroposteriorly. The distal shaft rapidly narrows transversely and would probably have terminated in a laterally compressed 'blade.' In lateral view, this shaft curves gently backwards towards the distal end.

It is clear from the above comparisons that *Pelorosaurus conybeari* represents either a brachiosaurid or a basal titanosauriform sauropod, quite separate from *Cetiosaurus oxoniensis* (see below). No true autapomorphies can be observed in the *P. conybeari* material, although the shallow anconeal fossa distinguishes the humerus from those of most sauropods except *Lapparentosaurus*. In other respects, such as caudal morphology, *P. conybeari* and *Lapparentosaurus* display marked differences. Thus, *P. conybeari* probably represents a distinct sauropod taxon, but the criteria by which this taxon can be diagnosed are very unsatisfactory. Such material would probably not merit a new name if found today, but since it already possesses a name, it may be of heuristic value to retain this taxon until more complete material is found.

C. brachyurus **Owen, 1842b**—The type material of *C. brachyurus* consists of single dorsal and caudal centra from the 'Wealden' (Hastings Beds) of Tetham, Kent. This material is probably in the collections of the BMNH, but has not yet been located by the authors. According to Owen (1842b:100) these vertebrae differ from those of *C. brevis* in terms of their pro-
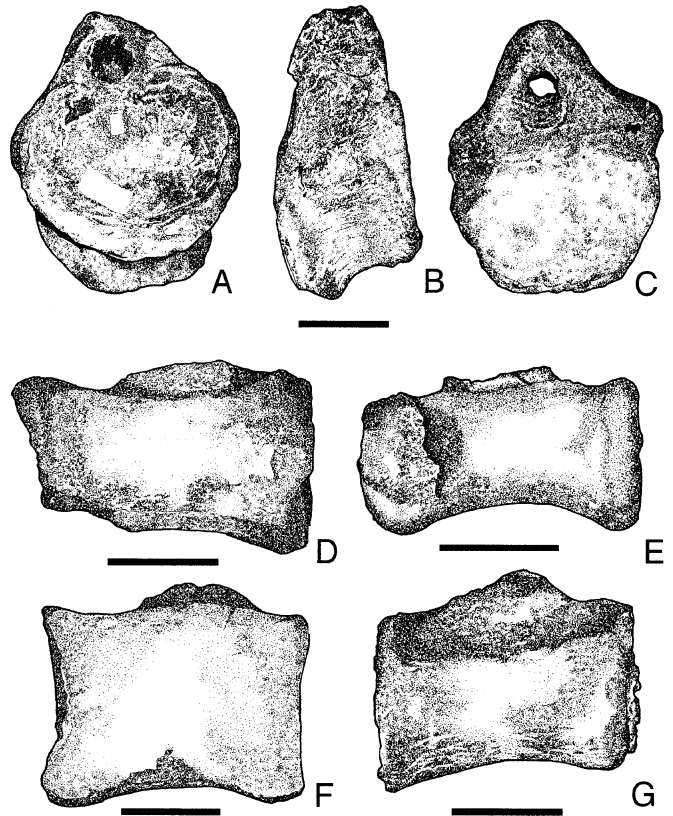

FIGURE 2.   Caudal centra forming part of the type series of '*C. medius*': **A–C**, OUMNH J13693; **D**, OUMNH J13700; **E**, OUMNH J13702; **F**, OUMNH J13697; **G**, OUMNH J13698. **A**, anterior view; **B** and **D–G**, right lateral views; **C**, posterior view. Scale bars equal 50 mm (**A–C** are drawn to the same size).

portions (length:height ratios of the dorsal and caudal are 0.69 and 0.75 respectively), and reduction of the expansion of the articular ends of the dorsal centrum. No other material has since been referred to *C. brachyurus*. Melville (1849) and Steel (1970) regarded these type vertebrae as referable to *Iguanodon*. Even if these specimens do belong to a sauropod, they lack diagnostic features. For example, the proportional differences between *C. brachyurus* and *C. brevis* lie within the range expected for the posterior end of the *Iguanodon* dorsal series and the anterior end of a eusauropod tail. *C. brachyurus* is here regarded as a junior subjective synonym of *Iguanodon*.

C. medius **Owen, 1842b**—In 1825, John Kingdon reported the discovery of large bones at Chapel House, near Chipping Norton, Oxon. (Owen, 1842b:100). At least part of this material was sent to the OUMNH (Buckland, 1836; Phillips, 1871:245). Richard Owen (1841a) named the Kingdon material *Cetiosaurus*, but did not designate any species (but see '*C. hypoolithicus*' above). In 1842, Owen assigned the Kingdon specimens to the new species *C. medius*, which, because of the subsequent problems associated with *C. brevis* and *C. brachyurus*, has generally been accepted as the type species (Steel, 1970; McIntosh, 1990).

The type series of *C. medius* consists of 11 caudal centra (OUMNH J13693–13703; Fig. 2), sacral ribs and a metatarsal (OUMNH J13704–13712), a metacarpal (OUMNH J13748) figured by Lyell (1838:fig. 219), an ungual (OUMNH J13721), part of a dorsal centrum (OUMNH J13877), representing the Kingdon collection, plus other remains from Oxfordshire, Northamptonshire and Buckinghamshire. The absence of adequate

locality data casts doubt on the degree of association of these various remains. Phillips (1871:245), for example, reported that specimens belonging to the Kingdon collection came from more than one site in the vicinity of Chapel House. The 11 caudal centra could potentially belong to a single individual, but this assessment is only supported by the relative size of the centra. These caudals do not form a continuous series. OUMNH J13693 (Fig. 2A–C) is larger than the others, has a short high centrum (length:height ratio <0.70), and possesses caudal ribs (Fig. 2A–C), indicating that it came from the anterior end of the tail. The centrum of OUMNH J13693 is strongly constricted in its middle portion relative to the articular ends. The anterior articular surface is slightly concave, whereas the posterior face is flat at its center and very mildly convex towards its margins. The lateral surfaces of the centrum extend downwards and medially to merge smoothly into the ventral surface. The latter is nearly flat, but bears a broad shallow midline groove which ends posteriorly in a deeper pit between the chevron facets. The latter are weakly developed on the anterior margin of the centrum, but posteriorly they are larger and face downwards and backwards. The caudal ribs are broken at their bases, but appear to have been simple dorsoventrally flattened processes. The neural arch is low and the spine is missing.

The remaining caudal centra (Fig. 2D–G) belong to the middle and distal parts of the tail. Centrum length:height ratios range from ~1.0 in middle caudals to 1.94 in the more distal elements. These specimens are essentially amphicoelous, although OUMNH J13695–6 have only very shallow anterior articular faces, and a distal(?) caudal (OUMNH J13703) has slightly convex articular faces with a deep pit at the center of each. In a few of these specimens the anterior articular face bears a small rounded 'boss' near its center. The area around the periphery of each articular face is flattened, creating a 'bevelled' appearance, as also occurs in *Haplocanthosaurus* and *Cetiosauriscus*. There are no lateral pits or pleurocoels in any of the centra. The centra are only moderately constricted in their middle portions relative to the expanded articular ends, except in OUMNH J13696 where a stronger constriction occurs. The lateral surfaces of these centra are mildly concave longitudinally and more strongly convex dorsoventrally. These surfaces merge smoothly into the ventral face, giving each centrum a subcircular transverse cross-section. OUMNH J13695 has a low horizontal ridge on each of its lateral surfaces, producing a slightly subhexagonal transverse cross-section, as is also seen in *Cetiosaurus glymptonensis*, *C. oxoniensis*, the anterior caudals of *Haplocanthosaurus* and *Cetiosauriscus*, and Cds15-30 in *Omeisaurus* (all based on Upchurch, pers. obs.). In most centra the ventral surface is mildly convex transversely, but in OUMNH J13696 there is a shallow midline groove, as occurs in anterior–middle caudals of the Rutland *Cetiosaurus*, *Camarasaurus*, *Haplocanthosaurus*, *Omeisaurus* (He et al., 1988), and *Vulcanodon* (Cooper, 1984). Chevron facets are well-developed in the more anterior caudals (except OUMNH J13696), but are greatly reduced in more distal elements. No ribs are present on the middle and distal caudals, a derived state uniting Sauropoda (Upchurch, 1998). Neural arches and spines are missing, but the bases of the former occupy approximately half the length of the centrum. The neural arches are shifted a little forwards, but the derived state characterizing the middle caudals of titanosauriform sauropods (where the arch is restricted to the anterior half of the centrum, Salgado et al., 1997; Upchurch, 1998) is absent. Broken surfaces, and the sagittally sectioned OUMNH J13697, indicate that the bone has a very fine 'spongy' texture (Owen, 1841a, 1842b), rather than coarse cancellation.

The portion of 'dorsal centrum' (OUMNH J13877) is in fact an anterior caudal centrum, currently broken into two portions.

This specimen closely resembles the other caudals assigned to *C. medius*, including the 'spongy' internal bone texture.

Nine specimens (OUMNH J13704–13712) come from Chapel House and are labelled as part of the Kingdon collection. This material could form part of the type, but it is not mentioned directly by Owen (1841a, 1842b). Seven of these elements (OUMNH J13704–13710) appear to be the 'metatarsals' and 'phalanges' described by Phillips (1871:287–288), but most are actually sacral ribs. The best preserved sacral rib (OUMNH J13704) is a stout element measuring 210 mm in length. It is expanded at both ends, with roughened convex articular surfaces. The central portion of the rib is constricted, causing the ventral surface to arch upwards in anterior view. The dorsal surface bears a broken longitudinal ridge which represents the base of a sheet of bone which would have originally extended upwards to the underside of the transverse process. This sheet is convex on one surface and concave on the opposite side. The latter surface bears a distinct ridge which extends upwards and sideways from one of the expanded ends. One specimen (OUMNH J13707) is a genuine right(?) metatarsal. It is a robust element which closely resembles the second metatarsals of other sauropods. There is no striated ridge on the dorsolateral margin near the distal end, unlike Mt.II in *Barosaurus* and *Diplodocus* (Upchurch, 1995). The ungual (OUMNH J13721) is a typical laterally compressed sauropod claw, probably from the first digit of the right manus. Its total length from distal tip to the dorsal corner of the proximal articulation is 170 mm. The historically important metacarpal (OUMNH J13748) comes from the Great Oolite of Enstone (Fig. 1), near Woodstock, Oxon. (Lyell, 1838; Owen, 1841a). Although the general size, shape and cross-sectional profiles of this bone indicate that it is a robust sauropod metacarpal, damage to both articular ends means that little further morphological data can be obtained.

The partial skeleton of a single individual from Blisworth, Northamptonshire, consisting of five vertebrae, a scapula, coracoid, sternal plate, and portions of limb bone, was also assigned to *C. medius* by Owen (1842b). Unfortunately, this material seems to have been lost soon after Owen's study, and Phillips (1871) was unable to locate it during his survey of *Cetiosaurus* material. Lydekker (1888), however, lists two anterior caudal centra (BMNH R16090-1) which came from Blisworth. This material was purchased by the BMNH in approximately 1843 and probably represents part of the partial skeleton discussed by Owen (1842b). Both centra are amphicoelous, and lack pleurocoels and ventral excavations. BMNH R16091 possesses damaged rib bases and belonged to the anterior part of the series, whereas R16090 preserves part of the arch and came from near the middle of the tail. Unfortunately, neither specimen could be found during our comprehensive survey of BMNH sauropod specimens.

The material from near Buckingham apparently consisted of a few large caudals and other elements, although only one caudal centrum (OUMNH J13876/1) could be located. This specimen is a plaster cast of a centrum from the anterior-middle part of the tail. The centrum is amphicoelous and lacks pleurocoels and a ventral excavation. The centrum is somewhat dorsoventrally compressed, but this could reflect post-mortem distortion. As in the anterior-middle caudals of several other sauropods (see above), there is a horizontal ridge situated above mid-height on each lateral surface. The posterior chevron facets are large, widely separated from each other, and face downwards and backwards. The caudal ribs are represented by small subcircular broken bases. The neural arch is missing but was slightly shifted towards the anterior margin of the centrum.

The final specimen referred to *C. medius* is a caudal centrum (SMG J46890) from Stony Stratford, Buckinghamshire. In all respects this specimen closely resembles the anterior-middle caudals described above.

In summary, the sacral ribs, metacarpal, and metatarsal described above, resemble equivalent elements in other sauropods but cannot be identified more precisely. The ungual on manual digit I is large in most sauropods, but reduced in *Brachiosaurus* and possibly absent in titanosaurs (Salgado et al., 1997), suggesting that the claw did not come from a titanosauriform. The caudal vertebrae largely possess plesiomorphic states which, at best, can only be used to eliminate them from certain advanced sauropod clades. For example, amphicoelous articulations, and the absence of pleurocoels and deep ventral excavations, tend to exclude assignment of the caudal centra to either the Diplodocidae or Titanosauroidea. No autapomorphic features can be observed on any of the *C. medius* specimens; this taxon is therefore regarded as an indeterminate sauropod. The discovery that the type species of *Cetiosaurus* is based on undiagnostic material creates nomenclatural problems which will be discussed later.

C. longus **Owen, 1842b**—The type series of *C. longus* comprises single dorsal and caudal centra from the Portland Stone (Kimmeridgian; Cope et al., 1980) of Garsington, near Oxford (Fig. 1), and two caudal centra from the same deposit near Thame, Oxon. Unfortunately, the Garsington specimens could not be identified in the OUMNH collections. From Owen's (1842b) description, it seems that the most characteristic feature of the specimens is their relatively high centrum length:height ratios (0.83–1.09). The problem with this character is that it varies along the length of the vertebral column as well as between taxa: it cannot provide an adequate basis for distinguishing genera or species unless nearly complete vertebral series are available. This issue is explored in more detail in the section dealing with *C. glymptonensis*.

One of the Thame specimens (OUMNH J13871) is conceivably a dorsal or sacral centrum, having one mildly convex, and one concave, articular surface. There are no ribs, although the top of the centrum is marked by a horizontal ridge which forms a rounded roughened area towards its anterior(?) end. OUMNH J13872 is mildly amphicoelous and lacks caudal ribs. Both centra have broad flat ventral surfaces and lack pleurocoels. Chevron facets are not well preserved and the arches and spines are missing.

Owen (1842b:102) also assigned to *C. longus* the vertebra and metatarsals from the 'inferior Oolite' of White Nab, West Yorkshire, which were originally named *C. epioolithicus* (Owen, 1842a). The collections of the Scarborough Woodend Museum contain four specimens which potentially represent the material mentioned by Owen (1842a, b). One specimen (SCAWM 10G) is a centrum embedded in a conglomeritic matrix. This vertebra is catalogued as a saurischian cervical, although poor preservation and the presence of matrix make this difficult to establish. The centrum appears to have been a dorsoventrally compressed element and shows some resemblance to the sacral centra of sauropods. The remaining specimens include the proximal end of a right Mt.II (SCAWM 4G) and a left Mt.II broken into two halves (SCAWM 11a/b G). These elements closely resemble the second metatarsals of other sauropods and lack the laterodorsal ridge, near the distal end, which is present in several diplodocoids (Upchurch, 1995). The complete metatarsal has a maximum length of 320 mm, indicating that it came from a relatively large individual. No autapomorphic features could be identified on any of these specimens.

The material assigned to *C. longus* is undiagnostic and this species is therefore regarded as a nomen dubium. McIntosh (1990) referred *C. longus* to *Cetiosauriscus* Huene, creating the new combination *Cetiosauriscus longus*. This new 'species' is regarded as a junior objective synonym of *Cetiosaurus longus* because it cannot be demonstrated that it possesses any of the autapomorphies present in *Cetiosauriscus*.
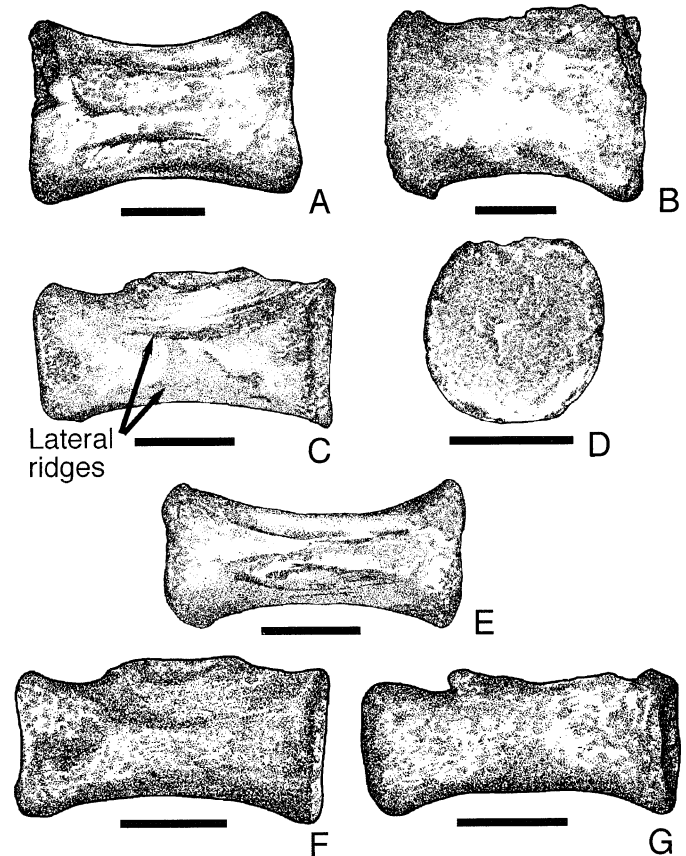

FIGURE 3. Caudal centra forming part of the type series of '*C. glymptonensis*': **A**, **B**, OUMNH J13750; **C–E**, OUMNH J13753; **F**, OUMNH J13754; **G**, OUMNH J13755. **A**, **E**, dorsal views; **B**, ventral view; **C**, **F**, **G**, right lateral views; **D**, anterior view. Scale bars equal 50 mm.

C. conybeari **Melville, 1849**—*C. conybeari* is a junior objective synonym of *C. brevis* Owen (see above).

C. giganteus **Owen in Phillips in Huxley, 1870**—This species name is attributed to Owen by Phillips in a letter published by Huxley (1870:16) (see also Phillips, 1871:247, 290). Owen apparently applied this name to a left sauropod femur (OUMNH J13617) from Gibraltar quarry, near Bletchingdon Station (Anon., 1848; Owen, 1859, 1875; Phillips, 1871). Neither Phillips' letter, nor the rest of Huxley's paper, provide any description or illustration of the specimen. Furthermore, there is no reference to a previous description by Owen. Thus *C. giganteus* is here regarded as a nomen nudum.

C. oxoniensis **Phillips, 1871**—Phillips (1871) did not specify a type specimen for this species, but lists a large series of remains including Owen's original type material of *C. medius*, the partial remains of three individuals from Bletchingdon Station, and several fragmentary specimens from Oxfordshire and Buckinghamshire. The largest individual from Bletchingdon can be diagnosed by autapomorphies and is described in detail after this taxonomic review.

C. glymptonensis **Phillips, 1871**—Phillips (1871:291) based *C. glymptonensis* on nine middle-distal caudal centra (OUMNH J13750–13758; Fig. 3) from Glympton, Oxon. (N.B. due to subsequent boundary changes Glympton was in Northamptonshire in 1871, rather than Oxfordshire as it is today). The major difference between these specimens and those assigned to *C. oxoniensis* is their relative length. Thus, typical *C. oxoniensis* middle caudals have length:height ratios of 1.0–1.5, whereas in *C. glymptonensis* this ratio ranges from 1.33 in larger (more

TABLE 1. Summary of the length:height ratios of sample caudal centra from different sauropod taxa. The length of the centrum excludes the articular convexity in forms with procoelous or opisthocoelous centra. '*' indicates caudals whose position in the tail series has been estimated.

Taxon	Specimen	Cd15	Cd25	Cd35	Cd45
Alamosaurus	USNM 15560 (Upchurch, pers. obs.)	1.50	1.88	—	—
Apatosaurus	CMNH 3018 (Gilmore, 1936)	1.05	1.64	3.44	4.75
Brachiosaurus	HMN Fund no (Janensch, 1950)	0.98	1.38	1.85	1.74
Camarasaurus	GMNH 101 (McIntosh et al., 1996)	0.82	1.19	1.66	2.33
Cetiosauriscus	BMNH R3078 (Upchurch, pers. obs.)	0.99*	1.32*	2.00*	—
Dicraeosaurus	HMN (Janensch, 1929)	1.04	1.70	—	—
Diplodocus	USNM 10865 (Gilmore, 1932)	1.23	2.01	2.28	—
Haplocanthosaurus	CMNH 572 (Hatcher, 1903)	0.98	—	—	—
Mamenchisaurus	CIT holotype (Upchurch, pers. obs.)	0.97	1.50	2.09	—
Omeisaurus	ZDM T5704 (He et al., 1988)	0.88	1.50	1.44	—
Opisthocoelicaudia	ZPAL MgD-I/48 (Borsuk-Bialynicka, 1977)	0.93	1.50	—	—
Shunosaurus	ZDM T5401 (Zhang, 1988)	1.14	1.53	1.83	—

anterior) specimens to 2.17 in more distal elements. This direct comparison should be treated with caution because: (1) neither *C. oxoniensis* nor *C. glymptonensis* have complete caudal series; and (2) sauropod tails display considerable variation in centrum proportions along their length and between taxa. Table 1 summarizes the length:height ratios for selected caudal centra from different taxa. The caudals of *C. glymptonensis* are more elongate than those of most sauropods, but equally high length: height ratios also occur in *Apatosaurus*, *Diplodocus* and *Cetiosauriscus*. Elongate middle caudals may characterize the Diplodocoidea (or a clade within this group), and *C. glymptonensis* may represent an early diplodocoid. The *C. glymptonensis* caudals are amphicoelous and lack pleurocoels and ventral excavations. The chevron facets are not as prominent as those in *C. oxoniensis*. The large, more anteriorly located specimens (e.g., OUMNH J13750, J13751, J13753–5, J13757; Fig. 3C, F, G) have a horizontal ridge situated at approximately two-thirds of the way up the lateral surface of the centrum, and a less prominent ridge at one-third centrum height. In conjunction with the flattened ventral surface, these ridges produce a suboctagonal transverse cross-section. The upper ridge is present in several other taxa (see '*C. medius*' above). The lower ridge is also found in *Cetiosauriscus*, but the latter possesses this feature only on its anterior-middle caudals and definitely lacks the lower ridge on middle caudals equivalent in size and shape to those preserved in *Cetiosaurus glymptonensis*. Thus, *C. glymptonensis* potentially possesses an autapomorphy. This lower ridge, however, is a subtle feature and may have been restricted to only a short part of the tail series. In OUMNH J13750–1, J13757, the neural arch occupies most of the length of the centrum (Fig. 3A), whereas in more distal caudals (e.g., OUMNH J13753–13755) the bases of the neural arches are long (up to 65% of centrum length) and are only slightly shifted towards the anterior end of the centrum (Fig. 3F, G).

Lydekker (1888) referred to *C. glymptonensis* two caudal centra (BMNH R47150, R47412), from the Forest Marble of Cogenhoe, Northamptonshire. The more distal element (BMNH R47150) has a length:height ratio of 2.04 as in many of the type caudals, but there is no other evidence to support Lydekker's assignment.

C. glymptonensis represents a taxon which is distinct from *C. oxoniensis* and all other sauropods. This taxon could be given a new generic name, but the type material is barely adequate for this purpose and it seems better to wait until a more complete specimen is discovered. McIntosh (1990) referred *C. glymptonensis* to *Cetiosauriscus* Huene, creating the new combination *Cetiosauriscus glymptonensis*. The Glympton material does not display any of the autapomorphies of *Cetiosauriscus* and vice versa; the new genus-species combination is therefore regarded as a junior objective synonym of '*Cetiosaurus glymptonensis*'.

C. humerocristatus Hulke, 1874—This species is based on a left humerus (BMNH R44635) from the Kimmeridge Clay (Kimmeridgian), near Weymouth, Dorset (Hulke, 1874:pl. 2). Hulke assigned this specimen to *Cetiosaurus* on the basis of 'general correspondence,' but suggested that a new species was required because the Dorset humerus had more prominent crests than in *C. oxoniensis*. The type humerus is a long slender element measuring 1,350 mm in length. The medial part of the proximal end is damaged, but it appears to be relatively narrow (~28% of shaft length), similar to that in *Brachiosaurus*, *Lapparentosaurus* and *Pelorosaurus conybeari* (see '*C. brevis*' above). The junction between the proximal and lateral surfaces forms the 'right-angle' characteristic of Titanosauriformes (Upchurch, 1999). As Hulke (1874) noted, the deltopectoral crest seems to be relatively prominent in BMNH R44635, but this may represent a synapomorphy of the Brachiosauridae (Wilson and Sereno, 1998). The most unusual feature is that the deltopectoral crest terminates ~44% of the way down the shaft from the proximal end. In most sauropods the deltopectoral crest terminates more proximally, although long crests are seen in many prosauropods, *Apatosaurus louisae* (Gilmore, 1936) and *Alamosaurus* (Gilmore, 1946). Unlike *Pelorosaurus conybeari* and *Lapparentosaurus*, the Dorset humerus has a deep and wide anconeal fossa.

The only other material assigned to *C. humerocristatus* is the proximal end of a pubis (BMNH R49165) from the same horizon and locality as the type humerus (Lydekker, 1888). This pubis lacks the hook-like ambiens process present in many diplodocoids (McIntosh, 1990; Upchurch, 1995, 1998), but in all other respects cannot be adequately distinguished from other sauropods.

In summary, the pubis assigned to *C. humerocristatus* is undiagnostic, but the humerus is potentially distinctive. Elongation of the humerus and distal prolongation of the deltopectoral crest are not, by themselves, autapomorphies: in combination, however, these features make the humerus unique. For the present, '*C. humerocristatus*' is regarded as a distinct taxon referable to the Brachiosauridae. We prefer to wait for more complete material before proposing a new name for this taxon.

C. leedsi (Hulke) Woodward, 1905—Hulke (1887) created the new species *Ornithopsis leedsi* on the basis of fragmentary remains (BMNH R1984–1988) from the Oxford Clay (Callovian; Cope et al., 1980), near Peterborough, Cambridgeshire. Woodward (1905) described a new specimen from near Peterborough (BMNH R3078) and assigned it, and Hulke's original material, to *Cetiosaurus* as *C. leedsi*. Huene (1927a, b) noted marked differences between *C. oxoniensis* and *C. leedsi* (especially BMNH R3078) and assigned the latter to the new genus *Cetiosauriscus*. At present, the referred partial skeleton (BMNH R3078) is known as *Cetiosauriscus stewarti* (Charig, 1993) and may represent a basal diplodocoid (Berman and Mc-

Intosh, 1978; Upchurch, 1995), while the type material (BMNH R1984–1988) has received little attention.

The type material of *C. leedsi* consists of a damaged dorsal centrum (BMNH R1986), four portions of thoracic rib (BMNH R1985), at least four fragmentary anterior caudal vertebrae (BMNH R1984), a distorted and fragmentary ilium (BMNH R1987?), and the right pubis and both ischia (BMNH R1988). The dorsal centrum possesses very large pleurocoels which are separated from each other by a thin midline septum. The anterior articular surface is poorly preserved but was probably strongly convex. The ventral surface is broad and nearly flat. The two best preserved thoracic ribs are nearly complete, although the capitulum and tuberculum are absent. These ribs are strongly curved relative to their length, suggesting that they came from the anterior end of the thoracic series. One rib has a flattened shaft (with the long-axis of the cross-section running lateromedially), while another is more subcircular in cross-section but flattened towards its distal end. No pneumatic openings can be observed in these ribs, but this may be due to poor preservation. The anterior caudal vertebrae have short high centra (length:height ratios <0.70), which lack pleurocoels. Each centrum is amphicoelous and has a subcircular transverse cross-section. The ventral surfaces are broad and shallowly concave. The caudal ribs are simple dorsoventrally compressed processes which project posterolaterally. The neural arches and spines are partially preserved, but are too fragmentary to describe. The ilium cannot yield useful anatomical data because of its fragmentary state. The pubis closely resembles those of other sauropods and lacks a 'hook'-like ambiens process. The length of the ischial articulation of the pubis is approximately 44% of pubis length, a derived state uniting the Camarasauromorpha (Salgado et al., 1997). The ischia have broad distal shafts which are directed strongly downwards as in brachiosaurids (Upchurch, 1995, 1998). The cross-sectional long-axes of the shafts are nearly coplanar, as occurs in *Haplocanthosaurus*, *Rayososaurus* and camarasauromorphs (Upchurch, 1998; Wilson and Sereno, 1998).

No autapomorphic features can be observed in the *C. leedsi* type material. This specimen is regarded as an indeterminate brachiosaurid and the name *C. leedsi* is a nomen dubium.

***C. rugulosus* (Owen) Steel, 1970**—*Cardiodon* Owen (1841b:pl. 75, fig. 7a, b) was named, without species, on the basis of a tooth from the Middle Jurassic Forest Marble of Bradford-On-Avon, Wiltshire. The species name *rugulosus* was added by Owen (1844). The whereabouts of this type specimen is not known. A second and apparently similar tooth crown (BMNH R1527), came from the Great Oolite near Cirencester, Gloucestershire, and was referred to *Cardiodon* by Lydekker (1890:236). Several isolated teeth were found at various localities in Oxfordshire, including one (OUMNH J13597, Fig. 4) from the Bletchingdon Station site which yielded the partial skeletons of *C. oxoniensis*. Consequently, Phillips (1871) referred these teeth to *Cetiosaurus*. The similarities between the *Cardiodon* and *Cetiosaurus* teeth suggested that the two taxa could be synonymous (Owen, 1875; Marsh, 1888), and Lydekker (1890) formalized this view by referring all *Cetiosaurus oxoniensis* material to *Cardiodon*. Subsequent workers largely ignored this synonymy, or accepted it but preferred to use the name *Cetiosaurus*; thus Steel (1970:64) created the new combination *Cetiosaurus rugulosus* based on the original *Cardiodon* tooth.

Before the name *Cardiodon* can replace the more widely used *Cetiosaurus*, three conditions must exist: (1) the teeth assigned to *Cetiosaurus* must genuinely belong to that genus; (2) the teeth assigned to *Cardiodon* and *Cetiosaurus* must share autapomorphic features; and (3) *Cardiodon* must have priority over *Cetiosaurus*. Condition (3) is controversial (compare Bush

FIGURE 4.   An isolated tooth crown (OUMNH J13597) from the Bletchingdon quarry, in labial view. Scale bar equals 10 mm.

[1903] and Steel [1970]), but this debate can be circumvented by considering conditions (1) and (2).

The degree of association between the tooth and the partial skeletons from Bletchingdon Station is difficult to determine. Phillips (1871:fig. 84) provides a site map showing the distribution of bones, but the position of the tooth is not marked. The only support for Phillips' view seems to be: (1) there is no evidence that any other sauropod taxon was present at Bletchingdon; and (2) the morphology of the tooth (see below) is similar to those of *Patagosaurus* (Bonaparte, 1986b) and is consistent with the proposed phylogenetic position of *Cetiosaurus*. There are obvious dangers associated with assuming that this tooth and the partial skeletal material belong to the same taxon. The use of circumstantial evidence (i.e., presence in the same locality and horizon) to group fragmentary sauropod remains together has been severely undermined by the taxonomic history of various Morrison Formation forms (Berman and McIntosh, 1978; McIntosh, 1990). Thus, although the Bletchingdon tooth could belong to *Cetiosaurus*, the evidence supporting this view is weak.

The tooth crown in *Cardiodon* curves somewhat lingually towards its apex. The labial surface is strongly convex mesiodistally and bears a shallow groove extending parallel to its distal margin. Unlike other spatulate sauropod teeth, the lingual surface is also convex, but much less so than the labial. The crown thins towards its tip and is generally relatively short and broad. There are no serrations along the crown margins, and the surface of the enamel is finely wrinkled, a synapomorphy of the Eusauropoda (Wilson and Sereno, 1998). The putative *Cetiosaurus* tooth from Bletchingdon (OUMNH J13597, Phillips, 1871:253, fig. 85) lacks its root and is damaged on its labial surface and along the distal(?) margin. This tooth generally resembles *Cardiodon* in most respects, except that the Bletchingdon specimen has the conventional concave lingual surface (bearing a vertical midline ridge) that is observed in basal sauropods and *Camarasaurus* (Upchurch, 1995, 1998). These brief descriptions indicate that the two tooth types do not share any autapomorphic features. Vitally, the absence of the lingual concavity in *Cardiodon* suggests that it may have come from a different taxon from that which produced the '*Cetiosaurus*' tooth.

In summary, the debate concerning the synonymy of *Cardiodon* and *Cetiosaurus* can now be resolved. There is no ev-

idence in support of the synonymy of these two genera, and the scant morphological data that are available actually argue against synonymy. *Cardiodon rugulosus* is provisionally retained as a valid taxon because it is based on the only known spatulate sauropod tooth with a convex lingual surface. This taxon is identified as Eusauropoda incerta sedis, but the type material is potentially lost and the referred specimen is barely adequate for the diagnosis of a distinct form. The name *Cetiosaurus rugulosus* is regarded as a junior objective synonym of *Cardiodon*.

Nomenclature

Thirteen species of *Cetiosaurus* have been based on British material. Although several of these have been eliminated by previous studies, or have simply been ignored after their first publication, recent taxonomic revisions have retained many species as valid taxa. Thus, Steel (1970) designated *C. medius* as the type species, and accepted the validity of a further five British species (*C. longus*, *C. oxoniensis*, *C. glymptonensis*, *C. leedsi*, and *C. rugulosus*). McIntosh (1990) produced a further revision in which *Cetiosaurus* itself contains two British species (*C. medius* as type and *C. oxoniensis*); *C. longus* and *C. glymptonensis* are placed within *Cetiosauriscus*, and *C. humerocristatus* is accepted as a valid taxon and regarded as an unnamed brachiosaurid of uncertain affinities. The taxonomic evidence outlined above agrees with certain aspects of these previous modifications, but also imposes further revisions. These revisions are summarized as follows:

1. Three species (*C. hypoolithicus*, *C. epioolithicus*, and *C. giganteus*) are nomina nuda and cannot be considered as available names (ICZN, Art. 12).
2. Two species (*C. conybeari* and *C. rugulosus*) are junior objective synonyms.
3. Four species (*C. brachyurus*, *C. medius*, *C. longus*, and *C. leedsi*) are nomina dubia because they are based on undiagnostic material.
4. Four species (*C. brevis*, *C. oxoniensis*, *C. glymptonensis*, and *C. humerocristatus*) can be recognized by autapomorphies, or at least unique combinations of character states, suggesting that they represent distinct taxa. These four species cannot be retained within a single genus because they represent distantly related forms (i.e., a brachiosaurid, a basal titanosauriform, a possible diplodocoid and a non-neosauropod), and they share no autapomorphies in common.
5. *C. brevis* is the only valid species name of those originally published by Owen (1842b) and, under a strict interpretation of ICZN rules (Art. 67(g)), should become the type species of *Cetiosaurus*. As a consequence, *C. oxoniensis* would have to be placed within a new genus.

A strict application of ICZN rules, regarding *C. brevis* and *C. oxoniensis*, might be considered inadvisable. The type material of *C. brevis* has been known by the name *Pelorosaurus conybeari* in most taxonomic works over the past century (Huene, 1927a, b; Kuhn, 1939; Steel, 1970; McIntosh, 1990; Upchurch, 1995). Thus, virtually all those working on sauropod systematics associate the name *Pelorosaurus* with brachiosaur or titanosauriform remains from the Lower Cretaceous of Britain. The name *Cetiosaurus* has been most closely associated with sauropod material from the Middle Jurassic of Britain, especially the *C. oxoniensis* specimens from Bletchingdon. Because the latter represent the most complete remains, they have been consistently used in comparisons of *Cetiosaurus* with other sauropods. Thus, restriction of the name *Cetiosaurus* to the Lower Cretaceous titanosauriform material, and the creation of a new generic name for the Middle Jurassic specimens from

near Oxford, would inevitably change current nomenclatural usage and generate considerable confusion.

At present, therefore, we believe there are two alternative and legitimate treatments of the nomenclature of *Cetiosaurus*: (1) a strict application of ICZN rules, so that *C. brevis* becomes the correct name for '*Pelorosaurus conybeari*' and '*Cetiosaurus oxoniensis*' is given a new generic name; or (2) a case for the conservation of the names '*Pelorosaurus conybeari*' and '*Cetiosaurus oxoniensis*', and suppression of '*C. brevis*', could be presented for a ruling by the ICZN under article 79 (the latter allowing the ICZN rules to be suspended in order to promote nomenclatural stability and avoid confusion). The authors prefer the second option and will submit a case for the conservation of '*Cetiosaurus*' in its current usage. For the remainder of this paper, therefore, the name *Cetiosaurus* refers to the Middle Jurassic basal sauropod from Oxfordshire, though the reader should be aware that such a treatment has no formal standing until ratified by the ICZN.

The Type Material of *Cetiosaurus*

Neither Phillips (1871), nor any subsequent worker, has designated the type material of *Cetiosaurus oxoniensis*. Given that the only diagnosable specimen assigned to this species is the large partial skeleton from Bletchingdon Station, we propose that this individual be regarded as the lectotype.

REDESCRIPTION OF *CETIOSAURUS OXONIENSIS* PHILLIPS, 1871

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842b
SAURISCHIA Seeley, 1888
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
CETIOSAURIDAE Lydekker, 1888
CETIOSAURUS, Owen, 1841a

Type and Only Species—*Cetiosaurus oxoniensis* PHILLIPS, 1871 (new designation).

Original Diagnosis—Owen (1841a, 1842b) listed the following diagnostic characters of *Cetiosaurus*: (1) dorsal centra broad and have subcircular articular faces; (2) dorsal centra constricted in the middle portions; (3) vertebral centra display unequal excavation of the anterior and posterior articular faces; (4) caudal neurapophyses are short anteroposteriorly and 'anchylosed' to the anterior part of the centrum; (5) caudal vertebrae have long prezygapophyses which project beyond the anterior end of the centrum; (6) caudal vertebrae have reduced postzygapophyses represented by facets at the base of the neural spine; and (7) internal texture of vertebral centra is 'spongy.' Owen (1875) repeated these characters and added: (1) chevron facets are paired and chevrons articulate intervertebrally; and (2) subquadrangular coracoid with rounded angles. All of these characters have a much wider phylogenetic distribution (see taxonomic revision above) and therefore cannot provide an adequate differential diagnosis for *Cetiosaurus*. Other major descriptions or taxonomic reviews (Phillips, 1871; Huene, 1927a; Steel, 1970; McIntosh, 1990) have not identified autapomorphic features or unique combinations of characters.

Revised Diagnosis—As for *C. oxoniensis*.

CETIOSAURUS OXONIENSIS PHILLIPS, 1871
(Figs. 4–12)

Ceteosaurus oxoniensis Phillips, 1871, figs. 86–112
Cetiosaurus longus Owen, 1842b: Owen (1875:figs. 3–11)
Ornithopsis oxoniensis (Phillips) Seeley, 1889

Cardiodon oxoniensis (Phillips) Lydekker, 1890

Lectotype—The partial skeleton of a large sauropod (OUMNH J13605–13613, J13615–16, J13619–J13688, J13899), including fragmentary dorsal and sacral elements, portions of thoracic rib, approximately 30 anterior and middle caudal centra (some with arches and processes), seven damaged hemal arches from the anterior and middle part of the tail, scapulae, damaged coracoids, left sternal plate, humeri, ulnae, portions of metacarpal, ilia, left pubis, right ischium, femora, left tibia and fibula.

Paralectotypes—The remains of a medium-sized individual including a portion of sternal(?) plate, a left humerus, and a femur (OUMNH J13614), and a small individual represented by a scapula, femur, tibia and fibula (OUMNNH J13617–8, J13780–1), from the same locality and horizon as the lectotype. The dorsal half of a braincase (OUMNH J13596) may belong to the lectotype but is provisionally regarded as a paralectotype (see below).

Referred Material—A partial skeleton (LCM G468.1968) from Great Casterton, Rutland, U.K.

Revised Diagnosis—Medium to large non-neosauropod dinosaur from the Middle Jurassic, distinguished by the following autapomorphies: (1) symmetrical 'pyramid'-shaped neural spines on posterior cervicals and anterior dorsals; (2) loss of the spinodiapophyseal lamina (or complete fusion of this lamina with the spinopostzygapophyseal lamina) on all dorsal neural spines; (3) distal caudal centra have 'tongue'-like projections on their articular faces which extend the floor of the neural canal anteroposteriorly; (4) distal shafts of anterior chevrons are anteroposteriorly compressed and do not taper to a transversely flattened distal end; (5) triangular hollow, bounded dorsally by a horizontal ridge, on the lateral surface of the base of the pubic process of the ilium.

Type Locality—A quarry near Bletchingdon (old Kirtlington) Station, near Enslow Bridge, Oxon. (Fig. 1), National Grid Reference SP 483 182 (P. Powell, pers. comm., 1997).

Type Horizon—The Bletchingdon Station specimens are often stated as being found in the Great Oolite (e.g., Owen, 1841a, 1842a, b; Lydekker, 1888). Phillips (1871:247–248) noted, however, that the *Cetiosaurus* bones were actually found in the Forest Marble (Bathonian, Cope et al., 1980) sediments immediately above the Great Oolite.

Discovery and Preservation of the Bletchingdon Station Material

The sauropod material from Bletchingdon Station potentially represents one of the best preserved sauropods from the Jurassic of Europe. Before describing this material in detail, however, some comments on the preservation and association of the elements are required.

In March 1868, quarry workers discovered a 1,600 mm long right sauropod femur at a site near Bletchingdon Station. Although no further specimens were found over the following year, the period from March 1869 to June 1870 witnessed the recovery of a very large number of bones scattered over a relatively small area. Phillips (1871:252) interpreted these remains as belonging to three individuals of different body size. The large animal is represented by a partial skeleton; the medium-sized individual is only known from a portion of sternal plate, a humerus, and a femur; and the small form is based on a scapula, femur, tibia and fibula. Phillips (1871:fig. 84) provided a sketch map showing the distribution of some large elements at the Bletchingdon site. It is clear from this map that, although the specimens were found in close association, most of the original anatomical relationships between elements were disrupted prior to burial. The question arises, therefore, whether Phillips could accurately distinguish three different individuals in a

bone assemblage of this type. In fact, there are several lines of evidence which broadly support Phillips's interpretation:

1. The relative completeness of the large individual may seem anomalous given the poor representation of the other two animals. According to Phillips (1871:251), however, most of the remains belonging to the smaller individuals were destroyed by quarrying before they could be saved. For quarrying to differentially destroy two skeletons and leave a third nearly intact, there must have been some spatial separation between carcasses and little post-mortem mixing of elements.

2. The large individual includes paired limb elements. Each pair of bones (e.g., the humeri) are virtually identical in size and proportions, and the relative proportions between elements are also consistent with the view that they belonged to a single individual (see below).

3. The large individual includes fragmentary dorsals and sacrals, the anterior half of the tail, limb girdle elements and the more proximal limb bones. This type of preservation is common in sauropods because their body shape and size facilitates loss of distal elements such as the skull, manüs, pedes and distal end of the tail.

Thus, despite the disarticulated state of the Bletchingdon material, and the absence of detailed site maps and records, we support Phillips's original allocation of material to one large and at least two smaller individuals.

Description and Comparisons

In the description which follows, the nomenclature of vertebral laminae follows that of Wilson (1999). The OUMNH catalogue, mentioned below, is an unpublished list of specimens created by P. Powell, with additional identifications and revisions by J. S. McIntosh.

Braincase—The dorsal portion of a sauropod braincase (OUMNH J13596) probably came from the Bletchingdon Station quarry and has recently been referred to *Cetiosaurus* sp. by Galton and Knoll (in prep.). In the light of the taxonomic revisions outlined above, and the probable provenance of this braincase, there is currently no reason why J13596 should be treated any differently from the postcranial material from Bletchingdon. Thus, the braincase is provisionally regarded here as belonging to *Cetiosaurus oxoniensis*. It is difficult, however, to make accurate comparisons of the relative proportions of disarticulated braincase and postcranial material, so it is impossible to establish with any confidence that the braincase belongs to the large individual (lectotype) from Bletchingdon: J13596 is here considered to be one of the paralectotype specimens of *Cetiosaurus oxoniensis*. The braincase itself, and the disagreements surrounding its provenance and identification, are dealt with in detail by Galton and Knoll (in prep.) and therefore will not be discussed here.

Dentition—A single tooth from Bletchingdon (OUMNH J13597, Fig. 4; Phillips, 1871:fig. 85) may belong to *Cetiosaurus* (see '*C. rugulosus*' for description and discussion).

Cervical Vertebrae—Although Phillips (1871:254) believed that no portions of cervical vertebra (Fig. 5A) or rib were present in the Bletchingdon collection, the OUMNH catalogue lists three specimens: a centrum (J13660), a crushed centrum (J13682) and a portion of right cervical rib (J13670). Examination of the OUMNH collections in 1997 revealed that OUMNH J13682 is indeterminate. The best preserved specimen (OUMNH J13660) is a cervical centrum which lacks its anterior end (Fig. 5A). Comparison with the cervical series of the Rutland *Cetiosaurus* (LCM G468.1968) suggests that J13660 most closely resembles Cv7. The lateral surfaces bear deep, longitudinally elongate pits or pleurocoels (Fig. 5A). There is no
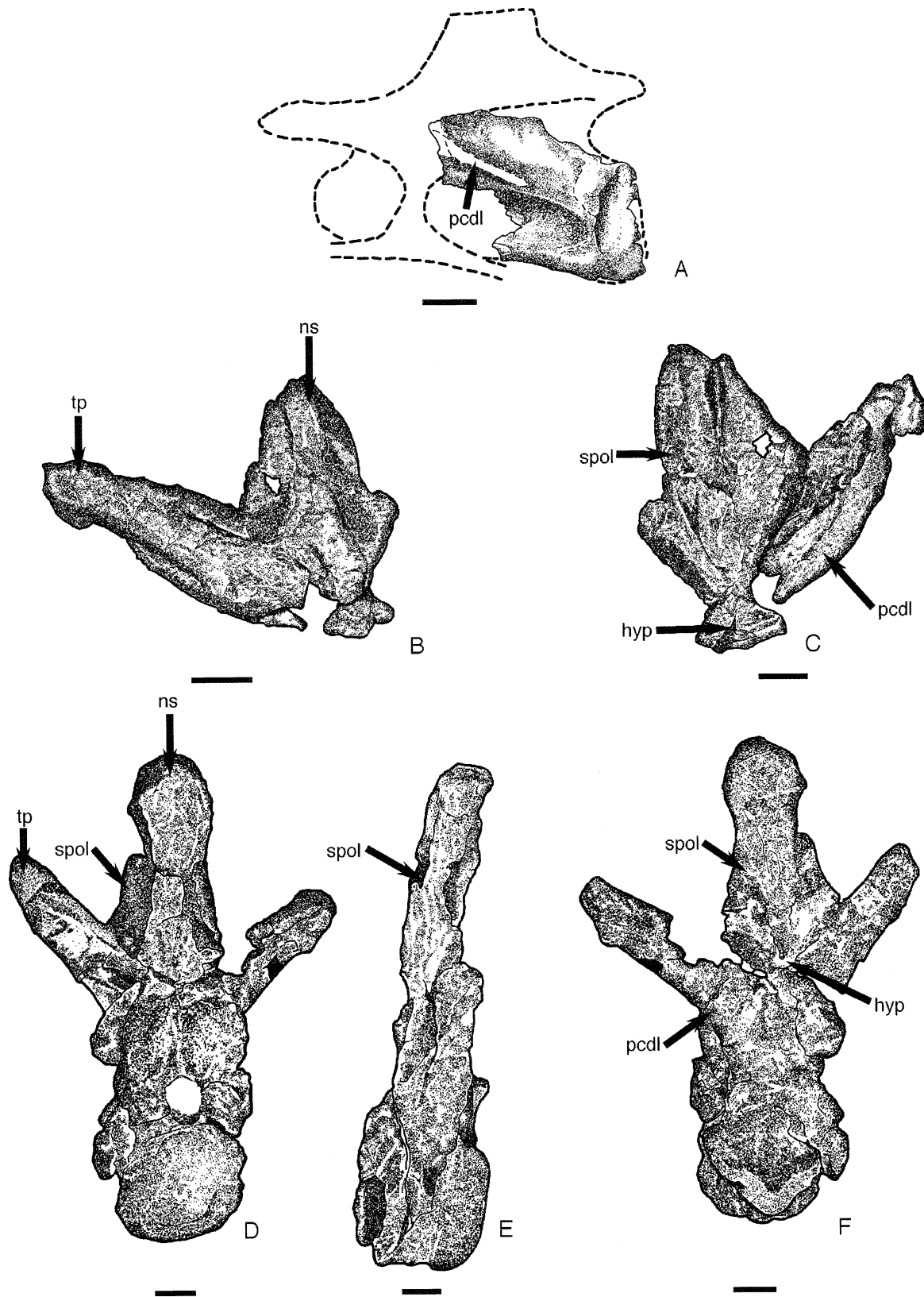
FIGURE 5. Presacral vertebrae from the lectotype of *Cetiosaurus oxoniensis*: **A**, portion of cervical centrum (OUMNH J13660) in left lateral view; **B**, portion of anterior dorsal neural spine and right transverse process (OUMNH J13646) in anterior view; **C**, as for B, in posterior view; **D**, mid-dorsal vertebra (OUMNH J13644/2) in anterior view; **E**, as for D, in right lateral view; **F**, as for D, in posterior view. **Abbreviations**; **hyp**, hyposphene; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **tp**, transverse process. Scale bars equal 50 mm.

evidence that the latter were divided into anterior and posterior portions by an oblique accessory lamina: in this respect this cervical is similar to those present in *Patagosaurus* (Bonaparte, 1986b) and the Rutland *Cetiosaurus* (LCM G468.1968, Upchurch and Martin, unpubl. data), and differs from those in *Omeisaurus*, *Haplocanthosaurus* and most neosauropods (Upchurch, 1998; Wilson and Sereno, 1998). The position of the parapophysis cannot be determined because of the damage to the anterior end. The posterior articular surface of the centrum is deeply concave and, unlike euhelopodids, is not compressed transversely (Upchurch, 1998). The ventral surface is broad, flat, and probably lacked a midline 'keel.'

Cervical Ribs—OUMNH J13670 is the proximal end of a cervical rib. The tuberculum is a flattened strap-like process. The angle between the capitulum and tuberculum is less than 90° suggesting that *Cetiosaurus* shares the derived state characterizing the Neosauropoda (Wilson and Sereno, 1998). This specimen is too poorly preserved to yield any other useful character data.

Dorsal Vertebrae—There are 20 specimens recognized as dorsal vertebrae in the OUMNH catalogue (Fig. 5B–F): a nearly complete vertebra (J13644/2, Phillips, 1871:fig. 86; Owen, 1875:29), nine portions of centrum and arch (J13643/2, J13647 [Phillips, 1871:fig. 88; Owen, 1875:fig. 10], J13648, J13649, J13650, J13651, J13669, J13680, J13685), six portions of spine (J13645/2, J13646, J13652–J13655), two centra (J1362/2, J13686) and two indeterminate fragments (J13656, J13681). OUMNH J13685 could not be located in 1997. The number of dorsal vertebrae in *Cetiosaurus* cannot be accurately reconstructed, but the above elements indicate that the trunk region contained a minimum of 12 dorsals.

In the description which follows, the approximate positions of the dorsal elements have been assessed using data from the Rutland *Cetiosaurus* (LCM G468.1968, Upchurch and Martin, unpubl. data) and complete dorsal series from other sauropods. For example, Phillips (1871:255) identified the most complete vertebra (OUMNH J13644/2, Fig. 5D–F) as an 'anterior dorsal'; the presence of a hyposphene, the parapophysis located on the neural arch, and the shape of the neural spine, however, all indicate that this specimen actually comes from the middle or posterior part of the dorsal series (Fig. 5D–F).

The anterior articular surface of the centrum is mildly convex in middle dorsals, but becomes flat or slightly concave in more posterior elements. This pattern is probably plesiomorphic because it occurs in *Barapasaurus* (Jain et al., 1979), *Patagosaurus* (Bonaparte, 1986b) and diplodocoids (Upchurch, pers. obs.), whereas camarasauromorphs possess a derived state in which a prominent 'hemispherical' articular surface is present throughout the dorsal series (Salgado et al., 1997; Upchurch, 1998). The *Cetiosaurus* centra are generally too badly distorted to determine their exact shape, but they were probably subcircular in transverse section throughout most of their length. The ventral surface of each centrum is formed from two ventrolaterally facing areas which meet each other on the midline to form a prominent longitudinal ridge, as also occurs in *Brachiosaurus* (Janensch, 1947:abb. 2). The lateral pits, or pleurocoels, are deep but do not ramify widely within the centrum or invade the base of the neural arch. The septum between the pleurocoels is usually 20–30 mm thick. The external margin of each pleurocoel is well defined ventrally by a stout rounded ridge which forms the boundary between the lateral and ventral faces of the centrum. The dorsal margin, however, is less well defined, and it is possible that these excavations opened laterally and a little dorsally. Such deep but simple lateral excavations are also present in *Patagosaurus* (Bonaparte, 1986b) and the Rutland *Cetiosaurus* (LCM G468.1968, Upchurch and Martin, unpubl. data), whereas *Haplocanthosaurus*, diplodocids and basal camarasauromorphs possess much more extensive pleurocoels

(Upchurch, 1998). The posterior articular surfaces of the dorsal centra are deeply concave.

The dorsal neural arches are tall in *Cetiosaurus*, approximately equalling the height of their centra. The anterior face of the arch is excavated, forming a deep hollow above the neural canal. Both the tall neural arch and the anterior excavation are derived states which unite a clade containing *Barapasaurus* and eusauropods (sensu Upchurch, 1995). The anterior margins of the arch form stout pillar-like ridges (centroprezygapophyseal laminae) which support the prezygapophyses from below. In the Oxford and Rutland *Cetiosaurus* specimens and other 'primitive' sauropods, these laminae have convex or even acute anterior surfaces in horizontal section, whereas in *Haplocanthosaurus* and many neosauropods these surfaces are flat or slightly concave towards the prezygapophyses (Upchurch, pers. obs.). The prezygapophyses are small and lie close together (at least in the middle dorsals), and have flat articular facets which face upwards and moderately inwards. Hypantral facets cannot be observed, but this is probably due to poor preservation.

Several broken specimens (e.g., OUMNH J13648), which preserve parts of the arch, suggest that a 'neural cavity' was present. The neural cavity is a hollow area within the arch, lying above the neural canal, which is present in *Barapasaurus* (Jain et al., 1979), *Patagosaurus* (Bonaparte, 1986b) and at least some neosauropods (Bonaparte, 1986a). In *Barapasaurus* and *Patagosaurus*, the neural cavity is linked to the external surface of the arch by a lateral foramen which lies immediately below the base of the transverse process, just in front of the posterior centrodiapophyseal lamina (Jain et al., 1979; Bonaparte, 1986b: figs. 39–41). Such a foramen may have been present in OUMNH J13648, but this depends on the interpretation of a curving broken margin. The most complete dorsal vertebra of *Cetiosaurus* (OUMNH J13644/2) apparently lacks both lateral foramina and the neural cavity itself: instead, there is a deep pit on either side of the arch (where the lateral foramen would normally be found) which is separated from its partner on the opposite side by a very thin midline septum. This second type of morphology is also observed in the anterior and middle dorsals of the Rutland *Cetiosaurus* (LCM G468.1968), and at least some of the dorsals of *Barapasaurus* and *Patagosaurus* (Jain et al., 1979; Bonaparte, 1986b). At present, it is not possible to determine the phylogenetic significance of the neural cavity, lateral foramina and lateral pits, because variation along the dorsal series, combined with fragmentary preservation, makes accurate comparisons impossible (Upchurch, 1998). The parapophysis is not clearly preserved in any of the dorsal elements and seems to have been absent from all of the available centra (the latter is consistent with the view that none of the most anterior dorsal centra are preserved). In the most complete dorsal (OUMNH J13644/2), worn areas on the lateral surfaces of the centroprezygapophyseal laminae may indicate the position of the parapophysis (Fig. 5E). As in other sauropods, the posterior centrodiapophyseal lamina is large and nearly vertical in middle and posterior dorsals. There is no evidence that this lamina bifurcated towards its ventral end, unlike those of many titanosauroids (Salgado et al., 1997). The *Cetiosaurus* middle and posterior dorsal vertebrae lack the posterior centroparapophyseal lamina which extends posteroventrally from the parapophysis in many neosauropods (Upchurch, 1998). The apparent absence of posterior centroparapophyseal, anterior centrodiapophyseal, and accessory centropostzygapophyseal laminae, however, could be the result of damage and weathering of the lateral arch surface.

The transverse processes are only well preserved in the nearly complete middle dorsal vertebra (OUMNH J13644/2), although the base of the right process can be observed in an arch-spine complex from an anterior dorsal (OUMNH J13646, Fig. 5B, C). Sauropods typically have either laterally or dorsolat-

erally directed transverse processes throughout the dorsal series. In the Rutland and Oxford *Cetiosaurus* specimens, and *Patagosaurus* (Bonaparte, 1986b), the transverse processes of the anterior and posterior dorsals are directed outwards and a little upwards, whereas those of the middle dorsals are more strongly inclined upwards. In parasagittal section, each process is triradiate, being formed from a stout 'horizontal' dorsal plate which links the bases of the pre- and postzygapophyses, and the vertically directed posterior centrodiapophyseal lamina. The transverse processes terminate in a heavy diapophyseal area, but the orientation of the articular facet cannot be determined.

In the middle dorsal (OUMNH J13644/2), the posterior face of the neural arch is formed by prominent centropostzygapophyseal laminae which extend dorsomedially from the centrum to the base of the hyposphene. The latter is a large block of bone, subtriangular in posterior view, which lies immediately below the midline contact between the postzygapophyses (Fig. 5F). The presence of a hyposphene-hypantrum articulation in the middle and posterior dorsal vertebrae is a saurischian synapomorphy (Gauthier, 1986), which is lost in some advanced titanosaurs such as *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977; Salgado et al., 1997; Upchurch, 1998). The postzygapophyseal articular surfaces face downwards and a little outwards.

The available dorsal neural spines display two distinct morphologies. In one type of spine (only represented by OUMNH J13646, Fig. 5B, C) there are very stout prominent spinopre- and spinopostzygapophyseal laminae. These laminae are symmetrical about the sagittal plane, and nearly symmetrical about a transverse plane through the spine summit. Between these laminae, on the anterior, posterior and lateral faces, deep hollows are present. The net effect of this morphology is to create a spine which is essentially a 'pyramid'-shape with excavated faces. This characteristic shape is also observed in the posterior cervicals and anterior dorsals of the Rutland *Cetiosaurus* (LCM G468.1968). The presence of well developed spinopre- and spinopostzygapophyseal laminae is a synapomorphy of the clade *Barapasaurus*+Eusauropoda (Upchurch, 1998), but the symmetry about the transverse plane through the spine summit is generally absent because the spinoprezygapophyseal laminae tend to be less prominent and more vertical than the spinopostzygapophyseal laminae in this region of the presacral series. The neural spines of *Patagosaurus* are taller and less symmetrical than those of *Cetiosaurus* (compare Fig. 5B, C with Bonaparte, 1986b:figs. 37–38), and it is therefore suggested that the symmetrical pyramidal spine shape should be regarded as an autapomorphy of the latter genus. All of the remaining dorsal neural spines from Bletchingdon closely resemble that belonging to the well preserved middle dorsal vertebra (OUMNH J13644/2). This type of spine is formed from low spinopre- and more prominent spinopostzygapophyseal laminae which are approximately vertical over most of their lengths before converging to form a robust, transversely rounded, summit. Compared to the anterior dorsal neural spine, middle and posterior dorsal neural spines are taller, widened transversely, lack the anterior and posterior excavations, and have tall anterolaterally facing hollows. The spinoprezygapophyseal laminae converge dorsally and fade into a rugose anterior surface, but *Cetiosaurus* lacks the derived prespinal and postspinal midline laminae found in Titanosauriformes and Diplodocoidea (Salgado et al., 1997; Upchurch, 1995, 1998). The sauropod spinodiapophyseal lamina is a small plate of bone which joins the dorsal surface of the transverse process to the anterior surface of the spinopostzygapophyseal lamina. This structure represents a derived state present in the middle and posterior dorsal vertebrae of virtually all sauropods, although it is rudimentary in *Shunosaurus* (Upchurch, 1998; Wilson and Sereno, 1998). Wilson and Sereno (1998) note that this additional lamina is restricted to the most posterior dorsals in *Haplocanthosaurus* and *Brachiosaurus*. The

dorsals of both the Oxford and Rutland *Cetiosaurus* specimens, however, clearly lack such a lamina, a condition which is here interpreted as an autapomorphic reversal to the plesiomorphic state. Whether this represents a reliable autapomorphy of *Cetiosaurus* is difficult to assess because complete articulated dorsal series are not available in this genus, and some sauropods (see above) lack the spinodiapophyseal lamina on their anterior and middle dorsals. The ventral end of the spinopostzygapophyseal lamina is unbifurcated, unlike those of diplodocoids (Wilson, 1999) and merges smoothly into the posterior margin of the transverse processes. The upper end of this lamina is a little expanded laterally in some specimens, but *Cetiosaurus* dorsal neural spines do not display the prominent triangular projections which occur in *Haplocanthosaurus* and camarasauromorphs (Upchurch, 1995:fig. 13; Wilson and Sereno, 1998).

Thoracic Ribs—Phillips (1871:267, fig. 97) reported the remains of 10–12 thoracic ribs from the large Bletchingdon individual. The only specimens in the OUMNH collections which are as complete as those figured by Phillips, however, belong to a sauropod from Chipping Norton (OUMNH J29784–5, J29789–90, J29794). Those fragments of thoracic rib from Bletchingdon, available in 1997, are too poorly preserved to provide useful anatomical data.

Sacral Vertebrae—Phillips (1871) did not mention any sacral material among the specimens from Bletchingdon. The OUMNH catalogue, however, lists three specimens (OUMNH J13657–8, J13687) which appear to be portions of sacral vertebrae. Each of these specimens consists of the combined centrum, base of neural arch, and bases of the sacral ribs (OUMNH J13657 has a broken neural arch exposing the floor of the neural canal). The sacral centra are compressed dorsoventrally and, unlike *Haplocanthosaurus*, *Camarasaurus*, *Brachiosaurus* and diplodocids, there are no lateral pits or pleurocoels. The articular faces of OUMNH J13658 are mildly concave, whereas in J13687 there is a convex surface at one end and a flat surface at the other. The ventral surface of each centrum is smoothly convex transversely. The neural canal is relatively large, approximately 20–30 mm in horizontal diameter. The rib bases are not well preserved, but as far as can be determined they resemble those of other sauropods.

Caudal Vertebrae—Phillips (1871:258) reported the presence of 27 caudal vertebrae (and some fragments) in a 'fine series' belonging to the large individual from Bletchingdon Station. The OUMNH catalogue lists 32 specimens, including 30 vertebrae or centra, one fragment of prezygapophysis (OUMNH J13689) and one portion of broken neural arch and zygapophyses (OUMNH J13899) (Fig. 6, Table 2). A subset of 19 caudals (OUMNH J13627–J13645/1, Phillips [1871:figs. 90, 99]; Owen [1875:fig. 10]) are labelled as caudals '1–34', with gaps in the series. This numbering suggests that the anterior part of the tail is represented by a disarticulated series with perhaps half of its elements missing. In fact, two lines of evidence support the view that these 19 vertebrae represent the nearly complete series from the anterior third of the tail. Firstly, according to the current numbering system, caudal ribs would be present as far back as caudal '24' (OUMNH J13639); this probably reflects Phillips's (1871:260) belief that the crocodile (which has caudal ribs on at least the anterior half of the tail) was a suitable analogue for reconstruction of *Cetiosaurus*. In fact, all known sauropods have caudal ribs which disappear in the region of caudal 14–16 (except *Alamosaurus* where Cd8 is the last to bear a rib [Gilmore, 1946]). There are 13 *Cetiosaurus* caudal vertebrae which bear ribs, implying that perhaps only two or three elements are missing from the anterior third of the tail. Secondly, the measurements of the subset of 19 caudals (Table 2) are consistent with the view that they form a nearly continuous series. The size and proportions of the remaining 11 vertebrae, indicate that these specimens probably represent the
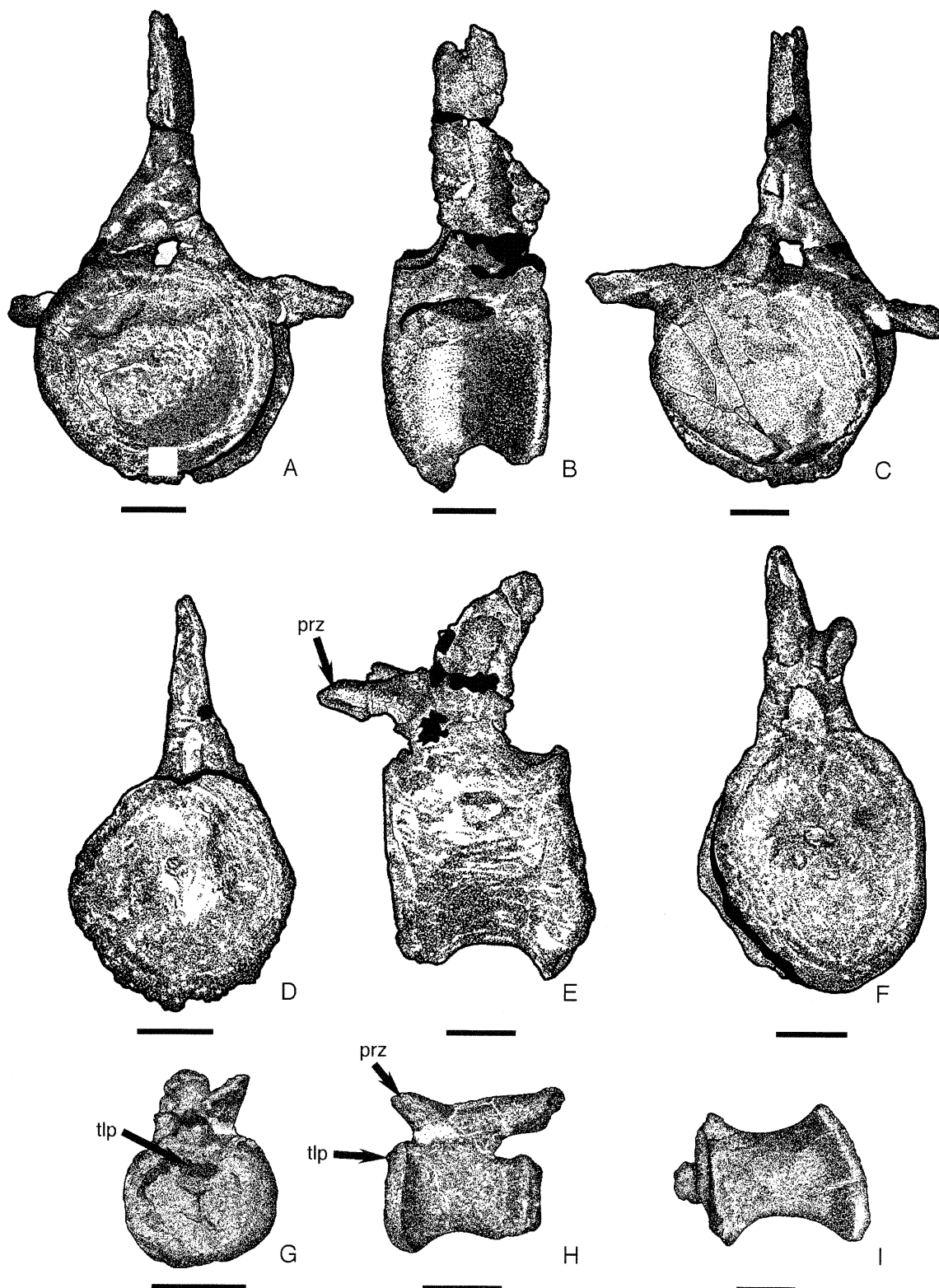
FIGURE 6. Selected caudal vertebrae from the lectotype of *Cetiosaurus oxoniensis*: **A–C**, anterior caudal (OUMNH J13634); **D–F**, anterior–middle caudal (OUMNH J13636); **G–I**, middle–distal caudal (OUMNH J13678). **A**, **D**, **G**, anterior views; **B**, right lateral view; **C**, **F**, posterior views; **E**, **H**, left lateral views; **I**, ventral view. **Abbreviations**: **prz**, prezygapophysis; **tlp**, 'tongue'-like process. Scale bars equal 50 mm.

TABLE 2. Measurements of the caudal vertebrae belonging to the large individual of *Cetiosaurus oxoniensis* from Bletchingdon. The 'estimated' position in the tail is based on Phillips (1871), and the OUMNH catalogue, and is not supported by the current study. **Abbreviations**: *****, measurements affected by distortion; **Anh**, height of centrum on its anterior surface; **Anw**, width of centrum on its anterior surface; **Arl**, length of the arch on the dorsal surface of the centrum; **Lc**, length of centrum; **Lpoar**, length of the centrum exposed posterior to the base of the neural arch; **Poh**, height of centrum on its posterior surface; **Pow**, width of centrum on its posterior surface. Measurements are in mm.

Cd	Specimen	Lc	Anh	Anw	Poh	Pow	Arl	Lpoar
'1'	J13627	84	200	240	—	—	—	—
'5'	J13629	120	215	184	—	—	—	—
'6'	J13628	113	240	222	—	—	—	—
'10'	J13631	120	—	203	—	—	—	—
'12'	J13630	Crushed	—	—	—	—	—	—
'14'	J13633	122	—	—	—	—	—	—
'15'	J13632	120	183	190	160+	200	—	—
'16'	J13634	133	160	196	146	190	—	—
'18'	J13638	140	151	143	143	—	74	47
'20'	J13636	—	—	—	—	—	—	—
'21'	J13635	149	123	190	125	180	73	44
'22'	J13637	135	122	163	133	168	—	—
	J13671	144	105	176	118	163	—	—
'24'	J13639	135	115	144	113	140	64	50
'25'	J13640	133	108	120	115	133	62	42
'26'	J13641	130	122	110	110	122	57	38
	J13668	132	106*	100*	—	—	—	—
	J13672	128	120	110	—	—	—	—
'30'	J13644/1	120	95	107	95	105	55	42
'31'	J13642/1	122	80	111	92	107	46	46
'32'	J13643/1	—	—	—	—	—	—	—
'34'	J13645/1	—	—	—	—	—	—	—
	J13674	96	83	96	76	83	50	30
	J13675	108	75	—	73	90	54	35
	J13676	103	70	98	71	90	50	30
	J13677	100	78	93	65	—	50	32
	J13678	98	66	81	—	83	50	25

middle part of the tail. We suggest, therefore, that the large Bletchingdon individual possesses most of the anterior half of the tail. Several of the smaller caudal vertebrae (OUMNH J13674, Phillips [1871:fig. 19], J13675–J13679, J13688, J13689, J13889) may have come from the distal half of the tail, separated from the anterior series by a large gap.

All of the caudal centra are solid, lacking pleurocoels and deep ventral excavations. The centra are amphicoelous, with equally concave anterior and posterior articular faces. In the most anterior vertebrae (OUMNH J13628, J13629, J13633), and in a few middle caudals (OUMNH J13640, J13641), however, the anterior articular face is noticeably shallower than the posterior one. A small mildly convex bone boss is found at the center of each articular face in middle caudals (OUMNH J13636 onwards, Fig. 6D–F). Several small, middle-distal, caudal vertebrae (OUMNH J13674, J13676–78, Fig. 6G–I) possess a short 'tongue'-like projection at the dorsal margin of their articular faces (Fig. 6G–I): these lie on the midline and increase the anteroposterior extent of the neural canal floor. This is an unusual feature not observed in any other sauropod known at present, and is therefore regarded as an autapomorphy of *Cetiosaurus*. The central portion of each centrum is constricted relative to the expanded articular faces. This constriction is mildly developed in anterior caudal vertebrae, but becomes more pronounced in middle caudals. The ventral surfaces of the anterior caudal centra (OUMNH J13628–30, J13634) are marked by a narrow midline groove (see '*C. medius*' above). This groove is deepest between the chevron facets and gradually fades out as one passes distally along the tail so that it is absent from OUMNH J13635 onwards. Chevron facets are weakly developed on the most anterior caudal vertebrae, but from OUMNH J13634 onwards, the facets on the posterior margin of each centrum are large, widely separated from the midline, and face posteroventrally. The lateral surfaces of the centra are generally concave anteroposteriorly and convex dorsoventrally, curving downwards to merge smoothly with the ventral

surface. In the anterior-middle part of the series, however, there is a horizontal ridge situated at approximately two-thirds of the way up the lateral surface (see '*C. glymptonensis*' above). In OUMNH J13638 this ridge is associated with the base of the caudal rib, whereas in J13636–37 the former lies below the latter.

Portions of neural arch and spine are only present in a few specimens (OUMNH J13627, J13629, J13630, J13634, J13636, J13674, JJ13675, J13678, Fig. 6), although the bases of the arches can be observed on all centra. In the anterior caudal OUMNH J13629, the arch is tall and laterally compressed. As in many sauropods, the anterior caudal vertebrae possess neural arches situated towards the anterior end of the centrum. The middle caudals, however, have neural arches placed on approximately the center of the centrum (with a slight bias towards the anterior end in some specimens), and do not display the extreme anterior location observed in Titanosauriformes (Salgado et al., 1997; Upchurch, 1998).

The prezygapophyses are preserved in OUMNH J13630 and J13636 (Fig. 6E). These are slender elongate processes which project forwards and a little upwards to a point beyond the anterior end of the centrum. The articular facets of the prezygapophyses face mainly medially and a little upwards. In the middle-distal caudal OUMNH J13674, the prezygapophyses are still paired structures, with articular facets directed dorsomedially. In all of these specimens, postzygapophyses are only represented by a small 'pinched' area at the base of the spine. None of the most anterior caudal vertebrae are sufficiently well preserved to determine whether a hyposphenal ridge was present (see '*C. brevis*' above).

The spine is damaged in the most anterior caudal vertebra (OUMNH J13627). The remaining portion at the base suggests that the spine was a simple laterally compressed vertical plate, expanded a little along its posterior margin. The spine in OUMNH J13636 is also laterally compressed and blade-like, but projects upwards and backwards (Fig. 6D–F). In the middle-
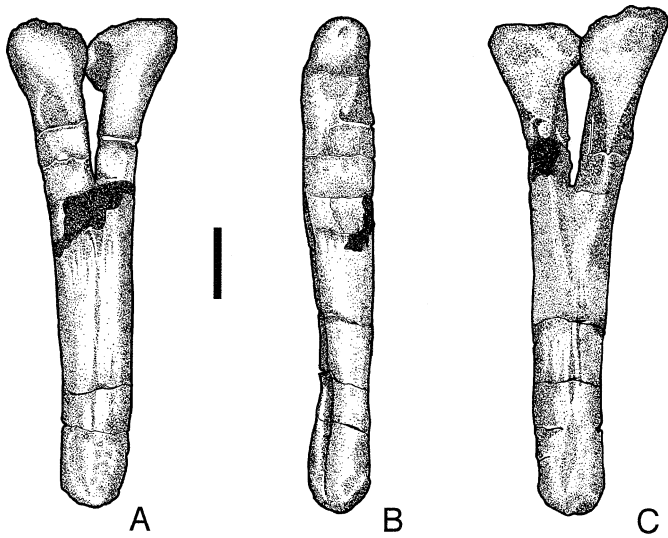
FIGURE 7. Hemal arch from the lectotype of *Cetiosaurus oxoniensis*. **A**, proximal chevron (OUMNH J13664) in anterior view; **B**, as for A, in right lateral view; **C**, as for A, posterior view. Scale bar equals 50 mm.

distal caudal vertebrae (OUMNH J13674, J13675, J13678) the neural spine projects backwards and a little upwards (Fig. 6G–I). In OUMNH J13674 and J13675, the spine is laterally compressed, whereas in J13678 it is subcircular in transverse cross-section throughout most of its length.

Caudal ribs are poorly preserved, but their bases can be detected in 13 specimens (OUMNH J13627–J13638, J13671). In the most anterior caudal (OUMNH J13627) the rib is represented by a tall thin plate which extends from the mid-height of the centrum to the top of the neural arch. Similar ribs are present on the first, and sometimes the second, caudal vertebrae of most sauropods (Upchurch, 1998) and indicates that OUMNH J13627 belongs to the extreme anterior end of the tail. In the remaining caudals, the ribs are simple lateral projections.

Hemal Arches—The material from Bletchingdon includes five nearly complete or partial chevrons (OUMNH J13661–2, J13664, J13667, Phillips [1871:fig. 89], Owen [1875:fig. 10]) and two fragments (OUMNH J13663, J13665) (Fig. 7). These elements are mainly from the anterior end of the series, except for J13667 and J13666 which appear to come from the anterior-middle and middle sections respectively. In the anterior chevrons, the hemal canal is 'closed' dorsally by a slender bridge of bone linking the left and right proximal articular facets (Phillips, 1871:261). This represents a plesiomorphic state present in *Omeisaurus* (He et al., 1988), *Patagosaurus* (Bonaparte, 1986b), diplodocids and dicraeosaurids: derived 'open' anterior chevrons characterize the Camarasauromorpha (Upchurch, 1998; Wilson and Sereno, 1998), but are also present in *Shunosaurus* (Zhang, 1988) and *Rayososaurus* ('*Rebbachisaurus*', Calvo and Salgado, 1995). The area for articulation with the caudal vertebrae is divided transversely so that there are two facets on each proximal ramus. The 'anterior' pair of facets are perpendicular to the long-axis of the chevron, whereas the 'posterior' set face backwards. Given the oblique orientation of the chevron facets on the centra, natural articulation of these anterior chevrons would cause their long-axes to be directed downwards and strongly backwards. The hemal canal is vertically elongate and occupies approximately one-quarter to one-third of chevron length. Ventrally, this canal leads into a midline groove which extends for several centimeters down the

posterior face of the distal blade. The latter is widened transversely and strongly compressed anteroposteriorly over most of its length: this means that the anterior chevrons apparently terminated distally in a blunt rounded end rather than a transversely narrowed edge as in other sauropods. This compressed type of chevron blade is also present in the Rutland *Cetiosaurus* and may represent an autapomorphy of the genus. A vertically striated ridge, subtriangular in cross-section, extends down the midlines of the anterior and posterior surfaces of the blade. Viewed from the side, the chevron curves gently backwards towards the distal end.

More distally located chevrons resemble the anterior ones in most respects, except for their smaller size. The most marked modifications include the loss of the anterior and posterior midline ridges on the blade, and a distinct transverse compression of the latter towards its distal end. In addition, the proximal articular facets face anterodorsally and posterodorsally, indicating that the chevrons were oriented more vertically than in the more anterior elements. Measurements of the most complete hemal arch, J13664: length = 355 mm; transverse width across proximal end = 120 mm; length of hemal canal = 110 mm; transverse width across distal shaft, immediately below hemal canal = 65 mm; anteroposterior width of distal shaft, immediately below hemal canal = 60 mm; transverse width of distal end = 52 mm; anteroposterior width of distal end = 48 mm.

Scapula—The OUMNH catalogue lists the left (OUMNH J13606, Phillips [1871:fig. 99]) and right (OUMNH J13605) elements from the large partial skeleton, and a left scapula (OUMNH J13781) belonging to the smallest animal, although the latter was not found in 1997 (Fig. 8A–C, Table 3). The two large scapulae are virtually complete apart from a portion missing from the dorsal edge of the distal end of the left element. The proximal plate is strongly expanded dorsally to form the broad acromion. This region has a wide concave area on its lateral surface, bounded posteriorly by a prominent vertical acromial ridge (Fig. 8A, C). In *Cetiosaurus*, the region posterior to the acromial ridge is slightly convex and extends postero-medially to the margin of the proximal plate. This contrasts with *Haplocanthosaurus* and many neosauropods where this region of the scapula is excavated. The glenoid area is robust and its articular surface faces anteroventrally; unlike the Somphospondyli, this area is not deflected medially (Wilson and Sereno, 1998). Between the anterior end of the scapula blade, and the posterior tip of the glenoid, the ventral margin is transversely rounded rather than flattened and longitudinally striated as in other sauropods. The medial surface of the proximal expansion is roughened and shallowly concave (Fig. 8A). The scapula blade expands gradually dorsoventrally from its mid-length to the distal end. The medial surface of the blade is essentially flat, and, unlike several titanosaurs (Powell, 1992; Bonaparte, 1996; Salgado et al., 1997), there are no ridge-like projections near its dorsal margin. There is a longitudinal ridge-like projection near the ventral margin of the scapula blade, at the point where the latter meets the proximal expansion (Fig. 8A). The lateral surface of the scapula blade is strongly convex dorsoventrally, with the dorsal margin somewhat thinner and more acute than the ventral one. Poor preservation means that the degree of expansion of the distal end of the scapula cannot be estimated accurately, but it seems probable that it lacked the extreme expansion found in *Haplocanthosaurus* (Hatcher, 1903), *Camarasaurus* (Osborn and Mook, 1921) and *Brachiosaurus* (Janensch, 1961).

Coracoid—Both the left (OUMNH J13609) and right (OUMNH J13610, Phillips [1871:figs. 84, 98]; Owen [1875:fig. 8]) coracoids of the large Bletchingdon animal are preserved (Fig. 8D, E, Table 3). The junction with the scapula, and the coracoid foramen, are missing in the left specimen, while the right coracoid is represented by only its ventral half. The cor-
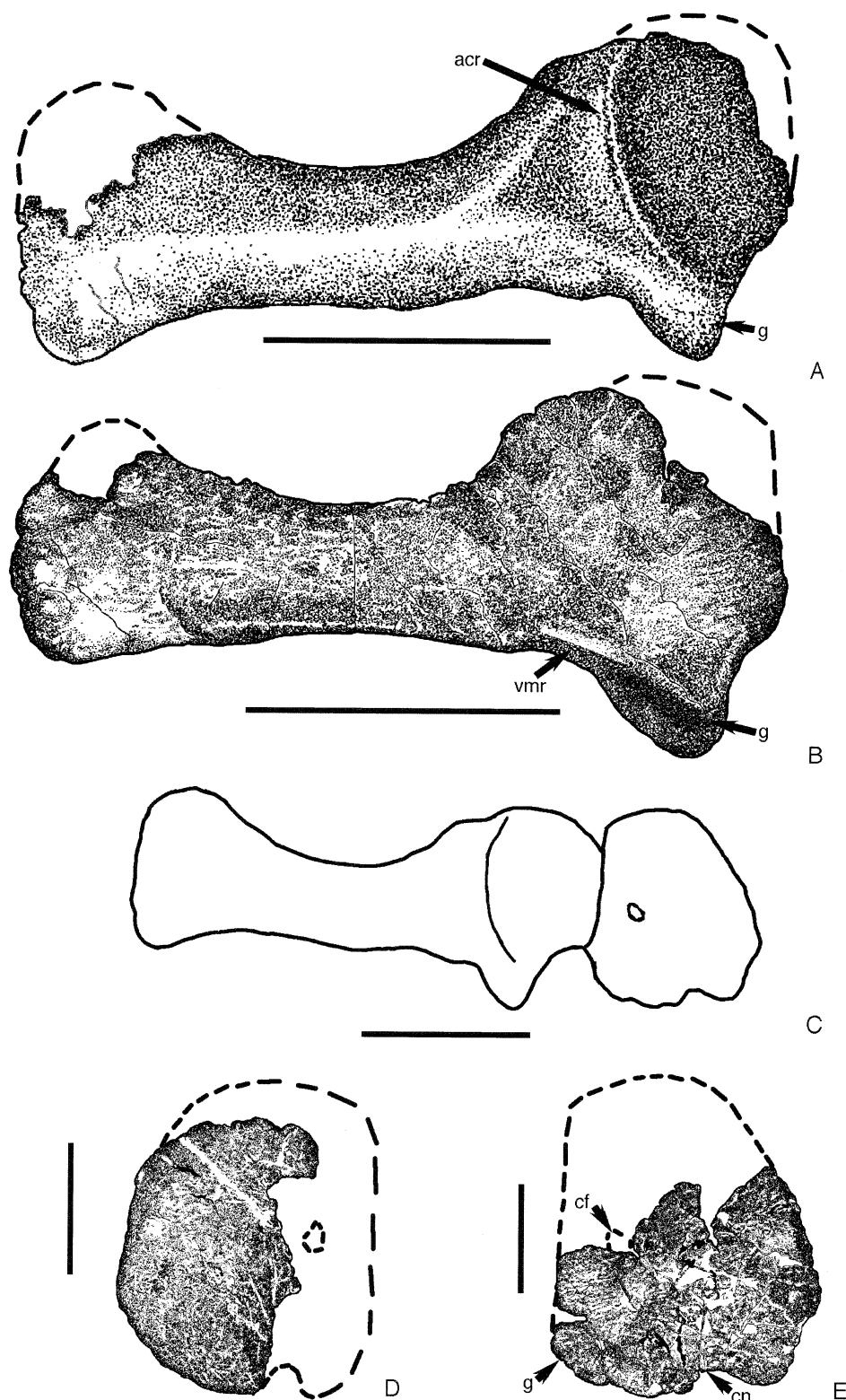
FIGURE 8.   The pectoral elements of the lectotype of *Cetiosaurus oxoniensis*: **A**, right scapula (OUMNH J13605) in lateral view; **B**, left scapula (OUMNH J13606) in medial view; **C**, restoration of the scapulocoracoid in lateral view; **D**, left coracoid (OUMNH J13609) in lateral view; **E**, right coracoid (OUMNH J13610) in lateral view. **Abbreviations**: **acr**, acromial ridge; **cf**, coracoid fenestra; **cn**, coracoid notch; **g**, glenoid fossa; **vmr**, ventral medial ridge. Scale bars equal 500 mm for **A–C** and 200 mm for **D** and **E**.

TABLE 3. Measurements of limb elements of *Cetiosaurus oxoniensis*. **Abbreviations**: **e**, estimated; **+**, minimum length (based on broken specimen). Measurements are in mm.

| Element/dimension	Left	Right
Scapula (OUMNH J13605, J13606)		
Greatest length	1,245+	1,370
Width across proximal expansion	665	660
Minimum width of scapular blade	240	250
Width across distal end of scapular blade	354e	400e
Coracoid (OUMNH J13609, J13610)		
Dorsoventral width	445+	—
Anteroposterior width	—	492+
Sternal plate (OUMNH J13607)		
Anteroposterior length	—	595
Maximum transverse width	—	370
Dorsoventral thickness at anterior end	—	65
Dorsoventral thickness at posterior end	—	31
Humerus (OUMNH J13612, J13613)		
Greatest length	1,260	1,236
Transverse width of proximal end	505	500
Length of deltopectoral crest	470	472
Minimum shaft circumference	594	575
Transverse width of distal end	365	364
Ulna (OUMNH J13611)		
Greatest length	—	930+
Width across proximal end (along anteromedial process)	—	280
Width across proximal end (along anterolateral process)	—	210
Minimum shaft circumference	—	346
Ilium (OUMNH J13622, J13623)		
Greatest length	990+	1,086+
Length of anterior process	—	390
Length of pubic peduncle	290	—
Height of iliac blade above pubic process	355	—
Diameter of acetabulum	421	—
Pubis (OUMNH J13624)		
Greatest length	950	—
Anteroposterior width across proximal end	385	—
Anteroposterior width of the shaft at mid-length	210	—
Length of ischial articulation	290e	—
Greatest diameter of the pubic foramen	115	—
Anteroposterior width of distal end	332	—
Transverse width of distal end	115	—
Ischium (OUMNH J13626)		
Greatest length	—	740+
Width across proximal end (from iliac articulation to ventral end of pubic articulation)	—	507
Length of chord across acetabular margin	—	264
Length of pubic articulation	—	270+
Greatest diameter of distal shaft, at its mid-length	—	167
Femur (OUMNH J13615)		
Greatest length	—	1,615
Transverse width of proximal end	—	525
Greatest anteroposterior width across proximal articular head	—	190
Distance from proximal end to top of 4th trochanter	—	605
Length of 4th trochanter	—	220
Minimum shaft circumference	—	683
Transverse width across distal end	—	438
Tibia (OUMNH J13621)		
Greatest length	—	945
Anteroposterior width across proximal end	—	390
Transverse width across proximal end	—	153
Minimum shaft circumference	—	455
Transverse width across anterior face of the distal end	—	300
Greatest anteroposterior width of distal end	—	160
Fibula (OUMNH J13619, J13620)		
Greatest length	—	945
Minimum shaft circumference	—	300
Anteroposterior width of distal end	—	208
Transverse width of distal end	—	78
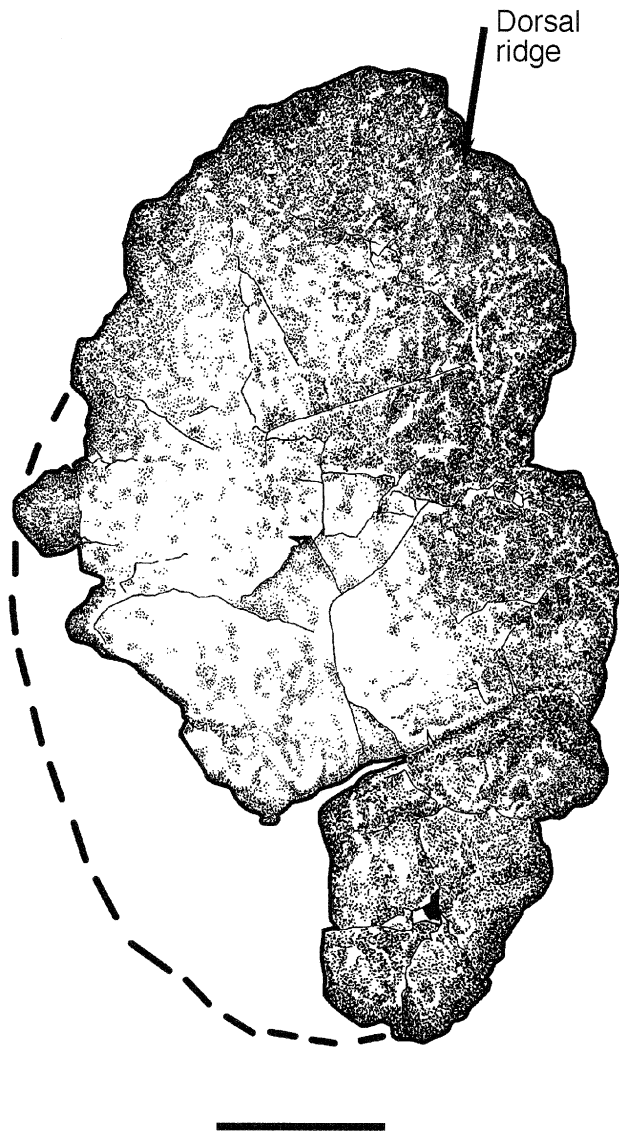
FIGURE 9. Dorsal view of the right sternal plate (OUMNH J13607) from the lectotype of *Cetiosaurus oxoniensis*. The stouter anterior end of the plate is situated towards the top of the page. Scale bar equals 100 mm.

acoid is a stout element which is strongly convex on its lateral surface and correspondingly concave medially. The lateromedial thickness of the coracoid is greatest near the glenoid and decreases anteriorly and dorsally, although these thinner areas were broken and lost in the field (Phillips, 1871). In lateral view, the coracoid retains the plesiomorphic rounded outline, rather than the derived subrectangular shape observed in *Opisthocoelicaudia*, *Saltasaurus* and several other titanosaurs (Salgado et al., 1997; Upchurch, 1998). A rounded notch-like indentation is present on the ventral margin of the right coracoid, lying anterior to the glenoid. The latter faces posteroventrally and is separated from the medial surface of the coracoid by a low rounded ridge. The coracoid foramen lies at approximately mid-height, a little displaced anteriorly from the junction with the scapula.

Sternal Plates—OUMNH J13607 (Phillips, 1871:fig. 98; Owen, 1875:fig. 1) is a nearly complete right sternal plate, lacking only a small part of the posteromedial portion (Fig. 9, Table 3). Both Phillips (1871) and Owen (1875) reconstructed the

sternal region with the greatest length of the plate oriented transversely. Articulated sauropod material, however, indicates that the long-axis of each sternal plate is typically subparalllel to the sagittal plane (Borsuk-Bialynicka, 1977; McIntosh, 1990). The *Cetiosaurus* sternal is an elongate oval plate which increases in dorsoventral thickness towards its anterior and lateral edges. The lateral margin is mildly convex in dorsal view; there is no concave emargination created by a prominent posterolateral expansion, unlike the 'kidney'-shaped sternals of titanosauroids (Salgado et al., 1997; Upchurch, 1998). The dorsal surface is mildly concave anteroposteriorly and convex transversely, making the sternal plate slightly 'saddle'-shaped. There is a low rounded eminence on the anterolateral portion of the dorsal surface. A ridge is also observed on the dorsal surface of each sternal plate in *Shunosaurus* and *Omeisaurus* (Upchurch, 1998), but these are much longer and more prominent than in *Cetiosaurus*. The sternal plate:humerus length ratio for *Cetiosaurus* is ~0.46, which represents the plesiomorphic state relative to the value of 0.75 or more in the titanosaurs *Alamosaurus* and *Opisthocoelicaudia* (Upchurch, 1998). No surfaces for articulation with sternal ribs can be observed on OUMNH J13608.

Humerus—The large Bletchingdon specimen is represented by nearly complete right (OUMNH J13612, Phillips [1871:figs. 84, 100]; Owen [1875:fig. 4]) and left (OUMNH J13613, Phillips [1871:figs. 84, 100]; Owen [1875:fig. 3]) humeri (Fig. 10A, Table 3). The proximal end of the humerus is broadly rounded in anterior view, rather than subrectangular as in Titanosauriformes (Upchurch, 1999). The posterior face of the proximal end has a vertical midline ridge which fades out at approximately one-third of the way down the shaft. The anterior face of the proximal end is shallowly concave, bounded laterally by the deltopectoral crest. The latter extends down the anterolateral margin, but at its most prominent point it expands medially across the anterior face: this is a less extreme version of a derived state observed in *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), *Saltasaurus* (Powell, 1992) and several other titanosauroids. As in most sauropods, this crest disappears well above the mid-length of the humerus. The central portion of the humerus has an anteroposteriorly compressed elliptical cross-section. The anconeal fossa is well developed and bordered laterally and medially by low rounded vertical ridges. Distally, the lateral and medial surfaces of the shaft are convex anteroposteriorly, but their detailed morphology is obscured by some crushing and wear. The distal articular surface is rugose and forms low condylar areas for the radius and ulna.

Ulna—Both the right (OUMNH J13611, Phillips [1871:fig. 103]) and left (OUMNH J13887) ulnae of the large Bletchingdon individual are nearly complete, apart from slight damage to the proximal and distal ends of the former (Fig. 10B–D, Table 3). As in all sauropods (Wilson and Sereno, 1998), the olecranon in *Cetiosaurus* is a low convex area, and the proximal end is divided into prominent anterolateral and anteromedial processes (Fig. 10D) which 'clasp' the radius (Fig. 10D). The articular surface of the anteromedial process is flat in the left ulna but longitudinally concave in the right specimen. The latter seems to have been produced by distortion, and it therefore appears that *Cetiosaurus* lacked the derived concave profile present in many titanosauroids (Upchurch, 1995, 1998). The medial surface of the proximal end is mildly concave, whereas the lateral surface is flat. The shaft of the ulna is subtriangular in cross-section at mid-length, where the bone is most slender. In lateral view the ulna is bowed somewhat forwards. Towards the distal end the shaft increases in robustness and a prominent vertical ridge appears on its anterolateral surface. The latter marks a ligamentous attachment to a corresponding ridge on the radius, and produces a subrectangular shaft cross-section at this point. The expanded distal end has a mildly convex and
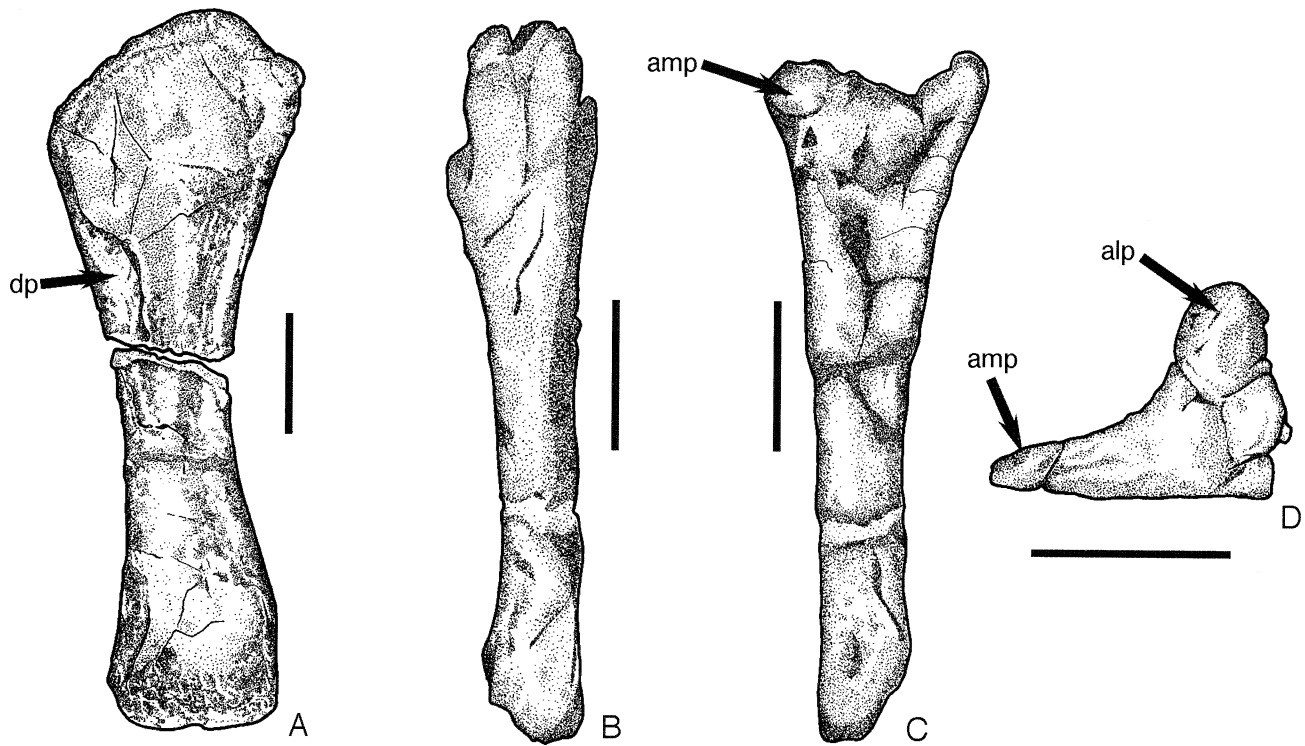
FIGURE 10.　Forelimb elements of the lectotype of *Cetiosaurus oxoniensis*: **A**, right humerus (OUMNH J13612) in anterior view; **B**, right unla (OUMNH J13611) in posteromedial view; **C**, as for B, in anterior view; **D**, as for B, proximal end view. **Abbreviations**: **alp**, anterolateral process; **amp**, anteromedial process; **dp**, deltopectoral crest. Scale bars equal 200 mm.

rugose articular surface which faces distally and a little posteriorly.

Manus—Phillips (1871:285) identified six specimens from the Enslow Rocks (Bletchingdon) as the proximal ends of metatarsals I–III from the left and right pedes. In the OUMNH catalogue, however, these specimens (J13742–J13747) are identified as distal portions of metacarpals. These elements are generally poorly preserved and have been heavily restored with plaster. OUMNH J13742 is indeterminate, while J13744 is potentially part of metatarsal I or II. The remaining four specimens, however, closely resemble the metacarpals of other sauropods. The most informative specimens are OUMNH J13743 (Mc.III?) and J13746 (Mc.II?), which are composed of real proximal and distal portions linked by reconstructed areas at mid-shaft. The proximal ends are flat and subtriangular in outline. There is a moderately deep striated excavation on the lateral surface of the proximal end, which forms the articulation with the adjacent metacarpal. These two features together suggest that the *Cetiosaurus* manus was formed from vertically oriented metacarpals in a 'U'-shaped arrangement, as occurs in eusauropods (Upchurch, 1998). Distal ends are strongly expanded transversely, forming lateral and medial rounded condyles separated on the midline by a very shallow and wide groove. The reconstructed lengths of these metacarpals are approximately 300 mm, which gives an estimated metacarpal:ulna length ratio of ~0.30. Although this figure represents only a crude estimate, it does suggest that *Cetiosaurus* probably did not have the elongate metacarpals characterizing camarasauromorphs (Wilson and Sereno, 1994, 1998; Salgado et al., 1997; Upchurch, 1998).

Ilium—Both the left (OUMNH J13622) and right (OUMNH J13623, Phillips [1871:fig. 105–107]; Owen [1875:fig. 9]) ilia of the large Bletchingdon individual are preserved (Fig. 11A, B, E, Table 3). The former lacks its posterior lobe and has a

portion missing from the middle of the dorsal margin, while the latter lacks much of the dorsal part and most of the pubic process. The anterior process is a curved subtriangular plate which tapers to an acute point. This plate lies in a nearly vertical plane, sloping a little dorsomedially, and projects mainly forwards. The precise orientation of this anterior process may have been affected by transverse compression; it seems probable, however, that *Cetiosaurus* lacked the laterally deflected anterior process which characterizes neosauropods (Wilson and Sereno, 1998). The ventral margin of the anterior process is slightly concave in lateral view, and is narrow and rounded in transverse section. The lateral surface of the ilium is moderately concave anteroposteriorly. The dorsal margin was probably strongly convex as in other sauropods (Gauthier, 1986). The pubic process is robust and semicircular in horizontal cross-section. This process appears to have provided more of a 'back wall' to the acetabulum than in other sauropod ilia, but this feature has probably been produced by crushing. At the proximal end of the pubic process, on its lateral surface, there is a shallow subtriangular concavity (Fig. 11A, B). The dorsal margin of this depression is formed by a longitudinal ridge which extends from above the acetabulum to the ventral margin of the anterior process. This lateral ridge/hollow structure has not been observed in any other sauropod and is therefore regarded as an autapomorphy of *Cetiosaurus*. The ischial peduncle is short and robust. A chord across the acetabulum (through the articular surfaces of the pubic and ischial peduncles) would pass above, or at least very close to, the ventral margin of the posterior lobe of the ilium (Fig. 11A, B): this reflects a derived degree of ischial peduncle reduction which also occurs in *Haplocanthosaurus* and the Neosauropoda (Upchurch, 1998). As in other sauropods (Gauthier, 1986), there is no brevis fossa on the posterior lobe of the *Cetiosaurus* ilium. Unfortunately, the large
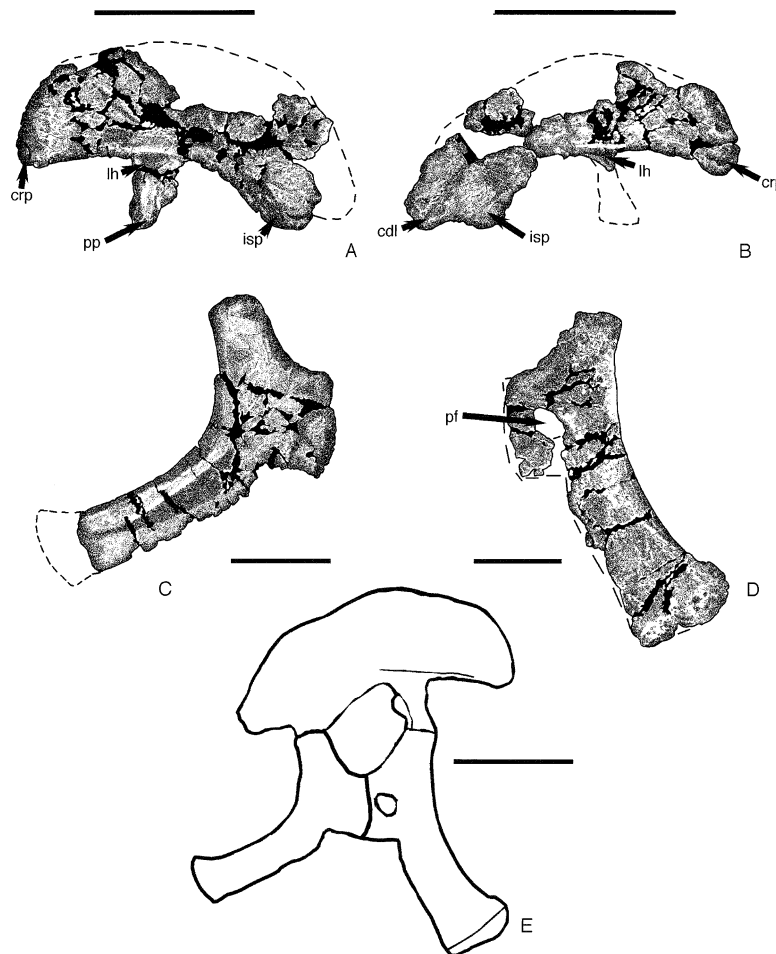
FIGURE 11. Pelvic elements from the lectotype of *Cetiosaurus oxoniensis*: **A**, left ilium (OUMNH J13622) in lateral view; **B**, right ilium (OUMNH J13623) in lateral view; **C**, right ischium (OUMNH J13626) in lateral view; **D**, left pubis (OUMNH J13624) in medial view; **E**, reconstruction of the pelvis in right lateral view. Scale bars equal 500 mm for **A**, **B**, **E**; 250 mm for **C** and **D**.

size and fragility of these ilia, which lie on their medial sides, means that the latter surface could not be examined.

Pubis—The left pubis (OUMNH J13624, Phillips [1871:figs. 84, 104]) is nearly complete apart from the loss of the ischial articulation and small portions missing from the distal end (Fig. 11D, E, Table 3). Part of the proximal end of the right pubis (OUMNH J13625) is also represented, but is too badly damaged to provide useful data. Phillips (1871:fig. 104) attempted a reconstruction of the relative positions of the pubis and ischium, but these elements were placed upside-down and contacted each other via their iliac articulations. The pubis is a relatively short robust element which is slightly bowed medially in anterior view. Just below its proximal end, the anterior margin is roughened, but the 'hook'-like ambiens process observed in *Dicraeosaurus* (Janensch, 1929), *Diplodocus* (Hatcher, 1901) and *Barosaurus* (Lull, 1919) is absent. The iliac articular surface is rough and ill-defined. Posterior to this region is a broad smooth area forming the acetabular margin. The pubic foramen is a large vertically elongate ellipse which extends ventromedially through the bone. Although the articulation for the ischium is not preserved, its length can be determined by reference to the pubic articulation of the ischium. On this basis, *Cetiosaurus* possessed a relatively narrow ischial articulation (~28% of pubis length) as occurs in all sauropods except camarasauromorphs (Salgado et al., 1997; Wilson and Sereno, 1998). At mid-length, the transverse section of the pubis resembles that in other sauropods, in that it is 'comma'-shaped with a stout anterior margin which expands laterally, and a thinner posterior portion. The ischium:pubis length ratio can only be estimated very approximately because of damage to the ischium: in *Cetiosaurus* this ratio is probably close to 1.0, suggesting that this form retained the derived shortening of the pubis which is present in all sauropods except titanosauroids (Salgado et al., 1997; Upchurch, 1998). As in all sauropod pubes, except that belonging to *Vulcanodon* (Cooper, 1984), there is little torsion between the long-axes of the proximal and distal ends (Upchurch, 1995). The distal end of the pubis is expanded, especially along its lateral margin, and has a convex rugose surface.

Ischium—The right ischium (OUMNH J13626, Phillips [1871:fig. 104]) is nearly complete, apart from some damage to its ventral margin and pubic articulation, and the loss of an estimated 150–200 mm long portion from the end of the distal shaft (Fig. 11C, E, Table 3). The mildly convex surface for articulation with the ilium is elliptical in outline, with the long-axis of this ellipse directed anteroposteriorly. The acetabular surface slopes directly medially rather than anteromedially as in other sauropods, but this may reflect damage to the more delicate medial margin of the acetabulum. A prominent groove extends along the dorsal surface of the anterior half of the distal shaft. This groove is divided into lateral and medial portions by a longitudinal rugosity, and probably represents the area of attachment of the M. flexor tibialis internus III (Romer, 1923;
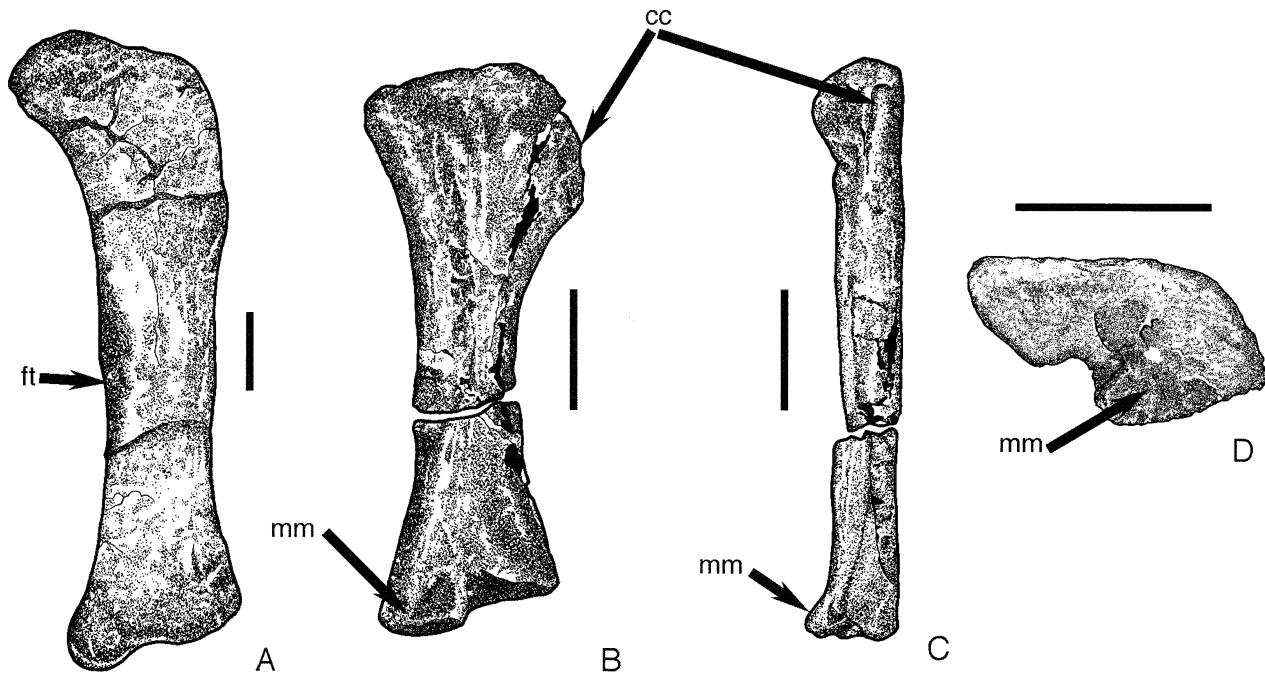
FIGURE 12.   Hindlimb elements of the lectotype of *Cetiosaurus oxoniensis*: **A**, right femur (OUMNH J13615) in posterior view; **B**, right tibia (OUMNH J13621) in posterolateral view; **C**, as for B, in anterior view; **D**, as for B, distal end view (anterior face oriented towards the top of the page). **Abbreviations**: **cc**, cnemial crest; **ft**, fourth trochanter; **mm**, medial malleolus. Scale bars equal 200 mm.

Borsuk-Bialynicka, 1977). There is no evidence that the distal blade was twisted relative to the plane of the proximal plate. Thus, *Cetiosaurus* probably lacked the derived state present in *Rayososaurus*, *Haplocanthosaurus*, and camarasauromorphs in which the flattened distal ends of the two ischia are coplanar (Upchurch, 1998:fig. 16; Wilson and Sereno, 1998). In lateral view, the distal shaft is slightly curved and its long-axis, if extrapolated forwards, would pass through the dorsal part of the pubic articulation or ventral part of the acetabulum. There is no suggestion that the shaft expanded towards its distal end, but it should be remembered that the terminal section is missing.

Femur—The femora of *Cetiosaurus* are represented by a right (OUMNH J13615) and left (OUMNH J13616) pair belonging to the large individual (Phillips, 1871:figs. 84, 108; Owen, 1875:fig. 6), and a left element (OUMNH J13617) from the small animal (Fig. 12A, Table 3). These femora closely resemble those of most other sauropods insofar as the main shaft is straight and anteroposteriorly compressed, there is no distinct 'neck' between the greater trochanter and the proximal articular head, the lesser trochanter is absent, and the fourth trochanter is reduced to a low ridge (Gauthier, 1986; McIntosh, 1990; Upchurch, 1998). The prominent lateral 'bulge', located near the proximal end of the femoral shaft in titanosauriform sauropods (Salgado et al., 1997:fig. 10; Upchurch, 1998; Wilson and Sereno, 1998), is absent in *Cetiosaurus*. The fourth trochanter lies at the posteromedial margin of the shaft as in *Haplocanthosaurus* and neosauropods (Upchurch, 1998). Just anterior to the fourth trochanter, on the medial surface of the shaft, there is a moderately deep and vertically striated concavity. The distal end of the femur is divided into a larger tibial and smaller fibular condyle by a deep intercondylar groove. The fibular condyle bears a wide vertical groove on its posterolateral face, as occurs in most dinosaurian femora. Poor preservation prevents any assessment of the extent to which the distal condyles projected forwards beyond the anterior face of the main shaft. The

medial surface of the tibial condyle is flat, vertically striated and faces a little upwards.

Tibia—The tibia of *Cetiosaurus* is represented by large right (OUMNH J13621, Phillips [1871:figs. 84, 109]; Owen [1875: fig. 7]) and small (OUMNH J13780, Phillips [1871:fig. 110]) specimens assigned to the largest and smallest Bletchingdon individuals respectively (Fig. 12B–D, Table 3). The large tibia is complete but broken at its center: the small specimen is shown as a complete well preserved element by Phillips (1871: fig. 110), but the only specimen in the OUMNH collection bearing the number J13780 is a poorly preserved limb bone which displays some similarities with a sauropod humerus. The description which follows, therefore, is based solely on OUMNH J13621. The tibia:femur length ratio is ~0.58, which is typical for the Sauropoda (McIntosh, 1990). The proximal end is strongly expanded relative to the shaft and has a transversely compressed profile unlike the derived, subcircular outline, characterizing the Neosauropoda (Wilson and Sereno, 1998). The lateral margin of the proximal end forms a prominent projection which extends distally into a ridge. The latter gradually merges with the shaft and disappears at approximately one-quarter of tibial length below the proximal end. The cnemial crest is a small stout plate which, as in other eusauropods, is directed mainly laterally (Wilson and Sereno, 1998). The posterolateral face of the cnemial crest is separated from the proximal lateral ridge by a deep vertical groove. The shaft is a little crushed, but seems to have been semicircular in cross-section with the flat surface facing laterally or posterolaterally. The distal end is expanded both anteroposteriorly and especially transversely. In this respect, *Cetiosaurus* possesses the plesiomorphic state present in prosauropods, *Vulcanodon* and titanosauroids (Salgado et al., 1997). The medial malleolus projects more distally and posteriorly than the lateral one, but seems to be reduced as in other eusauropods (Wilson and Sereno, 1998). There is a vertical groove between the lateral and medial malleoli on the pos-

terolateral face of the distal end. The anterior face of the tibia, just above the distal end, forms a broad flat triangular area.

Fibula—The OUMNH catalogue lists three fibulae from Bletchingdon: a large, nearly complete, right fibula (OUMNH J13619); a similar specimen which may represent a left fibula or a crushed radius (OUMNH J13620); and a small left fibula discovered by Strickland in 1848 (OUMNH J13618, Phillips [1871:fig. 107]) which was not found during our survey of the collections in 1997 (Table 3). The large right fibula is slightly damaged along the anterior margin of the proximal end and there is some restoration in places along the shaft. The *Cetiosaurus* fibula is similar to those of other sauropods, with a transversely compressed proximal end and a long slender shaft. The medial surface of the proximal end possesses the broad triangular scar, for articulation with the tibia, which is a derived state uniting *Barapasaurus*, *Omeisaurus* and neosauropods (Wilson and Sereno, 1998). At approximately one-third of the way from the proximal end, the anteromedial margin has a thickened striated prominence. Eusauropod fibulae typically have a lateral trochanter at mid-length (Wilson and Sereno, 1998); this derived state cannot be detected in *Cetiosaurus*, but this may be due to breakage and restoration. Towards the distal end, the anterior margin of the shaft forms an acute vertical ridge, whereas the corresponding posterior margin is somewhat thicker and more rounded. The distal articular surface is convex and expands medially.

DISCUSSION AND CONCLUSIONS

Systematic revision of *Cetiosaurus* suggests that this genus contains only a single British species, *C. oxoniensis*, which is currently known from the Bathonian of Oxfordshire and the Bajocian of Rutland. The partial skeleton of a large individual from Bletchingdon Station, Oxon., is designated as the lectotype of *C. oxoniensis*.

This re-examination of British sauropod material also indicates the presence of: a diplodocoid(?) ('*Cetiosaurus glymptonensis*') from the Bathonian of Oxfordshire; a brachiosaurid ('*Ornithopsis leedsi*') from the Callovian of Cambridgeshire; a potentially distinct brachiosaurid ('*Cetiosaurus humerocristatus*') from the Kimmeridgian of Dorset; and a titanosauriform (*Pelorosaurus conybeari*) from the Valanginian of Sussex. Prior to this study, the oldest known diplodocoid was *Cetiosauriscus* from the Callovian of Cambridgeshire: '*C. glymptonensis*' potentially extends the stratigraphic range of this clade back into the Bathonian. Similarly, '*Ornithopsis leedsi*' joins *Lapparentosaurus* (from the Bathonian of Madagascar), *Volkheimeria* (from the Callovian of Argentina), and *Atlasaurus* (from the Bathonian-Callovian of Morocco), to provide glimpses of the early diversification of the Brachiosauridae. The current work, and several previous studies (Upchurch, 1995; Wilson and Sereno, 1998), demonstrate that neosauropods had originated and diversified into several major clades by the Bathonian. Such an early diversification is consistent with the Middle Jurassic fragmentation of Pangaea (Upchurch, 1995; Upchurch et al., 2002), and is directly supported by the early representatives of the major lineages reported above.

The revised diagnosis of *Cetiosaurus* provides the first opportunity for a preliminary reassessment of the Moroccan taxon *C. mogrebiensis* Lapparent, 1955. The type material of the latter species consists of three cotype partial skeletons from separate localities in Morocco (Lapparent, 1995; Monbaron et al., 1999). Lapparent (1955:23) referred this material to *Cetiosaurus* on the basis of the following shared characters: (1) the pleurocoels in dorsal vertebrae lie in an elevated position; (2) strongly developed anterior chevrons; (3) robust middle caudals; (4) reduced curvature of the scapula; (5) similarly shaped humeri; (6) triangular cross-section through the shaft of the ulna; (7) radii

which differ from that of *Bothriospondylus*; (8) the ischium is elongate and has an expanded shaft; (9) the pubis is robust and strongly expanded in its proximal part; (10) similarly shaped femur. Most of these features are defined in vague terms and/or are present in a variety of other sauropod genera. None of the characters listed by Lapparent correspond with the autapomorphies identified in the current study. In fact, it is difficult to justify Lapparent's referral of the Moroccan specimens to *Cetiosaurus* because the former are damaged in key areas such as the cervical and dorsal neural spines. Certain differences between the English and Moroccan specimens, such as the presence of more extensive dorsal pleurocoels in the latter, also suggest that they are not congeneric. The type material of '*C. mogrebiensis*' clearly requires detailed re-evaluation, but there is currently no compelling evidence that this Moroccan material genuinely belongs to *Cetiosaurus*.

It is hoped that the revised taxonomy and anatomy presented above will encourage the incorporation of *Cetiosaurus oxoniensis* into future phylogenetic analyses. The only phylogenetic studies which have included *Cetiosaurus* were carried out by Upchurch (1995, 1998). These analyses were hampered by substantial quantities of missing data for *Cetiosaurus*, but suggested that this taxon lies outside of, but closely related to, the Neosauropoda. In the near future, Upchurch and Martin (in prep.) will provide a description of the Rutland specimen of *Cetiosaurus*, and undertake a full assessment of the phylogenetic relationships of this genus using the revised information on its anatomy. In this way, *Cetiosaurus* should yield new insights into the sequence of events leading to neosauropod origins.

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