

# THE RUTLAND *CETIOSAURUS*: THE ANATOMY AND RELATIONSHIPS OF A MIDDLE JURASSIC BRITISH SAUROPOD DINOSAUR

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**ABSTRACT.** A relatively well-preserved specimen of *Cetiosaurus oxoniensis*, from the Middle Jurassic (Bajocian) of Rutland, United Kingdom, is described in detail. The material includes a nearly complete cervical series, representative dorsal vertebrae, a fragment of sacrum, anterior caudals, the right femur, and numerous rib and limb fragments. Contrary to previous suggestions that this specimen possesses 14 cervical and ten dorsal vertebrae, it seems more probable that there were at most 13 cervicals and at least 12 dorsals. The vertebral column displays several autapomorphic features which supplement the generic diagnosis of *Cetiosaurus*, including: (1) a stout, anteriorly directed process located at the top of the neural spine of the twelfth (?) cervical vertebra; and (2) the presence of lateral pits, separated by a thin midline septum, below the transverse processes of middle dorsal vertebrae. Cladistic analysis indicates that *Cetiosaurus* is probably the sister-taxon to the advanced neosauropod clade. This relationship affects the distribution of particular character states that have played an important role in determining sauropod phylogeny.

**KEY WORDS:** cladistic analysis, phylogeny, Sauropoda.

IN June 1968 the driver of an excavating vehicle, working in a pit belonging to Williamson Cliffe Brickworks (Great Casterton, Rutland), noticed bone protruding from a number of siderite nodules. By the time Leicester City Museums (LCM) staff arrived at the quarry on June 20th, all the bone-bearing nodules had been removed to another part of the pit so that clay extraction could resume. No detailed stratigraphical or sedimentological information was obtained at the time, nor was it ever confirmed that all of the preserved material had been collected. The estimated four tonnes of nodules were taken to Leicester, where M. D. Jones (LCM) organized the preparation of some of the elements over the following two years. The remaining nodules were prepared between 1981 and 1985, revealing that the various specimens probably belonged to a single medium-sized partial sauropod skeleton. Jones (1970) announced the discovery of this material, briefly described representative cervical, dorsal and caudal vertebrae, and identified them as belonging to *Cetiosaurus oxoniensis* Phillips; however, no detailed description has been provided until the current study.

Until recently, the genus *Cetiosaurus* has been largely neglected, mainly because of the confusion produced by an inadequate generic diagnosis and the creation of numerous ill-defined species. Upchurch and Martin (in press) reviewed the taxonomy of the British *Cetiosaurus* species and demonstrated that only *C. oxoniensis*, based on a partial skeleton from Bletchington, Oxfordshire, can be characterized by clear autapomorphic features. This Bletchington material provides important anatomical data on the morphology of the tail, girdles and limbs: although it includes one damaged cervical and at least 20 portions of dorsal vertebrae, the detailed structure of the presacral vertebrae cannot be seen. By contrast, the Rutland *Cetiosaurus* specimen possesses a nearly complete cervical series and several well preserved dorsal vertebrae. The current paper, therefore, has two principal aims: (1) to increase our knowledge of *Cetiosaurus* anatomy by describing the Rutland specimen in detail; and (2) to incorporate the new anatomical data into existing data-matrices so that the phylogenetic relationships of *Cetiosaurus* can be established more precisely.

**Abbreviations.** Anatomy: Cd, caudal vertebra; Cv, cervical vertebra; D, dorsal vertebra; S, sacral vertebra. Institutions: BMNH, The Natural History Museum, London; CMNH, Carnegie Museum of Natural History, Pittsburgh; LCM,

Leicester City Museums, Leicester; OUMNH, Oxford University Museum of Natural History, Oxford; ZDM, Zigong Dinosaur Museum, Zigong.

#### MATERIAL

The Rutland *Cetiosaurus* specimen, LCM G468.1968, includes the following material: cervicals '2–14' (see discussion of vertebral formula below), some with ribs of the left or both sides; neural arches, spines or centra of at least 11 dorsals and many thoracic rib fragments; at least four sacral centra, with parts of the parapophyses; four sacral ribs and possible sacral spines; 13 anterior caudals; several damaged chevrons; fragments of both ilia and the left ischium; and the right femur. As noted above, no field data were collected on site in 1968. The extent to which the skeleton was disarticulated before burial can only be deduced from the associations of bones in blocks of matrix recorded as the specimens were unwrapped and prepared during 1981–85.

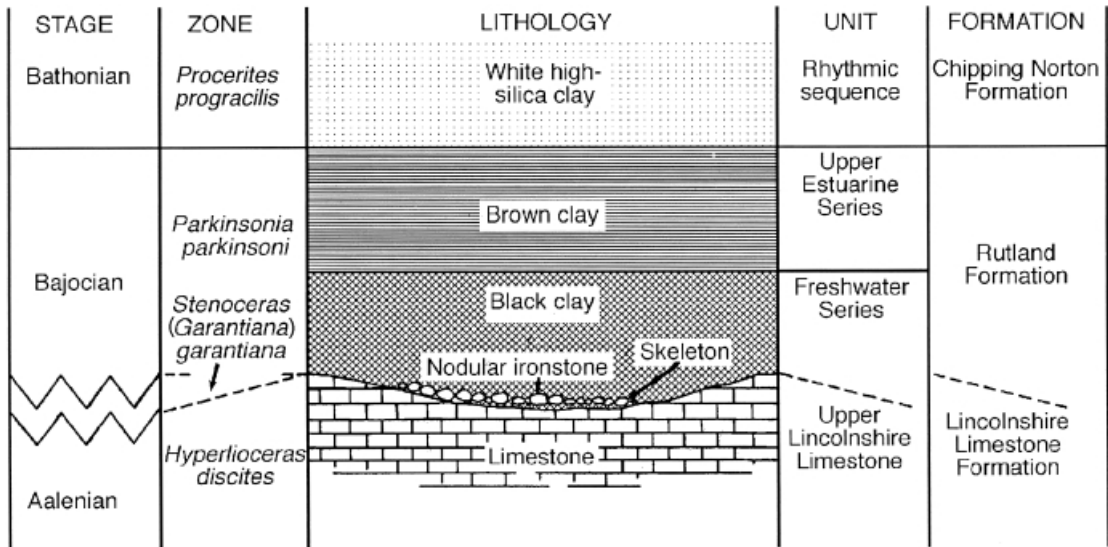
Preservation of the individual elements varies from excellent to very poor. The presacral vertebrae can be arranged into a 'natural series' which implies few gaps in the sequence. These vertebrae are generally best preserved on their left sides. This preservation, combined with the relative sizes of the different elements and the absence of duplicated elements, suggests that LCM G468.1968 represents the remains of a single sauropod carcass which lay on its left side during burial. While the cervical and caudal series were relatively well protected, the central portion of the skeleton was more severely affected by erosion, resulting in fragmentation of the ribs, disruption of the dorsal series, and loss of much of the sacrum and limb elements.

#### GEOLOGICAL SETTING

##### *Stratigraphy*

The probable stratigraphical age of the Rutland sauropod can be determined with reasonable accuracy. Jones (1970, p. 145) wrote that '... the productive horizon occurs near the base of the upper Estuarine Series [Rutland Formation] (Bathonian), the lower nine feet of which consists of black carbonaceous shale...'. Jones' unpublished manuscript notes provide more detail on the nature of the Upper Estuarine Series at the Great Casterton quarry. Three sedimentological units can be distinguished: (1) an upper, brown, high-silica clay; (2) a middle, black, high-alumina clay; and (3) a lower 'ironstone', 1 m thick, resting on the Lincolnshire Limestone. Subsequent work (see below), however, identified the brown clay as the Upper Estuarine Series, while the black clay and ironstone are considered to represent a lower Freshwater Series (Text-fig. 1). The sauropod remains are recorded, by Jones, as having been found 'below the middle black clay', although the sketch section in Jones' manuscript shows the bones between the middle black clay and the lower ironstone. A more likely interpretation (supported by some of the matrix preserved with the specimen), therefore, is that the skeleton was incorporated in the top of the ironstone.

Above the brown clay Estuarine Series there is a high silica white clay known as the 'Rhythmic Sequence' which is possibly marine in origin (Text-fig. 1). Bradshaw (1978) has traced the top rhythms of the Rhythmic Sequence into the middle Bathonian (*Procerites progradilis* Zone) Hampen Marly Formation of the south Midlands of England (see also Cope *et al.* 1980). This suggests that the base of the Rhythmic Sequence represents the start of Bathonian-age deposits across the East Midlands, including the Great Casterton locality. Bradshaw (pers. comm. 1983) estimated (by downward event counting) that the black basal clay with ironstone (containing the dinosaur skeleton) is of late Bajocian [*Stenoceras* (*Garantiana*) *garantiana* Zone] age (Text-fig. 1). This would make the Freshwater Series the lateral equivalent of the late Bajocian part of the Hook Norton Member of Oxfordshire. A late Bajocian age for the lower part of the Rutland Formation is supported by other workers. For example, Fenton *et al.* (1994) correlated the lower member of the Rutland Formation with the 'White Sands' of central England and dated the latter as late Bajocian on the basis of dinoflagellates. The Rutland *Cetiosaurus* may therefore be two biozones older than the Bathonian specimens of '*Cetiosaurus medius*' from Chipping Norton (OUMNH J13693–13703; Owen 1842), and up to seven biozones older than *C. oxoniensis* from Bletchington Station, Oxfordshire (Phillips 1871; Upchurch and Martin in press).



TEXT-FIG. 1. Schematic diagram showing the probable original stratigraphic position of the Rutland *Cetiosaurus* skeleton (LCM G468.1968) relative to stratigraphic formations, stages, units, ammonite biozones, and lithology (based on Jones 1970, and field notes; Bradshaw 1978).

#### *Lithology, environment and associated palaeontology*

In the East Midlands generally, the Rutland Formation (in particular the Freshwater Series mentioned above) consists of brown, mauve or white high-silica clays and sands resting directly on an eroded surface of the marine, Bajocian, Lincolnshire Limestone Formation (Horton 1977; Fenton *et al.* 1994; Berridge *et al.* 1999). Plant debris is always an important constituent of these basal deposits and is sometimes concentrated enough to form a coal, as at Elton sand pit, Cambridgeshire (TL 087960). At Great Casterton (and also Grange Quarry, Ketton, Leicestershire, SK976056) there are black high-alumina clays (the basal metre of which is iron-rich) interposed between the paler clays above and the limestone below (Text-fig. 1). Bradshaw (1978) described these black carbonaceous deposits lying in a marked 'depression or hollow' in the Lincolnshire Limestone, and noted that the lowest metre (probably Jones' 'ironstone' of 1968) might be heavily iron-stained and contained mudstone nodules with drifted plant material. On this basis, the black clays were probably lake bottom and bottomset beds. Bradshaw (1978) also showed that the black infrabasals Rutland Formation clay at Great Casterton occupied a depression, which was at least 400 m across, in the eroded, perhaps karstic, surface of the Lincolnshire Limestone Formation. Similar clay-filled hollows of relatively small size (up to 1 km wide) are found throughout the East Midlands area. They are thought to have been the sites of first deposition of late Bajocian or early Bathonian sediments following the end of the low sea-level and emergent condition of much of Britain during the early Late Bajocian (Bradshaw 1978). Sediment input to this lake was probably controlled by rainfall in the catchment area of contributory streams, influxes of coarser material, with wave rippling and plant debris, being produced at times of flood upstream. Indeed the *Cetiosaurus* carcass itself may have been introduced to the lake by one of these events.

Other fossils from the lake-fill deposits of the Rutland Formation at Great Casterton are listed in Table 1.

#### SYSTEMATIC PALAEOLOGY

SAURISCHIA Seeley, 1888

SAUROPODOMORPHA von Huene, 1932

TABLE 1. A list of the fossils found in the lake deposits at Great Casterton, Rutland, England (based on Sharp 1873, Judd 1875, Jones 1970, Bradshaw, pers. comm. 1983, Clements, pers. comm. 1985, and Martin, pers. obs.).

Lacustrine environment	
Plantae	<i>Equisetites</i> sp.
Ostracoda	<i>Cypridea</i> sp.?
Bivalvia	<i>Unio</i> cf. <i>andersoni</i> (Hudson)
Gastropoda	<i>Viviparus</i> spp., ' <i>Valvata</i> sp.'
Vertebrata	fish scales, shark teeth, bone debris, crocodilian tooth
Hinterland	
Plantae	coniferous bisaccate pollen, <i>Neocalamites</i> sp., <i>Bennettitales</i> sp., Ginkgoales sp.

SAUROPODA Marsh, 1878  
 EUSAUROPODA Upchurch, 1995  
 CETIOSAURIDAE Lydekker, 1888  
 Genus CETIOSAURUS Owen, 1841

*Type species.* *Cetiosaurus oxoniensis* Phillips, 1871 (proposed by Upchurch and Martin in press), from the Forest Marble Formation (Bathonian) of Bletchingdon Station, Oxfordshire.

*Diagnosis.* As for type species.

*Cetiosaurus oxoniensis* Phillips, 1871

Text-figures 2–10, Tables 2–3

- 1871 *Cetiosaurus medius* Owen; Phillips, p. 245.
- \*1871 *Cetiosaurus oxoniensis* Phillips, p. 245, figs 86–112.
- 1875 *Cetiosaurus longus* Owen; Owen, p. 27, pl 10, figs 3–11.
- 1888 *Cetiosaurus oxoniensis* Phillips; Lydekker, p. 137.
- 1889 *Ornithopsis oxoniensis* (Phillips); Seeley, p. 391.
- 1890 *Cardiodon oxoniensis* (Phillips); Lydekker, p. 236.
- 1927 *Cetiosaurus oxoniensis* Phillips; von Huene, p. 21.
- 1932 *Cetiosaurus oxoniensis* Phillips; von Huene, p. 221, fig. 21 (an isolated braincase).
- 1970 *Cetiosaurus oxoniensis* Phillips; Steel, p. 1.
- 1970 *Cetiosaurus oxoniensis* Phillips; Jones, p. 144.
- 1990 *Cetiosaurus oxoniensis* Phillips; McIntosh, p. 345.

*Lectotype.* The partial skeleton of a large individual from Bletchingdon Station, Oxfordshire (OUMNH J13605–13613, J13615–13616, J13619–13688, J13899). This lectotype designation is proposed by Upchurch and Martin (in press).

*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 (OUMNH J13617–8, J13780–1), from the same locality and horizon as the lectotype.

*Referred material.* The partial skeleton of a medium-sized sauropod (LCM G468.1968) from the Rutland Formation (Bajocian), Great Casterton Quarry, Rutland, UK.

*Revised diagnosis.* Medium to large eusauropod; cervical vertebrae relatively short (centrum length:height ratio less than 3.0), with simple deep pleurocoels and undivided neural spines; middle dorsal vertebrae have dorsolaterally directed transverse processes; caudal centra are amphicoelous and lack pleurocoels and

ventral excavations; anterior chevrons with bridge of bone over the haemal canal; forelimb:hindlimb ratio *c.* 0.86; girdle and limb elements resemble those of other sauropods but generally lack the derived features present in particular neosauropod clades.

*Autapomorphies.* \* marks those autapomorphies observed in both the type material and that from Rutland: (1)\* symmetrical, pyramid-shaped, neural spines on posterior cervicals and anterior dorsals; (2) Cv12 (and possibly other posterior cervicals) possesses an anteriorly directed stout process at the top of the neural spine; (3)\* middle dorsal vertebrae possess a deep excavation on either side of the neural arch, immediately below the transverse process, which leave only a thin septum of bone on the midline; (4)\* loss of the spinodiapophyseal lamina (or complete fusion of this lamina with the spinopostzygapophyseal lamina) on all dorsal neural spines; (5) distal caudal centra have 'tongue-like' projections on their articular faces which extend the floor of the neural canal anteroposteriorly; (6) distal shafts of anterior chevrons are anteroposteriorly compressed and do not taper to a transversely flattened distal end; (7) triangular hollow (bounded dorsally by a horizontal ridge) on the lateral surface of the base of the pubic process of the ilium.

#### TAXONOMY OF *CETIOSAURUS* OWEN, 1841

The taxonomy and nomenclature of British *Cetiosaurus* material was fully revised by Upchurch and Martin (in press), and is briefly summarised below. Thirteen species of *Cetiosaurus* are listed in the literature. Three of these (*C. epioolithicus*, *C. giganteus* and *C. hypoolithicus*) are *nomina nuda*; two species (*C. conybeari* and *C. rugulosus*) are junior objective synonyms; four species (*C. brachyurus*, *C. leedsi*, *C. longus* and *C. medius*) are based on undiagnostic material and are therefore *nomina dubia*; and four species (*C. brevis*, *C. glymptonensis*, *C. humerocristatus* and *C. oxoniensis*) can be diagnosed by autapomorphies but display characters that suggest they come from distantly related genera. *C. glymptonensis* is potentially a basal diplodocoid sauropod, whereas *C. brevis* and *C. humerocristatus* appear to belong to titanosauriform sauropods.

This revised taxonomy creates some nomenclatural difficulties because *C. medius* Owen 1842 has generally been regarded as the type species (Steel 1970; McIntosh 1990). Since the type material of *C. medius* is undiagnostic, the options available are: (1) to designate a new type species from those available within *Cetiosaurus*; (2) to retain the name *C. medius*, but base it on diagnosable material; or (3) to create a new genus and species to contain diagnosable *Cetiosaurus* material. Upchurch and Martin (in press) preferred option 1 because conservation of the name *Cetiosaurus* seems less disruptive than option 3, and option 2 is ruled out by lack of adequate material.

*C. brevis* Owen 1842 is the only valid species name of the original four designated by Owen. Under a strict interpretation of ICZN rules [Art. 67(g)], therefore, *C. brevis* should become the type species of *Cetiosaurus*. The name *C. brevis*, however, has rarely been used in the literature, partly because its type material consists of caudal vertebrae that have subsequently been referred to *Pelorosaurus conybeari* from the Lower Cretaceous of Sussex. In most cases, workers have used the name *Cetiosaurus* to refer to the well-preserved *C. oxoniensis* Phillips 1871 material from the Middle Jurassic of Oxfordshire. Upchurch and Martin (in press), therefore, suggested that the strict interpretation of ICZN rules would cause confusion and nomenclatural instability, and should be set aside under the provisions of Article 79. In summary, there appears to be only one valid species within *Cetiosaurus*, though it is not entirely clear which species name should be adopted. It should be stressed that the use of *C. oxoniensis* as the type species of *Cetiosaurus*, here and in Upchurch and Martin (in press), represents our personal preference and can have no formal standing until an ICZN ruling permits the suspension of the normal rules of priority. A formal case for the suppression of the name *C. brevis*, and designation of *C. oxoniensis* as the type species of *Cetiosaurus*, will be submitted to the IZCN in the near future.

#### DESCRIPTION OF THE RUTLAND SPECIMEN

##### *Axial skeleton*

The vertebrae of the Rutland *Cetiosaurus* are referred to below by their position in the mounted skeleton, or by their accession number if not included in the latter. As will become clear in the discussion of vertebral formula, the position

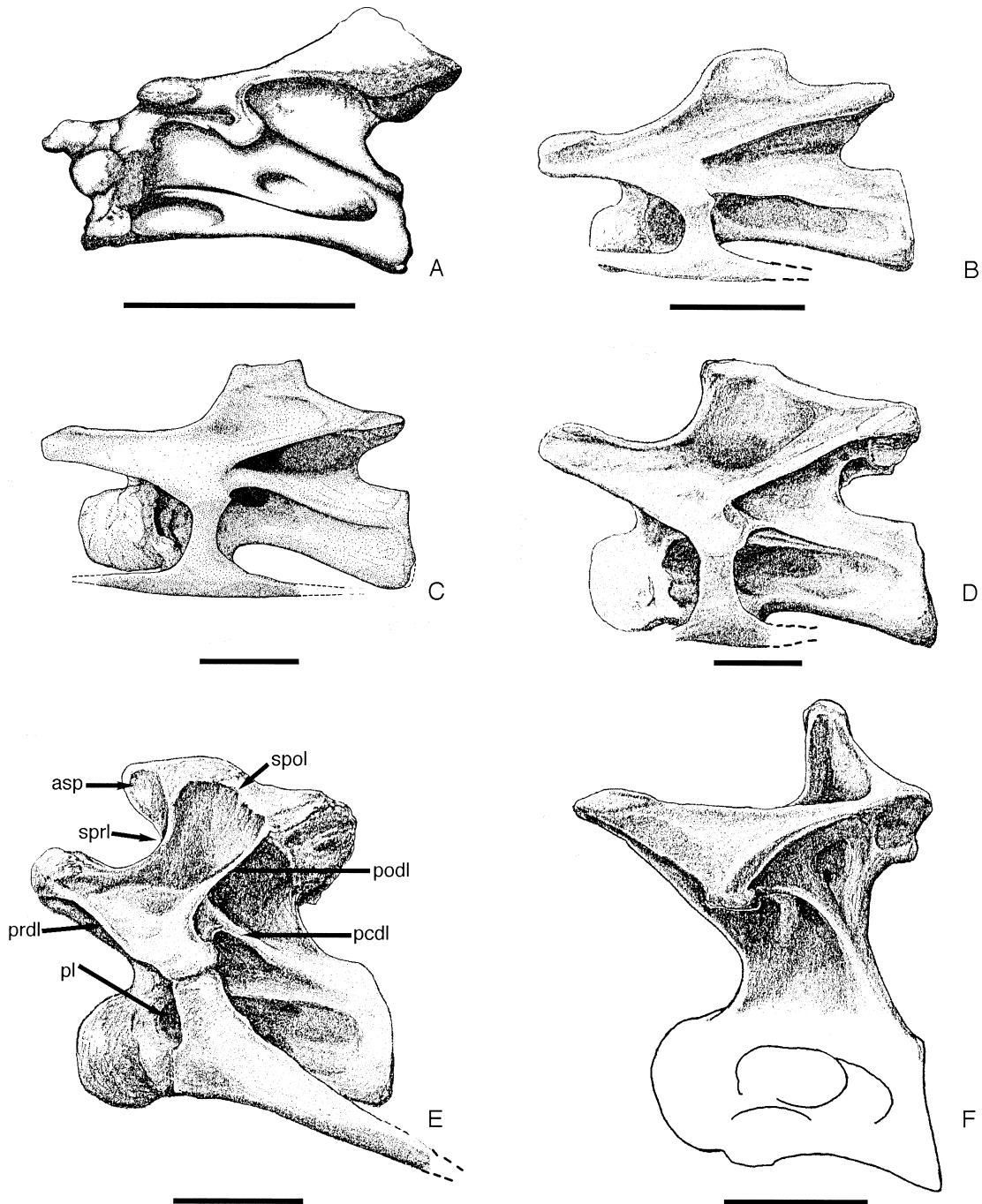
of the vertebrae in the mounted skeleton may not reflect the true sequence in the living animal. The following description employs Wilson's (1999) nomenclature for vertebral laminae.

*Odontoid* (Text-fig. 2A). The odontoid is fused to the anterior end of the axis, as occurs in the larger (and perhaps older) individuals of other sauropod genera (Upchurch 1993). This element is cone-shaped, tapering to a bluntly rounded anterior end. In *Cetiosaurus*, the odontoid seems to be rather low dorsoventrally relative to its anteroposterior and transverse diameters. The dorsal surface is mildly concave transversely.

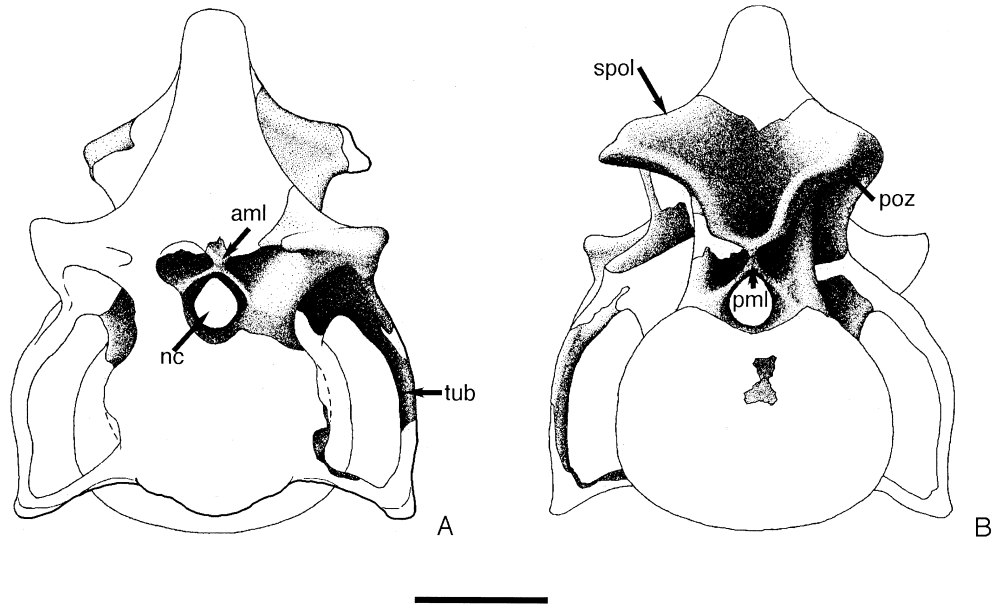
*Axis* (Text-fig. 2A, Table 2). The ventral surface of the centrum and much of the anterior and dorsal portions of the neural spine were missing in the original specimen and have been restored. The centrum is relatively elongate (length:width ratio equals 2.23), as in other sauropodomorphs (Upchurch 1993), and possesses a depression on each of its lateral surfaces (Text-fig. 2A). These depressions are long anteroposteriorly and low dorsoventrally. They are not true pleurocoels since they do not ramify within the body of the centrum. The posterior end of the centrum forms a shallowly concave articular surface. The long, low, neural arch is best preserved at its posterior end, although the anterior portion on the right side is also present. The right prezygapophysis projects forwards but terminates posterior to the anterior end of the centrum. The prezygapophyseal articular facet faces outwards and upwards, as is typical for the axes of diapsids (Sereno 1991). A small lateroventrally directed transverse process lies approximately midway between the pre- and postzygapophyses. The latter are larger and higher than the prezygapophyses, and possess lateroventrally directed articular facets which project beyond the posterior end of the centrum. The anterior margin of each postzygapophysis is linked to the transverse process by the postzygodiapophyseal lamina, which curves steeply downwards and forwards. None of the laminae which support the transverse process from below has survived intact.

TABLE 2. Measurements of the presacral vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968). Abbreviations: e, estimated; Hcp, height of centrum across posterior face; Hsp, neural spine height (from postzygapophyses to spine crest); Lda, axial length of the spine crest; Lc, length of centrum; TH, total height of vertebra; Tpw, distance between the tips of the transverse processes; Vert., vertebra (no. in mounted skeleton); Wcp, width of centrum across posterior face; Wdp, transverse width of the spine crest across its posterior surface; Wpoz, transverse width across postzygapophyses; Wprz, transverse width across prezygapophyses. All measurements are in mm.

Vert.	Lc	Hcp	Wcp	Lda	Wdp	Hsp	TH	Wprz	Wpoz	Tpw
Axis	145	65	65	–	–	56	148	72	97	–
Cv3	193	75e	84e	–	–	52	154e	120	129	–
Cv4	243	85	93	–	–	55	163	110	118	–
Cv5	265	97	115	–	–	56	192	123	124	–
Cv6	265	100	129	–	–	68	215	–	140	–
Cv7	315	127	142	–	–	70	236	167	147	–
Cv8	337e	126e	145e	–	–	103	283e	167	175	–
Cv9	356e	144e	160e	–	–	115e	333e	213	220e	–
Cv10	360	159	180	–	–	165e	357	235	210e	–
Cv11	–	–	–	–	–	143e	337	–	–	–
Cv12	254	165	177	125	66	154	–	242	218	378
Cv13	–	–	–	–	–	–	–	240	238	–
Cv14	–	–	–	–	–	–	–	267	–	–
D1	–	–	–	40	49	155	–	180	193	310
D2	–	–	–	62	56	194	–	154	148	416
D3	–	–	–	81	47	160	–	132	139	410
D4	–	–	–	–	–	–	–	152	150	304
D5	186e	150	174	–	57	210	–	–	–	400e
D6	–	–	–	–	–	–	–	–	–	–
D7	–	154	183	–	–	–	–	134	176	354
D8	–	–	–	–	–	–	–	–	155	416
D9	–	–	–	–	–	–	–	120	144	390
D10	–	–	–	93	116	219	–	135	240	424e



TEXT-FIG. 2. Cervical vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968) in left lateral view. A, axis. B, Cv5. C, Cv8. D, Cv10. E, Cv12. F, Cv'14' (probably an anterior dorsal vertebra). Abbreviations: asp, anterior spine process; pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; podl, postzygodiapophyseal lamina; prdl, prezygodiapophyseal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Key: shaded/stippled areas represent bone; plain areas represent plaster reconstruction (either complete fabrication or plaster covering and supporting real bone). Scale bars represent 100 mm.



TEXT-FIG. 3. Cervical vertebra no. 10 of the Rutland *Cetiosaurus* (LCM G468.1968) in A, anterior view, and B, posterior view. Abbreviations: aml, anterior midline lamina; nc, neural canal; pml, posterior midline lamina; poz, postzygapophyses; spol, spinopostzygapophyseal lamina; tub, tuberculum. For key to shading, see explanation of Text-figure 2. Scale bars represent 100 mm.

The neural spine is formed largely by the stout spinopostzygapophyseal laminae. Although only the bases of these laminae are preserved, it seems likely that they ran upwards, forwards and medially, to converge at the top of the neural spine. The height of the spine is greater in *Cetiosaurus* than in *Omeisaurus tianfuensis* (ZDM T5703, He *et al.* 1988, fig. 18), but probably lower than those in neosauropods (e.g. *Camarasaurus*, CMNH 11338, Madsen *et al.* 1995).

*Cervical vertebrae 3–'14'* (Text-figs 2B–F, 3; Table 2). Centra are well preserved in Cv3–8, 11, and 12, damaged in Cv9 and 10, and missing in Cv13 and '14'. The cervical centra increase in length and overall size towards the posterior end of the series (Table 2). They do not, however, become especially elongate: the length:height ratios for the cervicals of *Cetiosaurus* are close to 2:3, with a maximum value of 2.6 in Cv4, whereas this ratio is greater than 4.0 in many cervicals belonging to diplodocids and euhelopodids (Upchurch 1994, 1995, 1998). Cv12 in *Cetiosaurus* has a length:height ratio of 1.44, indicating a relative shortening of the centra towards the posterior end of the cervical series. As in virtually all sauropods, the cervical centra possess a hemispherical anterior articulation and a concave posterior articular 'cup'. In lateral view (Text-fig. 2), the ventral rim of this 'cup' projects more posteriorly than the lateral and dorsal margins. The ventral surface of each centrum is arched upwards anteroposteriorly: transversely, this surface is concave between the anteriorly placed parapophyses and becomes flat towards the posterior end. With the exception of Cv12, where there is a low midline ridge, *Cetiosaurus* cervicals lack a ventral keel. As in other sauropods, the parapophyses are situated at the anteroventral corner of the lateral surface of the centrum throughout the cervical series. The dorsal surface of the parapophysis is excavated, a derived state present in neosauropods but absent in euhelopodids and possibly *Patagosaurus*. In *Cetiosaurus*, this depression is continuous with the pleurocoel, whereas in neosauropods these two areas are separated by a longitudinal ridge (Upchurch 1998). The parapophyses of middle and posterior cervicals become anteroposteriorly elongate. The depression/pleurocoel on the lateral surface of each centrum is underlain by a stout ridge [the 'postparapophyseal lamina' (NB, this is a new term which only applies to cervicals and is not recorded by Wilson 1999)] which extends backwards from the posterior margin of the parapophysis. The anterior cervical centra display a shallow depression on each lateral surface. In middle and posterior cervicals these depressions deepen and become true pleurocoels, which ramify within the body of the centrum. By Cv6, the midline septum between left and right pleurocoels has become very thin, and in several of the more posterior cervicals this area is perforated (probably due to damage). Although the posterior portion of each



pleurocoel is often shallower than the anterior part, these regions are not separated by an oblique lamina, unlike those of *Omeisaurus* and most neosauropods (Upchurch 1995, 1998; Wilson and Sereno 1998). The pleurocoels of *Patagosaurus* appear to be similar to those of *Cetiosaurus*, lacking a dividing accessory lamina and becoming shallower towards the posterior end of each vertebra (Bonaparte 1986a).

The neural arches of the anterior and middle cervicals are relatively low, but increase in height from approximately Cv10 onwards. The prezygapophyses are supported from below by stout centroprezygapophyseal laminae. These laminae do not bifurcate into medial and lateral branches at their dorsal ends, unlike those of diplodocoid sauropods (Upchurch 1993). The medial edge of each prezygapophysis runs backwards and a little medially in dorsal view. In the anterior and middle cervicals, the medial margins of the prezygapophyses meet, on the midline, at the top of the anterior neural canal opening. In more posterior cervicals this midline junction occurs at a point some way above the top of the neural canal; the former is joined to the latter by a small vertical midline lamina (the 'anterior midline lamina'; Text-fig. 3A). This short lamina was not named by Wilson (1999). The anterior face of the arch is marked by a shallow hollow on either side of the anterior midline lamina, as occurs in many neosauropods. The prezygapophyses themselves are large and project forwards to a point beyond the anterior end of the centrum. From Cv11 onwards, the prezygapophyses project somewhat upwards, as well as forwards, in lateral view (Text-fig. 2). The prezygapophyseal articular facets are flat (unlike those of *Barosaurus* and *Diplodocus*, which are convex transversely) and face dorsally and moderately medially. In the posterior cervicals and anterior dorsals, both pre- and postzygapophyses develop transversely broadened articular facets, and are situated further from the midline (Table 2). The prezygapophyses are joined to the transverse processes by the prezygodiapophyseal laminae (Text-figs 2–3). In the anterior cervicals, this lamina runs lateroventrally in anterior view, and posteroventrally in lateral view. The lateral surface of the cervical neural arch is divided into three cavities by the anterior and posterior centrodiapophyseal laminae. The middle cavity, below the diapophysis, is separated from the pleurocoel by a horizontal ridge which probably represents the suture between the arch and centrum. This ridge and the small deep pocket-like excavation above it, appear to be absent in *Patagosaurus* (Bonaparte 1986b, figs 36–37) and other sauropods. The anterior centrodiapophyseal lamina is generally short and steeply inclined whereas the posterior centrodiapophyseal lamina is longer and directed backwards and a little downwards in anterior and middle cervicals. Towards the posterior end of the cervical series the latter lamina is shorter and becomes more steeply inclined. This pattern of laminae and cavities, and the changes in orientation of the laminae along the series, is typically found in all other sauropods.

The transverse process is joined to the postzygapophysis by the postzygodiapophyseal lamina. In the anterior cervicals, this lamina curves upwards and backwards from the dorsal surface of the transverse process to the anterior margin of the postzygapophysis (Text-fig. 2). The transverse processes themselves curve outwards and downwards in anterior view. The articular facets of the postzygapophyses are flat and face outwards and downwards. In those cervicals where the posterior region of the arch is well preserved, the anterior portions of the postzygapophyses meet each other on the midline. In the more anterior cervicals this midline junction occurs at the top of the posterior neural canal opening. From Cv9 onwards, however, the midline junction between the postzygapophyses is joined to the top of the neural canal by a vertical lamina (the 'posterior midline lamina'). As with the anterior face of the neural arch, the posterior face has an excavated area on either side of the midline lamina. In more posterior cervicals, each postzygapophysis is supported from below by a vertical centropostzygapophyseal lamina.

The neural spines remain unbifurcated throughout the presacral series. The spines of the anterior and middle cervicals are relatively long (anteroposteriorly) and low. These spines are formed from the spinopre- and spinopostzygapophyseal laminae and a central portion (the 'spine crest'). The long, prominent, spinoprezygapophyseal laminae originate just behind the prezygapophyses and extend medially and posterodorsally to converge at the anterior end of the spine crest. Between these laminae there is a shallow, longitudinally striated, anterodorsally facing hollow. The spine crest itself is an anteroposteriorly elongate, transversely narrow, ridge representing the highest point of the spine. The spinopostzygapophyseal laminae originate from the dorsal surfaces of the postzygapophyses and extend medially and anterodorsally to converge at the posterior end of the spine crest. Between these laminae, above the postzygapophyses, there is a deep postspinal hollow which apparently extends forwards below the spine crest. In the anterior cervicals of *Patagosaurus* (Bonaparte 1986b, fig. 36), the spine crest is relatively taller, and narrower anteroposteriorly, than in *Cetiosaurus* (Text-fig. 2). Passing posteriorly along the neck, the neural spines increase in height and shorten anteroposteriorly. Unlike the cervicals of other sauropods, the Rutland specimens maintain the prominence of the spinoprezygapophyseal laminae in the posterior part of the series. As a result, posterior cervical and anterior dorsal neural spines have spinopre- and spinopostzygapophyseal laminae which are nearly symmetrical across both a sagittal and a transverse plane through the spine crest. The net effect of this morphology is to create a neural spine which is pyramid-shaped, with deep excavations in its anterior, lateral, and posterior faces. This distinctive morphology has not been observed in any other sauropod except *Cetiosaurus oxoniensis* from Bletchington Station, Oxfordshire, and it is therefore regarded as an autapomorphy of this genus. A second unique feature is also present in at least one posterior cervical (Cv12), where there is a stout process, projecting forward, at the top of the spine (Text-fig.

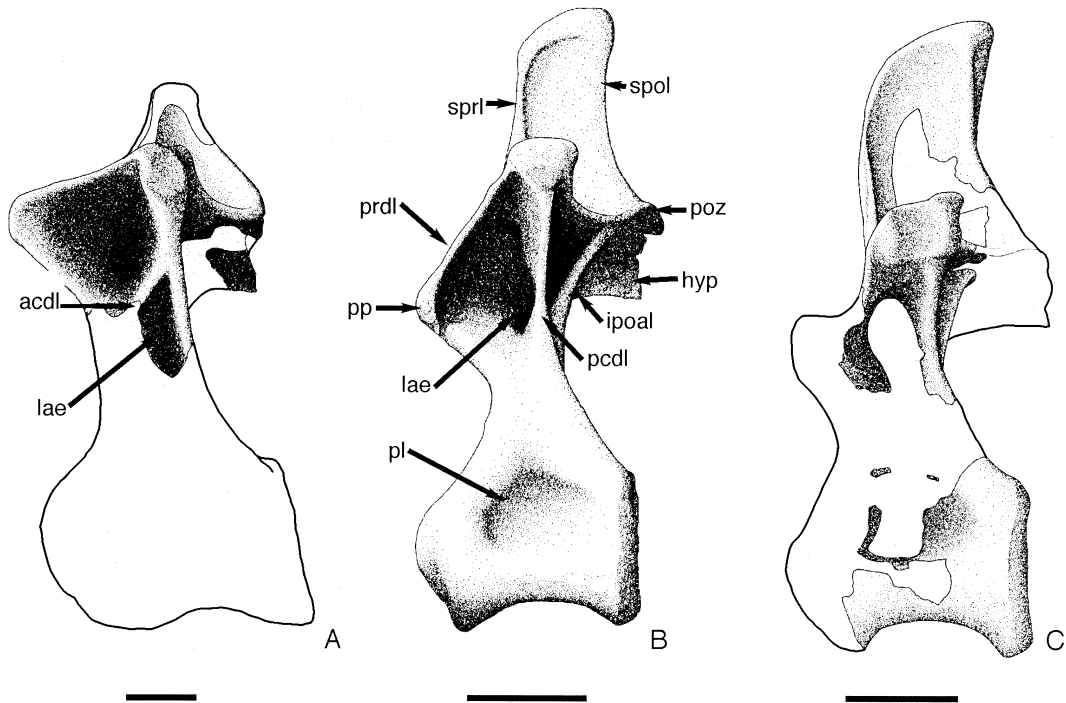
2E). Unfortunately, the anterodorsal portions of the spines of Cv11, 13 and '14', are poorly preserved, and it is not clear whether they also possessed a similar anterior projection. Nevertheless, no other sauropod possesses such a process on any of the cervicals, and the anterior projection is therefore tentatively regarded as an autapomorphy of *Cetiosaurus*. The spinopre- and spinopostzygapophyseal laminae, and the surface of the spine crest, have a rough texture. The anterior and posterior faces of the spines, especially in the more posterior cervicals, display marked longitudinal striations. Such areas presumably mark muscle and ligament attachments.

*Cervical ribs.* Portions of cervical rib are preserved in Cv3, 4, 7–8, and 10–12 (Text-figs 2–3). In most cases only the anterior process, capitulum and tuberculum are preserved: most of the distal shafts have been broken off and are not represented in the skeletal mount. Numerous fragments of these distal shafts are preserved in the collections of the LCM. It is difficult to determine accurately the relative length of the cervical ribs, but the long anterior process and the slender nature of the distal shaft fragments suggest that *Cetiosaurus* probably had long overlapping ribs in at least the middle of the cervical series. Thus, *Cetiosaurus* probably possessed the plesiomorphic state found in most sauropods rather than the derived shortened ribs present in various diplodocids (Upchurch 1998). The anterior process is best preserved in Cv7, where it is long and tapers anteriorly to a blunt point. The angle between the capitulum and tuberculum is close to, or slightly less than, 90 degrees. This means that the rib shaft lies almost level with the ventral margin of the cervical centrum. Wilson and Sereno (1998) noted that the capitulum-tuberculum angle is greater than 90 degrees in basal sauropods such as *Shunosaurus*, and is reduced to less than 90 degrees in *Omeisaurus* and neosauropods (where the ribs lie well below the ventral margin of the cervical centra). As far as can be ascertained from the Rutland material, the capitulum-tuberculum angle in *Cetiosaurus* is intermediate between the plesiomorphic and derived states. The rib associated with Cv12 is shorter, broader and more flattened than those belonging to middle cervicals.

*Dorsal vertebrae* (Text-figs 4–5; Table 2). Dorsal centra are only preserved in D5–8 of the Rutland *Cetiosaurus*. These centra are a little longer (anteroposteriorly) than high. The form of the anterior articular surface is not well preserved. It may have been flat, but there is some suggestion, in at least two of the centra, that this region was mildly convex as in the middle dorsal (OUMNH J13644/2) of *C. oxoniensis* from Bletchington Station, Oxfordshire (Phillips 1871; Upchurch and Martin in press). The posterior articular surfaces are concave. The ventral surfaces are arched upwards anteroposteriorly and flat transversely. The latter feature represents one of the few differences between the Rutland and Oxford specimens of *Cetiosaurus*; in the latter material, the ventral surface of each dorsal centrum is formed from ventrolaterally facing surfaces which meet each other at a midline ridge. It is not clear at present whether this discrepancy should be given any taxonomic significance (see Discussion). The lateral surface of each centrum is marked by a deep depression in its anterodorsal part (Text-fig. 4). In D5, the midline septum between the left and right depressions is replaced by plaster, but was probably quite thin in life. There is no indication that these depressions ramified widely within the centrum or base of the neural arch, unlike the pleurocoels of *Brachiosaurus*, *Camarasaurus*, *Haplocanthosaurus*, and several other neosauropods (Upchurch 1998).

The neural arches of 'Cv14' and the dorsal vertebrae are relatively tall (arch height exceeds centrum height), as occurs in other sauropods (Bonaparte 1986a; Upchurch 1998). The position of the parapophysis is unknown on D1–3. In D4, however, the parapophysis has 'migrated' dorsally to a point approximately two-thirds of the way up the neural arch. Although not well preserved, the parapophyses of D5–10 are apparently situated close to the level of the prezygapophyses, as occurs in the majority of middle and posterior dorsals of most dinosaurs. Each prezygapophysis is supported from below by a stout, vertical, centroprezygapophyseal lamina. In neosauropods, the centroprezygapophyseal lamina bifurcates into lateral and medial branches towards its dorsal end. This creates three laminae: the medial lamina below the prezygapophysis resembles the original centroprezygapophyseal lamina; the lateral branch, supporting the parapophysis from below, is termed the anterior centroparapophyseal lamina; and finally there is a prezygaparapophyseal lamina linking the prezygapophysis to the parapophysis. In *Cetiosaurus* and other basal sauropods, however, the centroprezygapophyseal lamina remains undivided throughout its length (Text-fig. 5A–C). These laminae form the lateral walls of a large hollow on the anterior surface of the neural arch. This hollow is partially roofed dorsally by a stout horizontal ridge of bone (the intraprezygapophyseal lamina) which links the bases of the prezygapophyses. According to Wilson and Sereno (1998), the intraprezygapophyseal lamina represents one of the synapomorphies uniting a clade containing *Barapasaurus*, *Omeisaurus* and Neosauropoda. D1 and D10 of the Rutland specimen have a stout vertical midline ridge running down the back wall of the anterior hollow. The prezygapophyses have flat articular surfaces which face dorsomedially (and a little forwards in the more anterior specimens). There is little evidence of the presence of hypantral facets on the medial surfaces of the prezygapophyses (except possibly in D10), but this may be a result of poor preservation.

On the lateral surfaces of D1, 2 and 10 (but not the other dorsals), there is a short anteroventrally directed anterior centriapophyseal lamina (Text-fig. 4A). All the dorsals of *Cetiosaurus* possess a prominent, nearly vertical, posterior

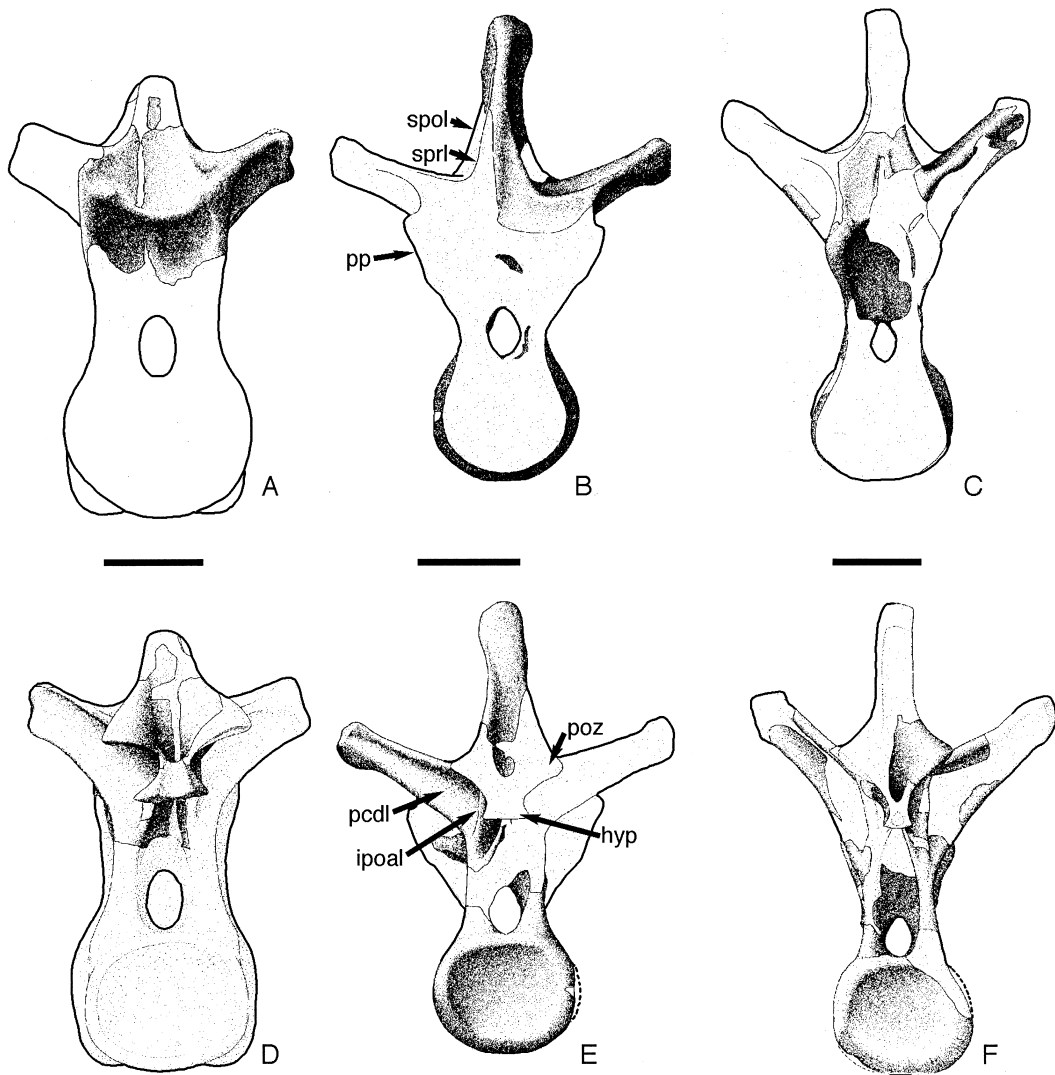


TEXT-FIG. 4. Dorsal vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968) in left lateral view. A, D1. B, D5. C, D7. Abbreviations: acdl, anterior centrodiapophyseal lamina; hyp, hyosphene; ipoal, infrapostzygopophyseal accessory lamina (NB, this is a new term, not used by Wilson 1999); lae, lateral accessory excavation (i.e. the fossa immediately below the transverse process); pcdl, posterior centrodiapophyseal lamina; pl, pleurocoel; poz, postzygopophysis; pp, parapophysis; prdl, prezygodiapophyseal lamina; spol, spinopostzygopophyseal lamina; sprl, spinoprezygopophyseal lamina. For key to shading, see explanation of Text-figure 2. Scale bars represent 100 mm.

centrodiapophyseal lamina, which supports the transverse process from below (Text-fig. 5). This lamina does not widen or bifurcate at its ventral end, unlike those of many titanosaurs (Salgado *et al.* 1997). The hollow defined by the postzygodiapophyseal and posterior centrodiapophyseal laminae possesses an accessory lamina extending posterodorsally towards the base of the postzygopophysis. Such accessory laminae are frequently present in the dorsals of neosauropods and some euhelopodids, but appear to be absent in *Patagosaurus* and *Barapasaurus* (Jain *et al.* 1979; Bonaparte 1986b; Upchurch 1998).

Bonaparte (1986a, b) has observed the presence of a 'neural cavity' (an excavated area within the body of the neural arch) in several sauropod genera. In most neosauropods (except *Haplocanthosaurus* and dicraeosaurids) the neural cavity is entirely enclosed by bone. In *Barapasaurus* and *Patagosaurus* anterior dorsals lack a neural cavity. Instead, there is a deep excavation on either side of the neural arch, immediately below the base of the transverse process, which leaves only a thin septum of bone on the midline (Jain *et al.* 1979, pl. 102; Bonaparte 1986b). The middle and posterior dorsals of these two genera possess neural cavities, but unlike those of other sauropods, these cavities are linked to the exterior of the vertebra via a foramen located in a position equivalent to the lateral excavation just described (Jain *et al.* 1979, pl. 102; Bonaparte 1986b, figs 39–41). Jain *et al.* (1979) have proposed that, at least in *Barapasaurus*, the lateral excavations of the anterior dorsals transform into the neural cavity plus lateral foramen of the middle and posterior dorsals, simply by becoming more extensive. In the Rutland material, the anterior and middle dorsal vertebrae possess the lateral excavations and thin midline septum below the transverse processes. None of the posterior dorsals is well enough preserved to reveal whether a neural cavity is present. The Oxford *Cetiosaurus* material also demonstrates that the lateral excavation system persists as far back as at least the middle dorsals (Upchurch and Martin in press), a unique condition which represents an autapomorphy of the genus.

The transverse processes of *Cetiosaurus* are directed dorsolaterally (Text-fig. 5). As in the type specimen from Bletchington and *Patagosaurus* (Bonaparte 1986b), the transverse processes of the most anterior and posterior dorsals



TEXT-FIG. 5. Dorsal vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968) in anterior (A–C) and posterior (D–F) views. A, D, D1. B, E, D5. C, F, D7. Abbreviations: hyp, hyosphene; ipoal, infrapostzygapophyseal accessory lamina (NB, this is a new term, not used by Wilson 1999); pcdl, posterior centrodiapophyseal lamina; poz, postzygapophysis; pp, parapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. For key to shading, see explanation of Text-figure 2. Scale bars represent 100 mm.

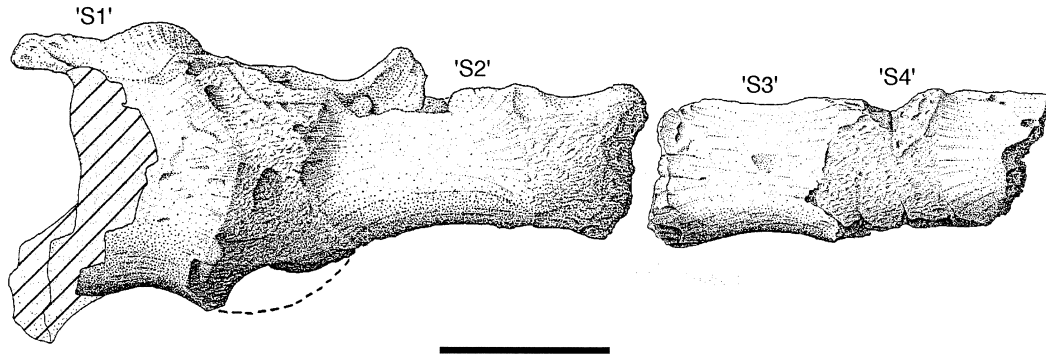
are inclined less strongly upwards than those of the middle dorsals. In other sauropods, transverse processes are either directed horizontally throughout the dorsal series (*Barapasaurus*, *Brachiosaurus*, *Camarasaurus*, diplodocids), or are strongly dorsolaterally inclined in the anterior dorsals and maintain this orientation through the series (*Shunosaurus*, *Haplocanthosaurus*, dicraeosaurids, and at least some titanosaurids). Each transverse process is essentially triradiate in parasagittal section, being formed from the posterior centrodiapophyseal, prezygo- and postzygodiapophyseal laminae. In at least some of the more posterior dorsals, such as D10, a pocket-like excavation is present on the anterior surface of the distal end of the transverse process.

A hyposphene appears to be present on all of the preserved dorsals, including D1 (Text-fig. 5D–F). In most sauropods (except titanosaurids where hyposphene-hypantrum systems are absent; Upchurch 1998) the most anterior dorsals lack a hyposphene, the latter first appearing on D3 or D4. The presence of a hyposphene on D1 of *Cetiosaurus* could be interpreted as a derived condition, but a more likely explanation is that this element was originally preceded by two or more dorsals in life (see below). In other respects, the hyposphenes of *Cetiosaurus* are like those of other sauropods, being triangular in posterior view, and situated on the midline immediately below the postzygapophyses. The lateroventral edges of each hyposphene pass forwards into laminae (the centropostzygapophyseal laminae) which extend ventrally and a little laterally, eventually merging into the back surface of the posterior centrodiapophyseal lamina (Text-figs 4–5). Between these centropostzygapophyseal laminae, and below the hyposphene, there is a large hollow on the arch, lying above the neural canal opening. The hyposphenes are not supported from below by a single midline lamina, unlike those of diplodocids. The portion of bone between the anterior and posterior arch hollows has a variable thickness; 40–50 mm thick just above the neural canal, becoming thinner dorsally. This structure differs from that present in *Haplocanthosaurus* and dicraeosaurids, where the thickness of the transverse septum between the two hollows is greatly reduced.

The dorsal neural spines of *Cetiosaurus* are generally well preserved, except in D4, and 6–8 (base preserved in latter). In lateral view, the spines ‘lean’ a little backwards, particularly those belonging to the more posterior dorsals. The neural spines are formed from a central portion or plate of bone (the spine core) which is nearly vertical, plus the left and right spinopre- and spinopostzygapophyseal laminae (Text-figs 4–5). In D1 and 2, spinopre- and spinopostzygapophyseal laminae are equal in prominence and extend from the base of the spine to its summit (forming the pyramid-shape described above). Passing posteriorly along the dorsal series, several trends can be observed: the spines become taller; the ‘core’ region widens anteroposteriorly and becomes laterally compressed; the spinoprezygapophyseal laminae are directed more laterally (rather than anterolaterally) at their bases and become less prominent than the spinopostzygapophyseal laminae; and from D3 onwards, both spinopre- and spinopostzygapophyseal laminae ‘fade out’ close to the summit. As a result of these changes, the middle and posterior dorsal neural spines of *Cetiosaurus* lose their pyramid-shape and generally resemble those present in *Patagosaurus* and *Barapasaurus*. Unlike titanosauriforms and diplodocoids, *Cetiosaurus* dorsals do not possess pre- or postspinal laminae. The anterior, dorsal and posterior surfaces of all spines are rugose. The summit of the neural spine of D10 is particularly robust and laterally expanded. This expansion overhangs the hollow formed on the lateral surface of the spine, but does not project beyond the lateral edge of the spinopostzygapophyseal lamina. Throughout the dorsal series, the spinopostzygapophyseal lamina remains single at its base rather than bifurcating as occurs in diplodocoids (Wilson 1999). The neural spines of the middle and posterior dorsals of LCM G468.1968 differ slightly from those in the Oxford material. In particular, the latter possesses spines which are more anteroposteriorly compressed, with a spine core which is relatively wide transversely. The spines belonging to the Oxford material are less well preserved than those from Great Casterton, and at least some of the differences in morphology are probably related to crushing and wear. Nevertheless, a morphological difference of potential systematic importance may exist between the two *Cetiosaurus* specimens.

Most sauropods possess a spinodiapophyseal lamina on their middle and posterior dorsals. This lamina extends from the dorsal surface of the transverse process to the anterior face of the spinopostzygapophyseal lamina at approximately one-third of the way up the spine. The presence of the spinodiapophyseal lamina is a synapomorphy uniting *Barapasaurus* + Eusauropoda (Upchurch 1998) or *Barapasaurus* + *Oemisaurus* + Neosauropoda (Wilson and Sereno 1998). The Oxford *Cetiosaurus* material suggests that there is no spinodiapophyseal lamina on at least the middle dorsals (Upchurch and Martin in press). The Rutland material confirms this and also indicates that this lamina is absent on the posterior dorsals as well. It is conceivable that the absence of the spinodiapophyseal lamina in *Cetiosaurus* represents a retention of the plesiomorphic state. Phylogenetic analysis (Upchurch 1995, 1998) demonstrates, however, that *Cetiosaurus* lies within the clade characterized by the presence of this lamina. Thus, the absence of the spinodiapophyseal lamina is here interpreted as an autapomorphy of *Cetiosaurus*.

*Thoracic ribs.* Numerous fragments of thoracic rib are preserved, but none has been incorporated into the mounted skeleton. The following description is based on four of the larger portions: accession nos. 10–11, 282, and 283. The proximal end is formed from the stout capitulum and tuberculum (the latter probably varying in height along the thoracic series, as in other sauropods). These two articular processes merge into a broad anteroposteriorly flattened region which tapers ventrally to form the rib shaft. The anterior and especially the posterior faces of this proximal plate are mildly concave. In lateral view, the proximal portion of the shaft is slightly bowed anteriorly. The anterolateral margin of the tuberculum and proximal plate forms a low ridge which extends ventromedially onto the anterior face of the proximal part of the shaft. As a result, the proximal part of the shaft is typically subtriangular in cross-section, with posterior, medial and anterolateral faces. There is no sign that the proximal ends of the ribs possess pneumatic foramina, nor is the internal structure of the rib pneumatic or cancellar. In this respect, *Cetiosaurus* retains the



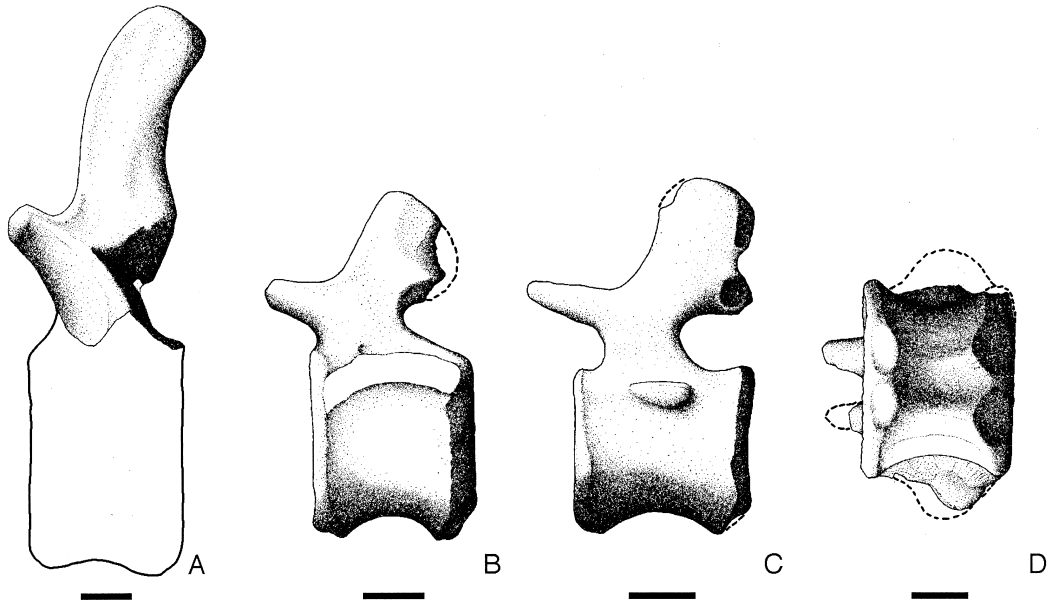
TEXT-FIG. 6. Four sacral centra of the Rutland *Cetiosaurus* (LCM G468.1968) in ventral view. For key to shading, see explanation of Text-figure 2. Scale bar represents 100 mm.

plesiomorphic condition relative to that found in titanosauriform sauropods (Wilson and Sereno 1998). The rib shaft, in its middle portion, becomes a little broader anteroposteriorly and compressed lateromedially. Unfortunately, the thoracic ribs are not well enough preserved to provide any further data on their structure, nor can variation along the thoracic series be accurately assessed.

*Sacrum* (Text-fig. 6). The sacrum of *Cetiosaurus* is only known from fragmentary remains. Two portions, representing the ventral part of a series of four coalesced sacral centra, are preserved (Text-fig. 6). The dorsal portions of these centra have been eroded away along an oblique plane, so that the centra appear to decrease in transverse width towards one end of the series. For the purposes of description, the wider end of this series will be arbitrarily considered to be the remnant of sacral 1. The ventral surfaces of the centra are transversely convex in 'S1' and '2', but become noticeably flatter in 'S3' and '4'. The centra apparently lack pleurocoels, although 'S1' is the only one well enough preserved for this character state to be determined accurately. Remnants of the bases of the sacral ribs are preserved on the left sides of 'S1' and '2'.

There are three isolated neural spines (unnumbered), which may have belonged to posterior dorsals, sacrals or anterior caudals. For the present, it will be assumed that they belong to the sacrum (the spines are damaged along their anterior and posterior margins in a manner which suggests that they may once have been part of a series of fused spines). The neural spines are relatively tall, plate-like elements, which are anteroposteriorly wide and transversely compressed. In lateral view, the long-axes of these spines are directed upwards and a little backwards. The summit of each spine is moderately expanded transversely, being widest along the posterior margin. The dorsal surface of each expansion is convex in posterior view. One specimen lacks the top of the spine but preserves part of the transverse process (i.e. the upper part of one of the sacral 'plates', which originally connected each sacral vertebra to the ilium). This specimen differs slightly from the two unnumbered spines in being more robust and wider transversely across its posterior surface. There are small spinopre- and spinopostzygapophyseal laminae (on the left side), but no spinodiapophyseal laminae. A stout lamina extends anterodorsally across the lateral surface of the base of one sacral spine, possibly representing a remnant of the spinopostzygapophyseal lamina of the preceding sacral vertebra. The left postzygapophysis is also present but too poorly preserved for description.

*Sacral ribs*. In *Cetiosaurus*, only portions of five broken sacral ribs are preserved (accession nos. 68, 78, 205–207). Specimen 205 may have come from the left side, whereas the remaining four ribs are probably from the right. These ribs vary in size and proportions, but share some features in common. The ventral surface is arched upward in anterior view. Each rib is expanded at its proximal (sacral) and distal (iliac) ends. The dorsal surfaces are broken, showing the base of the sheet of bone (posterior centrodiapophyseal lamina), which once joined the rib to the transverse process. In most specimens (except 68) the ventral surface of the rib, at the proximal end, is concave. Specimen 207 is particularly large, and there is some indication that the dorsal sheet curved forwards towards its distal end, away from the long axis of the rib itself. Similar features have also been observed in the ribs of S1 (and to a lesser extent S2) belonging to other sauropods. Several sauropod genera possess a large foramen near the proximal and/or distal ends of their sacral plates (e.g. *Haplocanthosaurus*, Hatcher 1903; *Apatosaurus*, Gilmore 1936; *Opisthocoelicaudia* Borsuk-Bialynicka, 1977). There is currently no evidence that similar foramina were present in the Rutland *Cetiosaurus*, but this may simply reflect the poor preservation of this specimen.

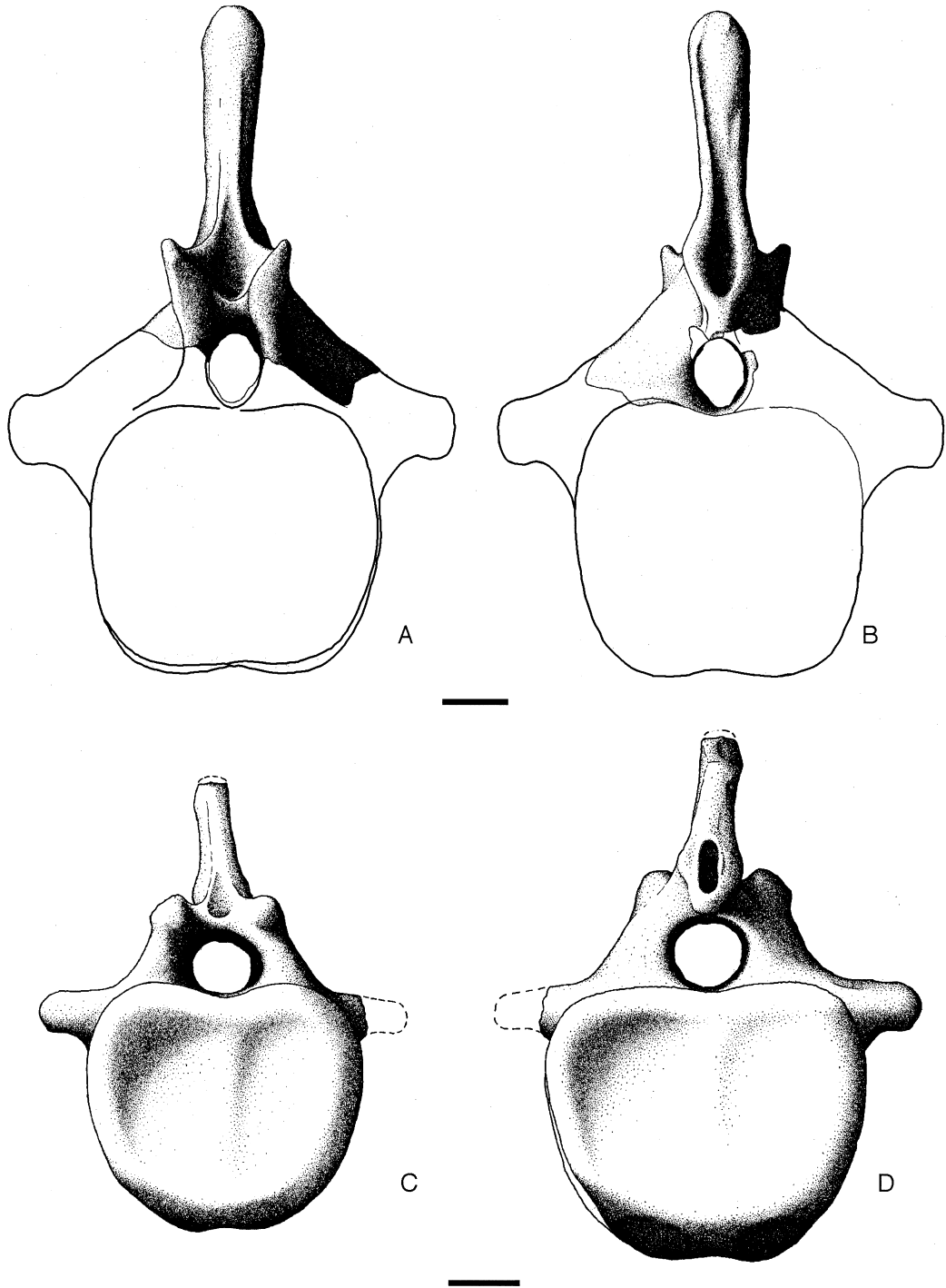


TEXT-FIG. 7. Caudal vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968) in left lateral (A–C) and ventral (D) views. A, ‘Cd2’. B, D, ‘Cd5’. C, ‘Cd11’. For key to shading, see explanation to Text-figure 2. Scale bars represent 50 mm.

*Caudal vertebrae* (Text-figs 7–8; Table 3). Portions of at least 13 anterior and middle caudals have been preserved. For convenience, these specimens will be referred to here as ‘Cd1–13’, the numbers following the order, but not the actual position, of the specimens as they are placed in the exhibition mount. The 13 caudals were found partially disarticulated. Several blocks of matrix preserved two or more caudals in association which, combined with the size and proportions of the specimens, allowed the relative positions of the vertebrae to be assessed reasonably accurately. Martin (1987) suggested that these specimens represented Cds1–3 and 13–23 in the original tail series. Ribs are present on 12 of the 13 caudals preserved in the Rutland *Cetiosaurus*. In virtually all sauropods (except *Alamosaurus*), caudal ribs are present as far posteriorly as Cd14–16 (Upchurch 1998). It is possible that *Cetiosaurus* differed from other sauropods by possessing caudal ribs that persist into the middle portion of the tail. It seems more likely, however, that all but one of the *Cetiosaurus* caudals came from the most anterior portion of the tail (see also the discussion of caudal vertebrae belonging to the Bletchingdon *Cetiosaurus*; Upchurch and Martin in press).

As in all sauropods (Upchurch 1998), the caudal centra of the Rutland *Cetiosaurus* are very short anteroposteriorly (centrum length:height ratio *c.* 0.67). Caudals from the middle part of the tail are more elongate, but they do not attain the extreme elongation seen in diplodocoid sauropods. All preserved centra are solid (i.e. there are no pleurocoels or ventral excavations). The centra are amphicoelous, although the posterior articular face of the more anterior caudals is generally less deeply excavated than the anterior face. The ventral surface is arched upwards in lateral view, and in the anterior caudals (‘Cd1’, ‘3’, and ‘5’) it is convex transversely. By ‘Cd12’, however, the ventral surface of the centrum is flatter and meets the lateral surface at a more abrupt angle. Each caudal has two anterior chevron facets and two larger posterior ones, which typically face anteroventrally and posteroventrally respectively (Text-figs 7–8). Each facet is separated from its partner on the midline by an excavation. In the more distal anterior caudals (i.e. ‘Cd10’ onwards) and middle caudals, these small excavations are linked by a groove or sulcus which runs along the ventral midline, as also seen in the Bletchingdon *Cetiosaurus* (Upchurch and Martin in press), *Camarasaurus* (Upchurch, pers. obs.), *Haplocanthosaurus* (Upchurch, pers. obs.), *Omeisaurus* (He *et al.* 1988) and *Vulcanodon* (Cooper 1984).

The best preserved neural arch and spine, from an anterior caudal, is found in ‘Cd2’ (Text-fig. 7A). The arch has thick walls and is moderately high. The prezygapophyses project anteriorly and a little upwards and outwards. The prezygapophyseal articular facets face mainly medially and a little dorsally (as typically occurs in Cd1–3 of most sauropods). At the base of the spine there are short spinoprezygapophyseal laminae which form the lateral margins of a small, anteriorly facing, triangular hollow. The dorsal surface of the caudal rib is connected to the lateral surface of the arch by a stout ridge. This ridge rises dorsomedially from the anterior edge of the rib, and meets the neural arch just



TEXT-FIG. 8. Caudal vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968) in anterior (A-B) and posterior (C-D) views. A, C, 'Cd2'. B, D, 'Cd5'. For key to shading, see explanation of Text-figure 2. Scale bars represent 50 mm.



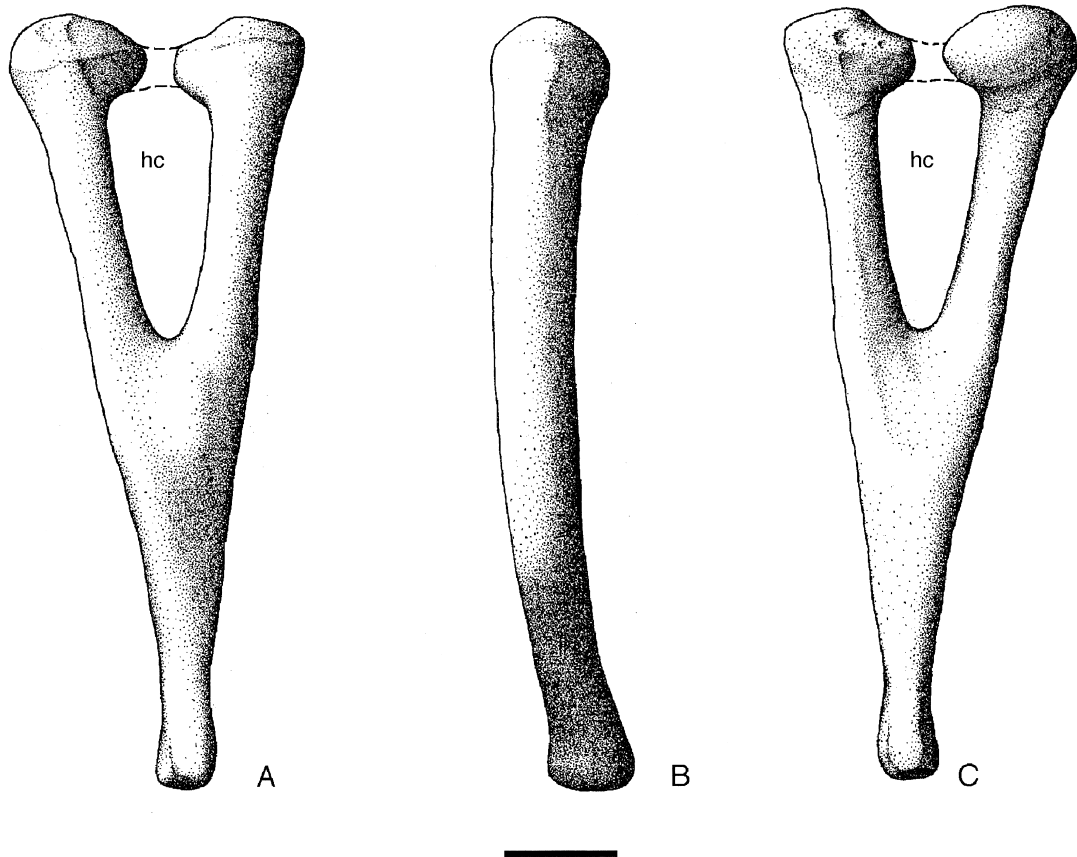
TABLE 3. Measurements of the caudal vertebrae of the Rutland *Cetiosaurus* (LCM G468.1968). Abbreviations: a, absent; e, estimated; Hcp, height of centrum across posterior face; Hsp, neural spine height (from postzygapophyses to spine crest); Lc, length of centrum; Tpw, distance between the tips of the transverse processes (caudal ribs); Wcp, width of centrum across posterior face; Wdp, transverse width of the spine crest across its posterior surface; Wpoz, transverse width across postzygapophyses; Wprz, transverse width across prezygapophyses. All measurements are in mm.

Cd	Lc	Wcp	Hcp	Tpw	Wprz	Wpoz	Hsp	Wdp
'1'	136e	188e	193	—	—	—	—	—
'2'	—	—	—	350	105	61	260	35
'3'	135	184	175	308	—	—	—	—
'4'	124	186	—	—	—	—	—	—
'5'	132	194	—	300e	—	—	—	—
'6'	133	176	143	—	—	—	—	—
'7'	135	177	148	—	—	—	—	—
'8'	—	—	—	—	—	—	—	—
'9'	143	162	120	—	—	—	—	—
'10'	130	158	120	—	—	—	—	—
'11'	121	150	115	—	—	—	125	—
'12'	130	150	—	—	—	—	—	—
'13'	132e	—	—	a	—	—	—	—

below the level of the zygapophyses (slightly nearer the prezygapophysis than the postzygapophysis). At this point, the ridge divides into anterior and posterior portions which extend to the pre- and postzygapophyses respectively. The latter are simple flat facets at the base of the neural spine. Ventrally, the postzygapophyses meet on the midline at the top of a portion of bone (the 'hyposphenal' ridge), which extends down to the dorsal rim of the neural canal. This feature is a derived state found in all sauropods except certain titanosaurs (Upchurch and Martin in press). The dorsal margins of the postzygapophyses give rise to short stout spinopostzygapophyseal laminae which form the posterolateral portions of the neural spine. The laminae fade out before reaching the spine's summit. As in many sauropods, these laminae form the lateral margins of a narrow, vertically elongate, slot-like postspinal cavity at the base of the neural spine (Text-fig. 8B, D). The neural spine of 'Cd2' is a moderately tall (Table 3), laterally compressed plate, which curves dorsally and a little backwards in lateral view (Text-fig. 7A). In horizontal cross-section, the spine tapers from a wider posterior margin to a narrower anterior edge. The arches and spines of the remaining caudals are generally less well preserved. It is clear, however, that the neural arches of the anterior-middle caudals were situated closer to the anterior end of the centrum. Passing distally along the tail, the neural spines remain laterally compressed and there is little sign that they altered their orientation to project more backwards and upwards. The latter point, however, may reflect the fact that only caudals from the anterior third of the tail are available.

*Caudal ribs.* The caudal ribs are simple dorsoventrally flattened projections, as is also the case for all sauropods except diplodocoids. Each rib projects posterolaterally, so that its distal end is level with the posterior margin of the centrum. The base of each rib is situated midway between the anterior and posterior margins of the dorsal half of the centrum.

*Haemal arches* (Text-fig. 9). At least ten partial or complete chevrons are preserved in the Rutland *Cetiosaurus* (accession nos. 46, 48–49, 70–71, 85, 193, 264–266). These were found partially disarticulated, although 46–49 were found in sequence on a single block of matrix, associated with four caudal vertebrae. All of these chevrons appear to be either large elements from near the anterior end of the tail, or slightly smaller anterior-middle chevrons: this is consistent with the view that only the most anterior part of the tail is preserved. None of the chevrons displays any evidence of having been 'forked' or skid-like. Indeed, the smallest, and presumably most posterior, of the *Cetiosaurus* chevrons does not possess even a hint of the expansion or bifurcation of its distal end which normally 'heralds' the appearance of forked chevrons. Given that the transition from normal to forked chevrons typically occurs between Cd9 (*Mamenchisaurus*; Young and Chao 1972) and Cd17 (*Omeisaurus*; He *et al.* 1988), forked chevrons were probably absent in *Cetiosaurus*. Forked chevrons represent a synapomorphy of the Eusauropoda which is reversed in titanosaurs (Wilson and Sereno 1998); whether *Cetiosaurus* possesses the original plesiomorphic state or the derived reversal can only be assessed after a phylogenetic analysis (see below).



TEXT-FIG. 9. Haemal arch (accession no. 46), from the proximal end of the tail, of the Rutland *Cetiosaurus* (LCM G468.1968) in anterior (A), left lateral (B) and posterior (C) views. Abbreviation: hc, haemal canal. Scale bar represents 50 mm.

In anterior view (Text-fig. 9A), the chevrons are Y-shaped and 'closed' proximally by a bridge of bone linking the left and right proximal rami above the haemal canal. Some chevrons appear 'open' proximally (i.e. the bone bridge is absent) but in each case the medial surfaces of the proximal rami appear to be damaged. Anterior chevrons with 'closed' proximal ends are found in many sauropods (most euhelopodids, *Vulcanodon*, *Patagosaurus*, dicraeosaurids and diplodocids) and are believed to be the plesiomorphic condition (Upchurch 1995). Derived 'open' chevrons are known in *Haplocanthosaurus*, *Rayososaurus*, *Shunosaurus*, and camarasauromorphs (Upchurch 1998; Wilson and Sereno 1998). The proximal end of each chevron bears a pair of anterior and posterior articular facets, reflecting their intervertebral articulation. In the more proximal chevrons, the anterior articular facets are nearly perpendicular to the long-axis of the chevron, whilst the posterior pair face almost directly backwards. This suggests that the shafts of the anterior chevrons were directed posteroventrally in lateral view, a feature that is emphasized by the posterior curvature of the distal shaft. In the anterior-middle chevrons, the anterior and posterior articular facets are oriented at approximately 45 degrees to the long-axis of the chevron, suggesting that the distal shaft projected mainly downwards. In lateral view, the shafts of the chevrons curve slightly backwards towards their distal ends. The more anterior chevrons have rather robust distal shafts. The horizontal cross-section through the shaft, just below the haemal canal, is wider transversely than anteroposteriorly (transverse:anteroposterior width ratio *c.* 2.23; Text-fig. 9), as also occurs in the Bletchinglydon *Cetiosaurus* (Upchurch and Martin in press), *Alamosaurus* (Gilmore 1946), *Brachiosaurus* (Janensch 1950), and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977). The remainder of the shaft is subcircular in cross-section, even close to the distal end itself. The latter feature distinguishes the Rutland and Oxford *Cetiosaurus* specimens from other sauropods where the anterior chevrons terminate in an anteroposteriorly expanded and transversely compressed

distal blade. The smaller *Cetiosaurus* chevrons, presumed to belong to the anterior-middle part of the series, possess shafts that are more anteroposteriorly expanded and transversely compressed at their distal ends. Striated ridges extend along the anterior midlines of the shafts of the more proximal chevrons. A similar pattern of midline ridges has been observed in other sauropods, including the Bletchington *Cetiosaurus*, and it is assumed that they represent attachment areas for part of the caudal musculature and ligament system.

### *Appendicular skeleton*

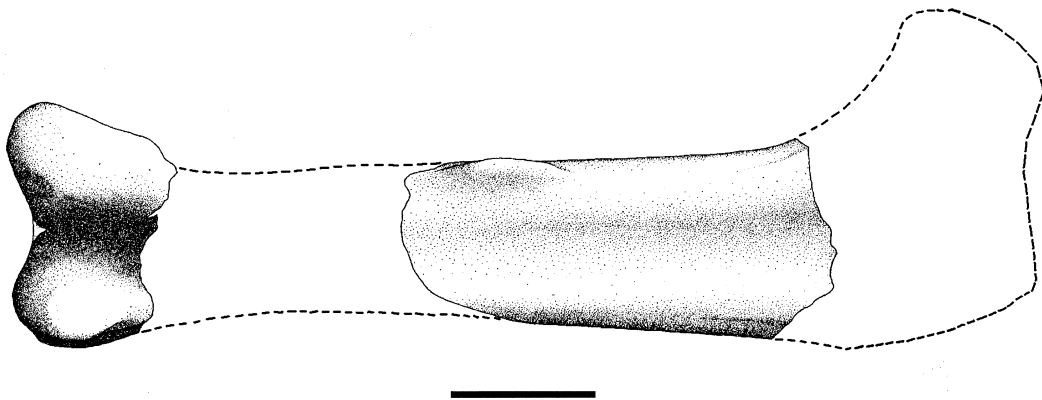
*Ilium.* The pubic process and the ventral part of the anterior process of the right ilium are preserved. The pubic process is rather stout and projects ventrally and a little anteriorly. The lateral edge of the pubic process is relatively narrow and rounded anteroposteriorly. The medial face of this process is expanded anteroposteriorly and broken (perhaps marking the attachment area for sacral ribs 1 and/or 2). A horizontal cross-section through the distal end of the pubic process is semicircular (or nearly subtriangular) in outline, as occurs in other sauropods. The articular surface of the acetabulum is not well preserved, but appears to have been flat and broad transversely.

Only the ventral part of the anterior process is preserved in the right ilium. This process is directed forward and only slightly laterally, supporting the view that *Cetiosaurus* lacks the derived outward flaring of the iliac anterior process which characterizes the Neosauropoda (Wilson and Sereno 1998; Upchurch and Martin in press). In lateral view, the ventral margin of the anterior process has a mildly concave profile. This margin is somewhat rounded in transverse section.

A second, poorly preserved specimen may represent part of the left ilium. There are no recognisable processes or articulations, but the preserved portion closely resembles part of the main plate of a sauropod ilium. If correctly interpreted, this left ilium indicates that the lateral surface was somewhat concave both dorsoventrally and anteroposteriorly. The medial surface of this element displays a roughened area which may represent the point of attachment for one of the sacral plates.

*Ischium.* A large fragment of bone probably belongs to one of the ischia. The preserved portion includes the proximal part of the distal shaft, and extends up towards the contact with the ilium. Unfortunately, this specimen is not well enough preserved to yield any useful anatomical data.

*Femur* (Text-fig. 10). The right femur is represented by the proximal half (lacking much of the articular head) and a smaller section which includes the posterior parts of the distal condyles. The lesser trochanter is extremely reduced. The shaft of the femur is straight in posterior and lateral views, and is anteroposteriorly compressed throughout much of its length. In euhelepodids and *Patagosaurus*, the fourth trochanter is relatively large and is situated close to the midline of the caudal face of the femoral shaft (Upchurch 1998). *Cetiosaurus* and neosauropods, however, share a derived condition in which the fourth trochanter is reduced to a small rounded ridge which lies on the posteromedial margin of the femur (Text-fig. 10).



TEXT-FIG. 10. Right femur of the Rutland *Cetiosaurus* (LCM G468.1968) in posterior view. For key to shading, see explanation of Text-figure 2. Scale bar represents 200 mm.

The distal end of the femur is divided into two condyles by a shallow intercondylar groove. This groove is quite shallow on the distal end of the femur, but becomes more prominent on the posterior faces of the shaft. The medial (tibial) condyle is a little larger than the lateral (fibular) one. A wide notch extends up the posterolateral margin of the distal end, dividing the fibular condyle into laterally and posteriorly directed lobes, as occurs in many other dinosaurs.

## DISCUSSION

### *The congeneric status of the Rutland and Oxford specimens*

Both the Rutland and Oxford specimens are rather fragmentary. As a result, only the dorsal and caudal vertebrae, chevrons, ilium and femur are represented in both specimens and allow comparisons to be made. The large individual from Bletchingdon Station (OUMNH J13605–13613, J13615–13616, J13619–13688, J13899) has been designated the lectotype of the sole (and via monotypy the type) species, *Cetiosaurus oxoniensis*, by Upchurch and Martin (in press). The evidence supporting the referral of the Rutland specimen to *C. oxoniensis* is briefly summarized below:

1. The Bletchingdon and Rutland specimens share several autapomorphic features, including: pyramid-shaped neural spines in the posterior cervical and anterior dorsal region; absence of the spinodiapophyseal lamina on all dorsal vertebrae; deep pits on the lateral surface of the neural arch immediately below the transverse processes, present on middle dorsal vertebrae; and anterior chevrons terminating in transversely broad distal ends rather than compressed blades.
2. The Rutland specimen possesses autapomorphies that are not observed in the Bletchingdon individual and vice versa. In every case, however, the failure to detect the autapomorphy is as a result of missing data rather than genuine absence. Only future discoveries can confirm or contradict the status of these features as autapomorphies of the genus *Cetiosaurus*.
3. There are a few differences between the Rutland and Bletchingdon specimens, including: slightly more extensive dorsal pleurocoels in the Oxford material; dorsal centra with transversely convex ventral surfaces in the Rutland specimen versus lateroventrally facing surfaces which meet at a midline keel in the Oxford specimen; and dorsal neural spines which appear to be more anteroposteriorly compressed in the Oxford material. Some crushing of the specimens, combined with the possibility of variation along the vertebral column, means that little taxonomic significance can be attached to these differences at present. Discoveries of more complete material, and a greater understanding of the phylogenetic distribution of these features, may necessitate re-evaluation of their importance in the future.

In summary, the current distribution of autapomorphic features indicates that the Rutland and Bletchingdon specimens are congeneric, but do not support their assignment to separate species.

### *Vertebral formula and numbering*

The large Bletchingdon *Cetiosaurus* provides relatively few data on the vertebral formula of this taxon. Upchurch and Martin (in press) noted that there were probably at least 12 dorsals, and the tail contains 30 anterior and middle caudal vertebrae. The current mount of the Rutland *Cetiosaurus*, including replica elements modelled for display, has a vertebral formula of 14 cervicals, ten dorsals, five sacrals and *c.* 50 caudals. This formula was determined partly on the basis of the associations observed in blocks of matrix during preparation. Block C contained Cv13 and '14', D1 and part of D2 in articulation, while block N held the rest of D2 through to D5 in articulation. Thus it would appear that Cv13–D5 represent a natural series. Other blocks confirm that the relative position of Cv6 and 7, Cv8 and 9, and Cv11 and 12, are also correct. The remaining cervicals and dorsals were found disarticulated and have been assigned positions on the basis of size and data on typical morphological transitions which occur in sauropod presacral series. This has resulted in a cervical series that appears to be complete and accurately organized. The vertebral formula is, therefore, most easily altered by shifting the proposed position of the cervicodorsal junction forwards or backwards, or by adding extra dorsals in the middle and posterior part of the truck. Other lines of evidence, however, indicate that the accurate determination of the presacral formula in *Cetiosaurus* may be more complex than previously realized:

1. 'Cv14' has the tall neural arch (with deep anterior cavity), and nearly vertical posterior

centrodiapophyseal lamina, which are commonly found in the dorsals of other sauropods. The poor preservation of centra and ribs in the region of the cervicodorsal transition makes it difficult to identify the last cervical and/or the first dorsal, so it is conceivable that 'Cv14' actually represents an anterior dorsal.

2. 'D1' possesses a well-developed hyposphene, which is usually absent on at least D1 and 2 of other sauropods (McIntosh 1990; Upchurch 1998).

3. The mounted skeleton does not include two neural arches and spines (held in store) which clearly belong to dorsal vertebrae. The pyramid-shaped neural spine, and the shape of the transverse process, suggest that one of these specimens probably belonged to an anterior dorsal vertebra.

These discrepancies can be partly resolved by assuming that the cervicodorsal junction occurred one vertebra further forwards than in the exhibition mount (i.e. between Cv13 and 'Cv14'), so that the hyposphene first appears on 'D2' in the revised system. The hyposphene might be expected to have first appeared even more posteriorly, and when combined with point 3 above, suggests that perhaps the 'articulation' of vertebrae implied by preservation in blocks C and N is misleading, perhaps reflecting some post-mortem jumbling of the vertebrae prior to final burial.

Taking all these lines of evidence into account, therefore, it seems likely that *Cetiosaurus* originally possessed 13 cervicals and at least 12 dorsals. This presacral formula closely resembles those of many other sauropods, including *Shunosaurus* (13 cervicals, 13 dorsals; Zhang 1988), *Camarasaurus* (12 cervicals, 12 dorsals; Gilmore 1925), *Brachiosaurus* (13? cervicals, 11? dorsals; Janensch 1950), and *Dicraeosaurus* (12 cervicals, 12 dorsals; Janensch 1929). The presacral formula seems to have changed from ten cervicals and 15 dorsals to 13 cervicals and 13 dorsals during the early stages of sauropod evolution, reflecting the conversion of perhaps two dorsal vertebrae into cervicals (Upchurch 1994, 1998; Wilson and Sereno 1998). The third additional cervical could represent a *de novo* structure, though more detailed data on the neck structure of basal sauropods are required before this can be confirmed.

The precise numbers of sacral and caudal vertebrae in *Cetiosaurus* cannot be accurately established. The sacrum must have had at least four coalesced vertebrae (a synapomorphy of the Sauropoda), but may have had more. The majority of sauropods (except dicraeosaurids and diplodocids) have 40–50 caudals, and this would appear to be a reasonable estimate for the number present in *Cetiosaurus*. In summary, therefore, the vertebral formula of *Cetiosaurus* was probably close to 13 cervicals, 13(+?) dorsals, 4+ sacrals, and *c.* 50 (?) caudals.

### *The phylogenetic relationships of Cetiosaurus*

*Analyses and results.* Only three cladistic analyses (Upchurch 1995, 1998, 1999) have included character data from *Cetiosaurus*. The most parsimonious trees (MPTs) found by Upchurch (1995) placed *Cetiosaurus* in three alternative positions, sister-taxon to: (1) a titanosaur-diplodocoid clade; (2) a brachiosaur-camarasaur clade; or (3) the Neosauropoda. The addition of new character data by Upchurch (1998) stabilized this situation, with both of the two MPTs placing *Cetiosaurus* as the sister-taxon to *Haplocanthosaurus* + Neosauropoda. The same result was replicated by Upchurch (1999) when the total number of characters was raised from 205 to 219.

The anatomical description presented above, and by Upchurch and Martin (in press), necessitates changes to 21 characters in the matrix outlined by Upchurch (1998, 1999) (see Appendix). A modified data-matrix, containing 26 sauropod taxa and 217 characters, was analysed using the Heuristic search in PAUP 4.0b4a (Swofford 2000). This analysis yielded ten MPTs (Text-fig. 11A). These ten trees possess essentially the same topology, with the differences between them reflecting: (1) variation in the relationships between *Omeisaurus*, *Euhelopus* and *Mamenchisaurus* within the Euhelopodidae; (2) placement of *Lapparentosaurus* as either a brachiosaurid or sister-taxon to *Phuwiangosaurus*; and (3) the breakdown in stability of the relationships of *Haplocanthosaurus*. The first two sources of uncertainty were also present in Upchurch (1998, 1999) respectively, and are, therefore, not the result of adding new data on *Cetiosaurus*. Although *Haplocanthosaurus* has been recognized as a problematic unstable taxon (Upchurch 1998; Wilkinson *et al.* 2000), instability at the level of the most parsimonious trees has not been observed in previous analyses and is here probably related to modifications made to the *Cetiosaurus* data. This phenomenon is not directly relevant to the issue of *Cetiosaurus* relationships and will be

addressed elsewhere. In all ten of the new MPTs, *Cetiosaurus* is placed as the sister-taxon to either the Neosauropoda or *Haplocanthosaurus* + Neosauropoda (Text-fig. 11A).

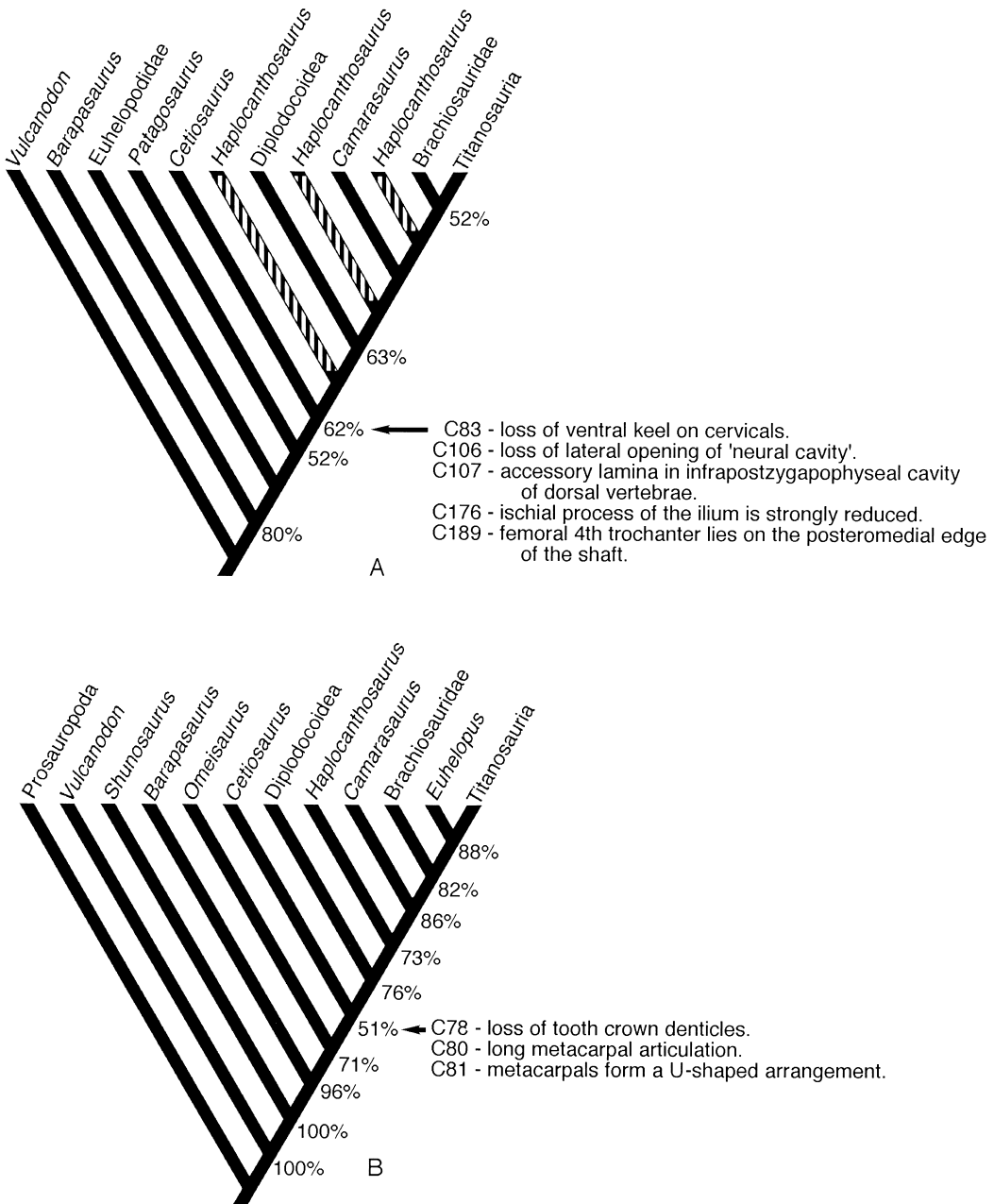
PAUP 4.0b4a (Swofford 2000) was used to run bootstrap analyses (2000 replicates) on the matrix produced by Upchurch (1998) and the new matrix which contains the modified *Cetiosaurus* data. The bootstrap values obtained are shown in Text-fig. 11A. It appears that the new *Cetiosaurus* data have improved the support for the position of this taxon from less than 50 per cent to approximately 62 per cent.

Wilson and Sereno (1998) provided a data-matrix containing ten sauropod taxa and 109 characters. Approximately 50 per cent of these characters are 'new' (i.e. they are not included by Upchurch 1998, 1999) and it is therefore conceivable that these data support a different position for *Cetiosaurus*. To test this possibility, *Cetiosaurus* was coded for the 109 characters employed by Wilson and Sereno (1998) (see Appendix) and the revised matrix was analysed using the Branch and Bound search in PAUP 4.0b4a (Swofford 2000). Only one MPT was produced, having the same topology as that found by Wilson and Sereno (1998), with *Cetiosaurus* placed as the sister-taxon to the Neosauropoda (Text-fig. 11B). A bootstrap analysis (2000 replicates) produced poor support for the node *Cetiosaurus* + Neosauropoda (Text-fig. 11B), apparently reflecting the fact that *Omeisaurus* is closer to the neosauropods than *Cetiosaurus* in a large proportion of the bootstrap fundamental trees. In general, the bootstrap values for the Wilson and Sereno matrix are higher than those produced by the modified Upchurch matrix. This does not, however, automatically indicate that the Wilson and Sereno cladogram topology is more robust: bootstrap values are often lower for larger data-matrices because of the inevitable increase in levels of homoplasy caused by increased numbers of taxa and characters. *Omeisaurus* and neosauropods share the following derived states, which are absent in *Cetiosaurus*: (1) cervical pleurocoels divided by one or more laminae; and (2) cervical rib shafts are positioned below the centra. Neither of these characters, however, provides strong evidence against the proposed MPT topology. For character 69 [cervical pleurocoels are simple excavations (state 0) or are divided by one or more accessory laminae (state 1)], Wilson and Sereno (1998) coded theropods, prosauropods, and the basal sauropods *Barapasaurus* and *Shunosaurus* as possessing an inapplicable state because they lack pleurocoels, while all remaining forms were assigned state 1. Thus, there is no evidence in Wilson and Sereno's (1998) matrix to support the view that simple pleurocoels are plesiomorphic with respect to those divided by accessory laminae. In the modified matrix, *Cetiosaurus* is the only sauropod to possess state 0. Without the addition of other basal sauropods with state 0, it is currently impossible to determine whether *Cetiosaurus* possesses a derived or plesiomorphic state. As discussed above, *Cetiosaurus* appears to possess an intermediate state regarding the capitulum-tuberculum angle in its cervical ribs (Wilson and Sereno 1998, character 71). In future analyses, it may be necessary to recode Wilson and Sereno's (1998) character 71 to form a multistate character. Furthermore, the difference in capitulum-tuberculum angle between *Omeisaurus* (He *et al.* 1988, fig. 21A) and *Cetiosaurus* appears to be very subtle. In any case, these discrepant characters are outweighed by other features (Text-fig. 11) that support the *Cetiosaurus* + neosauropod sister-group relationship.

Ultimately, the phylogenetic relationships of *Cetiosaurus* should be tested by producing a combined data-matrix which synthesizes the characters used by Upchurch (1998, 1999) and Wilson and Sereno (1998). Such a revised matrix, however, lies beyond the scope of the current work. For the present, the largest data-sets available 'independently' agree that *Cetiosaurus* is the sister-taxon to the Neosauropoda, while the relationships of *Haplocanthosaurus* remain problematic.

## CONCLUSION

*Cetiosaurus* is a medium-sized to large sauropod dinosaur from the Bajocian and Bathonian of England. At present, it includes only one valid species, *C. oxoniensis*, which is based on lectotype and paralectotype material from Bletchington Station, near Oxford, and a referred specimen from Great Casterton quarry, Rutland. Although both the Oxford and Rutland specimens are fragmentary, they combine to provide a detailed picture of the anatomy of the axial and appendicular skeleton of this basal sauropod. The probable vertebral formula for *Cetiosaurus* is 13 cervicals, 13(+?) dorsals, 4(+?) sacrals, and *c.* 50(?) caudals. Phylogenetic analyses agree that *Cetiosaurus* represents a taxon that is very closely related to, but lies



TEXT-FIG. 11. Most parsimonious trees generated by cladistic analysis of A, the modified data-matrix based on Upchurch (1998, 1999); and B, the data-matrix provided by Wilson and Sereno (1998). The cladogram shown in A is a simplified version based on the ten most parsimonious trees. The striped branches show the three alternative positions for *Haplocanthosaurus* in these ten MPTs. Bootstrap values above 50 per cent are shown as percentages. The derived character states supporting the position of *Cetiosaurus* are listed (only those character state distributions which are unequivocal under delayed and accelerated transformation, across all MPTs, are shown). See text and Appendix for further details of these analyses.

outside of, the Neosauropoda. *Cetiosaurus* therefore makes an important contribution to our understanding of the sequence of events leading to the origin of the advanced neosauropod clade.

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