

AN UNUSUAL NEW NEOSAUROPOD DINOSAUR FROM THE LOWER CRETACEOUS HASTINGS BEDS GROUP OF EAST SUSSEX, ENGLAND

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Abstract: *Xenoposeidon proneneukos* gen. et sp. nov. is a neosauropod represented by BMNH R2095, a well-preserved partial mid-to-posterior dorsal vertebra from the Berriasian–Valanginian Hastings Beds Group of Ecclesbourne Glen, East Sussex, England. It was briefly described by Lydekker in 1893, but it has subsequently been overlooked. This specimen's concave cotyle, large lateral pneumatic fossae, complex system of bony laminae and camerate internal structure show that it represents a neosauropod dinosaur. However, it differs from all other sauropods in the form of its neural arch, which is taller than the centrum, covers the entire dorsal surface of the centrum, has its posterior margin continuous with that of the cotyle, and slopes forward at 35 degrees relative to the vertical. Also unique is a broad, flat area of featureless bone on the lateral face of the arch; the accessory infrapapophyseal and postzygapophyseal laminae which meet in a V; and the asymmetric neural canal, small and round posteriorly but large and teardrop-shaped anteriorly, bounded by arched supporting laminae. The specimen

cannot be referred to any known sauropod genus, and clearly represents a new genus and possibly a new 'family'. Other sauropod remains from the Hastings Beds Group represent basal Titanosauriformes, Titanosauria and Diplodocidae; *X. proneneukos* may bring to four the number of sauropod 'families' represented in this unit. Sauropods may in general have been much less morphologically conservative than is usually assumed. Since neurocentral fusion is complete in R2095, it is probably from a mature or nearly mature animal. Nevertheless, size comparisons of R2095 with corresponding vertebrae in the *Brachiosaurus brancai* holotype HMN SII and *Diplodocus carnegii* holotype CM 84 suggest a rather small sauropod: perhaps 15 m long and 7600 kg in mass if built like a brachiosaurid, or 20 m and 2800 kg if built like a diplodocid.

Key words: Dinosauria, Sauropoda, Neosauropoda, *Xenoposeidon proneneukos*, Wealden, Hastings Beds Group, Lower Cretaceous.

THE remains of sauropod dinosaurs have been known from the Lower Cretaceous Wealden strata of the English mainland since the 1840s. Although sauropods were not recognized as a distinct dinosaurian group until somewhat later (Phillips 1871; Marsh 1878*a*), the first named sauropod species, *Cetiosaurus brevis* Owen, 1842, was coined for Wealden material (Naish and Martill 2001; Upchurch and Martin 2003).

Most Wealden sauropods are from the Barremian Wessex Formation of the Isle of Wight. Far less well represented are the sauropods of the older Berriasian–Valanginian (Allen and Wimbledon 1991) Hastings Beds Group of the mainland Wealden. Specimens have been collected from Cuckfield, West Sussex (Owen 1841; Mantell 1850), Hastings, East Sussex (Mantell 1852), and most recently from Bexhill, East Sussex (Anonymous 2005). There are indications that a taxonomic diversity similar to that of the Wessex

Formation is present among these forms, as discussed below.

Here we describe a Hastings Beds Group specimen first reported, briefly, by Lydekker (1893*a*). This specimen was collected by Philip James Rufford and subsequently acquired by the British Museum (Natural History), now the Natural History Museum, London, where it is deposited as specimen BMNH R2095.

Though consisting only of a single incomplete vertebra, R2095 preserves many phylogenetically informative characters that allow it to be confidently identified as a neosauropod. Furthermore, it is highly distinctive, possessing several autapomorphies. While it is generally difficult to assess the affinities of isolated bones, sauropod vertebrae, especially dorsal vertebrae, are highly diagnostic (Berman and McIntosh 1978, p. 33; Bonaparte 1986*a*, p. 247; McIntosh 1990, p. 345), and this is particularly true of the specimen described here.

Lydekker (1893*a*, p. 276) reported that this specimen was discovered in ‘the Wealden of Hastings’ (Text-fig. 1), but beyond that no locality or stratigraphic data were recorded. Watson and Cusack (2005, p. 4) confirmed that Rufford generally collected ‘from the Wealden beds of the Hastings area, East Sussex’. Specific plant fossils known to have been collected by Rufford came from East Cliff (Watson and Cusack 2005, p. 75) and from the Fairlight Clays of Ecclesbourne Glen (Watson and Cusack 2005, pp. 64, 80, 87, 107, 112, 125, 128, 138, 152–153), both in the Fairlight area. The units exposed at both East Cliff and Ecclesbourne Glen are part of the Ashdown Beds Formation, which straddles the Berriasian/Valanginian boundary (Text-fig. 2). The vertebra was probably collected from Ecclesbourne Glen since (1) it is closer to Hastings than is East Cliff and Lydekker (1893*a*) stated that the specimen was collected near Hastings; and (2) the majority of Rufford’s documented specimens came from there. The part of the Ashdown Beds Formation exposed at Ecclesbourne Glen is Berriasian in age (e.g. Watson and Cusack 2005), so this is the most likely age of R2095.

Anatomical nomenclature. The term ‘pleurocoel’ has been widely used to refer to the lateral excavations in the centra of sauropods and other saurischian dinosaurs. However, the blanket use of this term obscures the morphological diversity of these cavities, which varies considerably between taxa, encompassing everything from broad, shallow fossae to small, deep foramina; and some taxa have both of these. Furthermore, the term has been used inconsistently in the literature, so that characters such as ‘pleurocoels present’ in cladistic analyses are difficult to interpret. For example, in the analysis of Wilson (2002), character 78 is defined as ‘Presacral centra, pneumatopores (pleurocoels): absent (0); present (1)’ (Wilson 2002, p. 261), and *Barapasaurus* Jain, Kutty and Roy-Chowdhury, 1975 is scored as 0 (‘pleurocoels absent’). While *Barapasaurus* does indeed lack pneumatic foramina, it has shallow lateral fossae (Jain *et al.* 1979, pls 101–102), a feature that is not conveyed by the traditional terminology. Accordingly, we recommend that the ambiguous term ‘pleurocoel’ (and Wilson’s equivalent ‘pneumatopore’) be deprecated in favour of the more explicit alternatives ‘lateral fossa’ and ‘lateral foramen’ (Britt 1993, 1997; Wedel *et al.* 2000*b*; Wedel 2003, 2005). The EI (elongation index) of Upchurch (1998) is here used as redefined by Wedel *et al.* (2000*b*), being the length of the centrum divided by the height of the cotyle.

Anatomical abbreviations. ACDL, anterior centrodiapophyseal lamina; ACPL, anterior centroparapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; PODL, post-



TEXT-FIG. 1. A–B, maps indicating location of Ecclesbourne Glen, near Hastings, East Sussex, England, the probable discovery site of the holotype of *Xenoposeidon proneneukos* gen. et sp. nov.

zygodiapophyseal lamina; PDDL, paradiapophyseal lamina; PRDL, prezygodiapophyseal lamina; PRPL, prezygoparapophyseal lamina. We follow the vertebral lamina nomenclature of Janensch (1929) as translated by Wilson (1999) except in using capital letters for the abbreviations, a convention that allows plurals to be more clearly formed.

Institutional abbreviations. BMNH, the Natural History Museum, London, England; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MIWG, Museum of Isle of Wight Geology (now Dinosaur Isle Visitor Centre), Sandown,

Barremian	Weald Clay Group	Upper Weald Clay Formation
		Lower Weald Clay Formation
Valanginian	Hastings Beds Group	Upper Tunbridge Wells Sand Formation
		Grinstead Clay Formation
		Lower Tunbridge Wells Sand Formation
		Wadhurst Clay Formation
		Ashdown Beds Formation <i>(Xenoposeidon proneneukos gen. et sp. nov.)</i>
Berriasian		

TEXT-FIG. 2. Schematic lithostratigraphy of the Wealden indicating the origin of the holotype of *Xenoposeidon proneneukos* gen. et sp. nov. within the Ashdown Beds Formation of the Hastings Beds Group.

Isle of Wight, England; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

SYSTEMATIC PALAEOLOGY

DINOSAURIA Owen, 1842
 SAURISCHIA Seeley, 1888
 SAUROPODOMORPHA Huene, 1932
 SAUROPODA Marsh, 1878a
 NEOSAUROPODA Bonaparte, 1986b

Genus XENOPOSEIDON gen. nov.

Derivation of name. Greek, *xenos*, strange or alien, and Poseidon, the god of earthquakes and the sea in Greek mythology, the latter in reference to the sauropod *Sauroposeidon* Wedel, Cifelli and Sanders, 2000a. Intended pronunciation: ZEE-no-puh-SYE-d'n.

Type species. *Xenoposeidon proneneukos* sp. nov.

Diagnosis. As for the type and only species, *X. proneneukos*.

Xenoposeidon proneneukos sp. nov.

Text-figures 3–5; Tables 1–2

Derivation of name. Latin, *pronus*, forward sloping, describing the characteristic morphology of the neural arch. Intended pronunciation: pro-nen-YOO-koss.

Holotype. BMNH R2095, the Natural History Museum, London. A mid posterior dorsal vertebra consisting of partial centrum and neural arch.

Type locality and horizon. Near Hastings, East Sussex, England; probably Ecclesbourne Glen, about 2 km east of Hastings. Hastings Beds Group (Berriasian–Valanginian, earliest Cretaceous); probably Berriasian part of the Ashdown Beds Formation. Precise locality and stratigraphic information either has been lost or was never recorded.

Diagnosis. Differs from all other sauropods in the following characters: (1) neural arch covers dorsal surface of centrum, with its posterior margin continuous with that of the cotyle; (2) neural arch slopes anteriorly 35 degrees relative to the vertical; (3) broad, flat area of featureless bone on lateral face of neural arch; (4) accessory infra-parapophyseal and postzygapophyseal laminae meeting ventrally to form a V; (5) neural canal is asymmetric: small and circular posteriorly but tall and teardrop-shaped anteriorly; (6) supporting laminae form vaulted arch over anterior neural canal.

Description. BMNH R2095 (Text-figs 3–4) is a partial dorsal vertebra from the middle or posterior portion of the dorsal column. Most of the centrum and neural arch are preserved, but the condyle is broken, and the neural spine and dorsal part of the neural arch are missing, as are the pre- and postzygapophyses and diapophyses. However, sufficient laminae remain to allow the positions of the processes to be inferred with some certainty (Text-fig. 5). Measurements are summarized in Table 1.

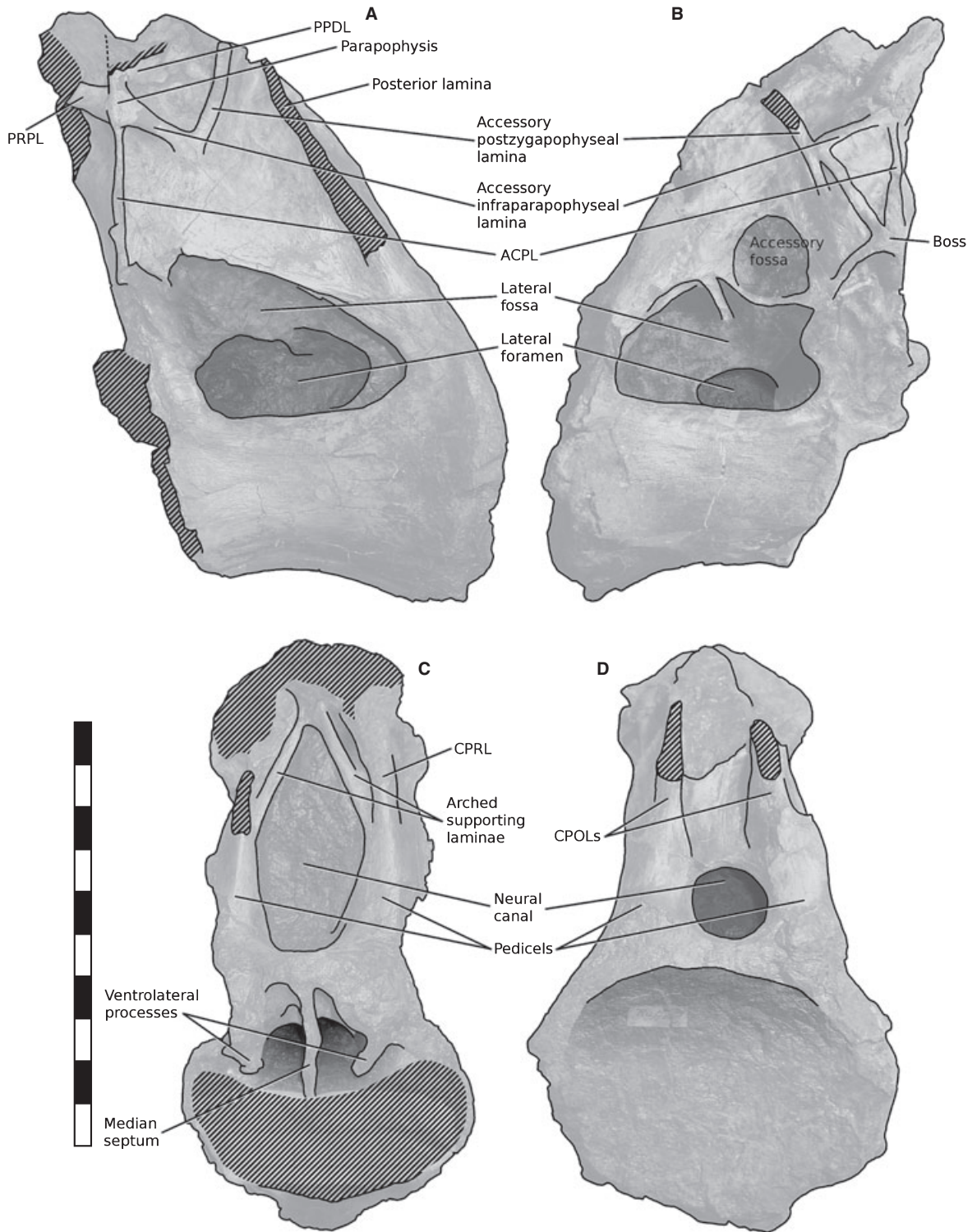
The most striking features of this specimen are the extreme height, anteroposterior length and anterodorsal inclination of the neural arch. These are clearly genuine osteological features and not the result of post-mortem distortion. Although the dorsalmost preserved part of the neural arch is ventral to the diapophyses, the height even of the remaining portion (160 mm above the anterodorsal margin of the centrum, measured perpendicular to the anteroposterior axis of the centrum) is equal to that of the cotyle. The centrum is 190 mm long measured along its dorsal margin; its anteroventral portion is missing but a maximum length of 200 mm is indicated, assuming that the curvature of the condyle is approximately equal to that of the cotyle. The base of the neural arch is 170 mm in anteroposterior length, 85 per cent of the estimated total length of the centrum, and its posterior margin is continuous with that of the cotyle, forming a single smooth curve when viewed laterally. The angle of the neural arch's inclination relative to the vertical cannot be precisely ascertained due to the absence of the condyle, but was



TEXT-FIG. 3. *Xenoposeidon proneukos* gen. et sp. nov. holotype in A, left lateral, B, right lateral, C, anterior, and D, posterior views. Scale bar represents 200 mm.

approximately 35 degrees and cannot have varied from this by more than 5 degrees or so unless the condyle was shaped very differently from that of other sauroptiles.

A clean break of the condyle exposes within the centrum the dorsal part of a median septum and a pair of ventromedially directed lateral septa, indicative of an extensively pneumatized



TEXT-FIG. 4. Interpretive drawing of *Xenoposeidon proneneukos* gen. et sp. nov. holotype in A, left lateral, B, right lateral, C, anterior, and D, posterior views. Scale bar represents 200 mm. Breakage is indicated by diagonal hatching. The PPDL (preserved only on the left side) is a sheet of bone projecting anterolaterally from the neural arch with its anterolateral margin running dorsoventrally, but which is broken off just dorsal to the parapophysis.

TABLE 1. Measurements (in mm) of *Xenoposeidon proneneukos* gen. et sp. nov. holotype, BMNH R2095, and comparison with mid-posterior dorsal vertebrae of other neosauropods. The suffix 'e' indicates an estimation; '+' indicates a minimum possible value, e.g. the length of the preserved portion of a broken element. Measurements for *Brachiosaurus altithorax* FMNH P25107 are taken from Riggs (1904, p. 234): D?7 and D?11 are the vertebrae described by Riggs as presacrals VI and II, respectively, on the assumption that *B. altithorax* had 12 dorsal vertebrae. Measurements for *Brachiosaurus brancai* HMN SII are taken from Janensch (1950, p. 44) except those suffixed 't', which were omitted from Janensch's account and so measured by MPT. Measurements for *Diplodocus carnegii* CM 84 are taken from Hatcher (1901, p. 38). Those suffixed 'i' were interpolated by measuring from Riggs (1904, pl. 72) for *B. altithorax*, Janensch (1950, fig. 56) for *B. brancai* and Hatcher (1901, pl. 7) for *D. carnegii*.

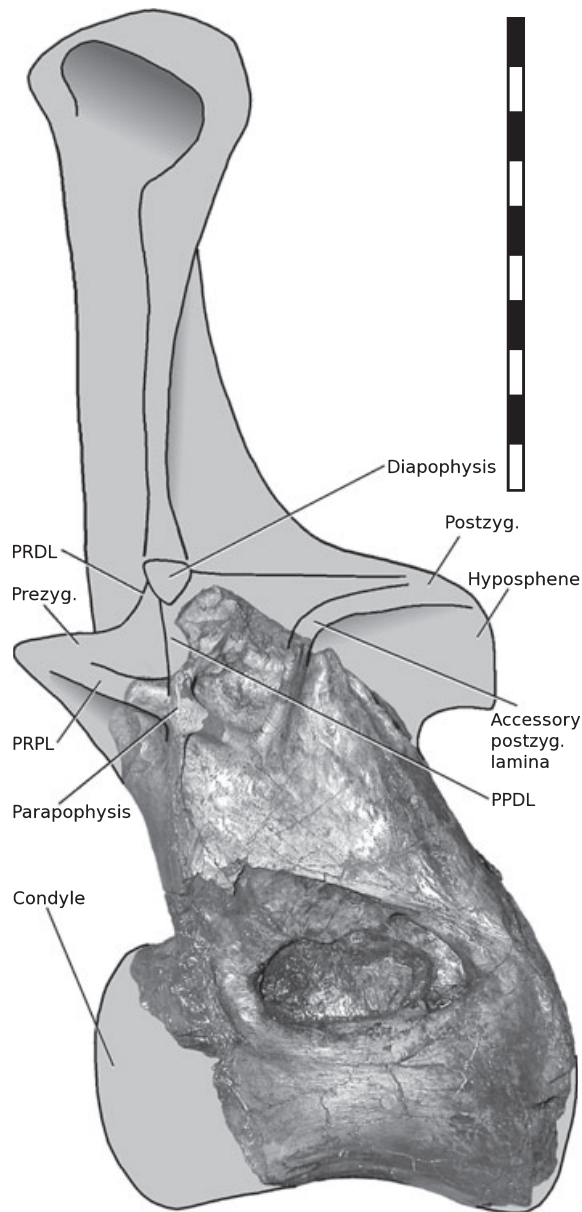
	<i>Xenoposeidon</i> BMNH R2095	<i>Brachiosaurus altithorax</i> FMNH P25107 D?7		<i>B. brancai</i> HMN SII D7	<i>Diplodocus carnegii</i> CM 84 D7		D8
Total height of vertebra	300+	900	800	770+	980i		970i
Total centrum length including condyle	200e	440	350	330	264		275
Total centrum length excluding condyle	190			294			
Cotyle height	160	270	280	220t			
Cotyle width	170	300	310	320t			
Average cotyle diameter	165	285	295	270t	280		309
Centrum length/cotyle height (EI)	1.25	1.63	1.25	1.50	0.94		0.89
Depth of cotylar depression	10	80	70				
Anteroposterior length of lateral fossa	95	–	–	–?	–		–
Dorsoventral height of lateral fossa	80	–	–	–?	–		–
Anteroposterior length of lateral foramen	80	190	160	97i	120i		130i
Dorsoventral height of lateral foramen	40	100	70	58i	85i		95i
Anteroposterior length of base of neural arch	170	220i	155i	170i	180i		165i
Neural arch base length/centrum length	0.85	0.50	0.44	0.52	0.68		0.60
Height of neural arch above centrum	160+						
Height of neural arch pedicels, posterior	130+						
Thickness of neural arch pedicels, posterior	30						
Height of neural canal, posterior	35						
Width of neural canal, posterior	35						
Height of neural arch pedicels, anterior	80+						
Thickness of neural arch pedicels, anterior	25						
Height of neural canal, anterior	120						
Width of neural canal, anterior	55						
Height of hyposphene above centrum	90+						
Height of postzygapophyses above centrum	140e						
Height of prezygapophyses above centrum	140e						

centrum with camerate, rather than camellate to somphospondylous, internal structure. The ventral portion of the broken condyle cannot be described as it is obscured by a catalogue note. The cotyle is slightly concave, its central portion indented 10–15 mm relative to its margin. It is 160 mm tall and 170 mm wide. A very subtle keel is present on the ventral surface of the centrum, and the ventral border of the centrum is gently arched in lateral view.

On the better preserved left side of the vertebra, a shallow lateral fossa is positioned dorsally on the centrum, and about midway between the anterior and posterior margins of the neural arch, onto which it intrudes. It is very roughly triangular in shape, taller anteriorly than posteriorly, with a maximum height of 80 mm and a total length of 95 mm. Set within this is a deeper lateral foramen, oval, anteroposteriorly elongate and measuring 80 by 40 mm. The fossa and foramen share their ventral borders. On the right side, the lateral fossa is situated even more dorsally, but is taller posteriorly than anteriorly, with a maximum height of 55 mm and a total length of 90 mm. The lateral foramen is much

smaller on this side, measuring only 20 by 15 mm, and is anteroventrally placed within the fossa.

On the left side, the dorsal border of the lateral fossa is formed by a prominent sharp-lipped lateral ridge, which extends anterodorsally for 90 mm; this is absent on the right side, apparently due not to damage but to intravertebral variation. Instead, an irregularly shaped and sharp-lipped border separates the fossa from a more dorsally placed subcircular 'accessory fossa' 30 mm in diameter. On this side, an accessory lamina connects the anterior part of the border between the main and accessory fossae to a prominent boss positioned on the anterior margin of the neural arch, 50 mm above the anterodorsal margin of the centrum. This is not a parapophysis or a diapophysis but seems to be an aberrant feature of this individual. Neither the accessory fossa nor the anterior boss has been reported in any other sauropod vertebra; however, these features are not considered taxonomically significant as their occurrence on only one side of the vertebra suggests that they are either pathological or a developmental aberration. Pneumatic features vary wildly and may be



TEXT-FIG. 5. *Xenoposeidon proneneukos* gen. et sp. nov. holotype, mid to posterior dorsal vertebra BMNH R2095, speculative reconstruction, in left lateral view. The location of the prezygapophyses, postzygapophyses and diapophyses are inferred with some confidence from the preserved laminae; the neural spine is based on an idealized slender neosauropod neural spine. Scale bar represents 200 mm.

opportunistic, if Witmer (1997, p. 64) is correct that ‘Pneumatic diverticula are ... opportunistic pneumatizing machines, resorbing as much bone as possible within the constraints imposed by local biomechanical loading regimes.’

The remaining features are described from the left side of the vertebra. The right side is consistent with this morphology, although not all features are preserved.

From a point anterior to the anterodorsal margin of the lateral fossa, a vertically orientated ACPL extends dorsally 70 mm to a

cross-shaped junction of laminae near the anterior margin of the arch, and may also have extended a similar distance ventrally although damage makes it impossible to establish this. The cross-shaped junction is interpreted as the location of the parapophysis. In sauropods, the position of the parapophysis migrates dorsally in successive dorsal vertebrae, being located ventrally on the centrum of anterior dorsals, dorsally on the centrum in mid to anterior dorsals, and on the neural arch of mid to posterior dorsals, level with the prezygapophyses in the most posterior dorsals: see, for example, Hatcher (1901, pl. 7). The high position of the parapophysis on the neural arch of R2095 indicates a mid to posterior placement of the vertebra within the dorsal column, but, because the prezygapophyses must have been dorsal to it, it was probably not among the most posterior vertebrae in the sequence.

In addition to the ACPL, three further laminae radiate from the parapophysis: part of an anteriorly directed PRPL, the ventral portion of a dorsally directed lamina, which is interpreted as a PPDL, and a posteroventrally directed accessory lamina supporting the parapophysis. This is presumably homologous with a PCPL, but cannot be so named as it does not approach the centrum, and indeed extends only 30 mm. Where the latter lamina merges with the neural arch, another accessory lamina arises. Directed posterodorsally, it presumably extended to the postzygapophysis and is here regarded as an accessory postzygapophyseal lamina similar to that found in posterior dorsal vertebrae of *Diplodocus carnegii* Hatcher, 1901 (Hatcher 1901, pl. 7). The PPDL, accessory infraparapophyseal and accessory postzygapophyseal lamina form three sides of a quadrilateral fossa; the fourth side, presumably formed by a PODL, is not preserved, although a very low and unobtrusive accessory lamina does join the dorsalmost preserved part of the PPDL to the accessory postzygapophyseal lamina. The near-vertical orientation of the PPDL indicates that the diapophysis was located some distance directly dorsal to the parapophysis, further extending the inferred height of the neural arch and ruling out an interpretation of the accessory postzygapophyseal lamina as the ACDL or as the ‘accessory PCDL’ of Salgado *et al.* (2005). Finally, a broken ridge of bone extends up the posterior margin of the lateral face of the neural arch. Its identity is problematic: it cannot be a PCDL owing to the anterior position inferred for the diapophysis.

Between the ACPL and the posterior lamina, above the dorsal margin of the lateral fossa and below the accessory laminae described above, the lateral face of the neural arch is a flat featureless area measuring 90 mm anteroposteriorly and 50 mm dorsoventrally. This feature is not observed in any other sauropod vertebra.

In posterior view, the pedicels of the neural arch are robust pillars, leaning somewhat medially, measuring 30 mm in width, extending at least 130 mm dorsally, and merging into the CPOLs before damage obscures their further extent. They enclose a neural canal that is almost exactly circular, 35 mm in diameter. There is no trace of the postzygapophyses or hyposphene, and no indication that these structures were attached to the preserved portion of the arch. It must be assumed, then, that these features were located on the lost, more dorsal, part of the neural arch. The hyposphene, if present, was located at least 90 mm dorsal to the centrum (measured from the floor of the neural canal), and the postzygapophyses at least 140 mm dorsal to the centrum.

In anterior view, too, the pedicels are robust, being 25 mm in width. They merge gradually into the CPRLs and extend dorsally for at least 80 mm, dorsal to which they are broken. In this aspect, however, the neural canal has no roof, instead forming a large teardrop-shaped vacuity 120 mm tall and 55 mm wide. The dorsal portion of this vacuity is bounded by a pair of gently curved, dorsomedially directed laminae unknown in other sauropods, which meet at a 55 degree angle to form an arch dorsal to the neural canal. The vacuity is filled with matrix, so the extent of its penetration posteriorly into the neural arch cannot be assessed. The prezygapophyses are absent; their articular surfaces were probably about 140 mm above the floor of the neural canal, judging by the trajectory of the PRPL.

The most anterodorsal preserved portion of the vertebra is obscured by a flat, anterodorsally directed 'apron' of matrix, 15 mm thick and 120 mm wide, which hampers interpretation of the prezygapophyseal area.

COMPARISONS AND INTERPRETATION

The large size of the specimen, combined with its concave cotyle, lateral foramina and complex system of bony laminae, indicate that it is a sauropod vertebra (Salgado *et al.* 1997, p. 6; Wilson and Sereno 1998, pp. 42–43). Within this group, the deep excavation of the anterior face of the neural arch and the height of the neural arch exceeding that of the centrum (Upchurch 1998, char. B7, B6) place the specimen within the clade (*Barapasaurus* + Eusauropoda). The deep lateral foramen indicates that the specimen is within or close to Neosauropoda (Salgado *et al.* 1997, pp. 8–9; Wilson and Sereno 1998, p. 44; Upchurch 1998, char. B5), as does the camerate internal structure of the centrum (Wedel 2003, p. 354). Possession of an ACPL suggests placement with Neosauropoda (Upchurch 1998, char. H3), a group of advanced sauropods consisting of diplodocoids, macronarians (camarasaurids, brachiosaurids and titanosaurs), and in some phylogenies *Haplocanthosaurus* Hatcher, 1903a. This identification is corroborated by the fact that no definitive non-neosauropod sauropods are known from the Cretaceous (Upchurch and Barrett 2005, p. 119): *Jobaria tiguidensis* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1999 from the Lower Cretaceous or Cenomanian of Niger, Africa, was recovered as a non-neosauropod by Sereno *et al.* (1999) and Wilson (2002), but as a basal macronarian by Upchurch *et al.* (2004).

ACPLs are also present, apparently by way of convergence, in mamenchisaurids, i.e. the mostly Chinese radiation of basal eusauropods including *Mamenchisaurus* Young, 1954 and *Omeisaurus* Young, 1939 (Upchurch 1998, char. D4), suggesting an alternative identity for R2095. [Upchurch termed these animals 'euhielopodids', but since *Euhelopus* Romer, 1956 itself is recovered outside this group in some analyses (Wilson and Sereno

1998; Wilson 2002), this name is misleading. Of the other available names for this group, we prefer the older name Mamenchisauridae Young and Zhao, 1972 over Wilson's (2002) Omeisauridae, as now does Wilson himself (pers. comm. 2006 to MPT)]. The posterior dorsal vertebrae of the mamenchisaurid *Mamenchisaurus hochuanensis* Young and Zhao, 1972 indeed have ACPLs, but they do not at all resemble those of R2095, being much shorter and less defined. The vertebrae resemble R2095 in having tall neural arches; however, they lack lateral foramina entirely and their centra are amphiplatyan (Young and Zhao 1972, fig. 7), thereby ruling out a mamenchisaurid identity for R2095.

We now consider each neosauropod group in turn, investigating the possibility of *X. proneneukos*'s membership of these groups.

Diplodocoidea

Tall neural arches are not unusual in the dorsal vertebrae of diplodocoids; and forward-sloping neural arches are known in this group, for example in dorsals 6–8 of CM 84, the holotype of *Diplodocus carnegii* (Hatcher 1901, pl. 7). Taken alone, these gross morphological characters of the neural arch suggest that R2095 may represent a diplodocoid. However, the length of the centrum, especially in so posterior a dorsal vertebra, argues against this possibility: the posterior dorsal centra of diplodocoids typically have $EI < 1.0$, compared with 1.25 for R2095. Furthermore, the lateral foramina of diplodocoids are more anteriorly located on the centrum and not set within fossae (e.g. Hatcher 1901, pl. 7; Ostrom and McIntosh 1966, pl. 19).

Among diplodocoids, rebbachisaurids differ in dorsal morphology from the better known diplodocids and dicraeosaurids, and in some respects R2095 resembles the dorsal vertebra of the type specimen of *Rebbachisaurus garasbae* Lavocat, 1954. As shown by Bonaparte (1999a, fig. 39), that vertebra has a tall neural arch whose posterior margin closely approaches, though it is not continuous with, that of the centrum. However, it differs from R2095 in many respects: for example, possession of a very prominent PCPL (LIP of Bonaparte's usage), large and laterally diverging prezygapophyses, depressions at the base of the neural arch (Bonaparte 1999a, p. 173), lateral foramina not set within fossae, and a strongly arched ventral border to the centrum. There is, then, no basis for assigning R2095 to this group.

In some phylogenies (e.g. Wilson 2002, fig. 13A), *Haplocanthosaurus* is recovered as a basal diplodocoid close to Rebbachisauridae, and its dorsal vertebrae are quite similar to those of *Rebbachisaurus* (compare Hatcher 1903b, pl. 1 with Bonaparte 1999a, fig. 39). R2095 therefore

bears a superficial resemblance to the dorsal vertebrae of *Haplocanthosaurus*, but a close relationship with that genus is precluded for the same reasons that R2095 is excluded from Rebbachisauridae. The dorsal vertebrae of *Haplocanthosaurus*, and some rebbachisaurids [e.g. *Limaysaurus* (= '*Rebbachisaurus*') *tessonei* Calvo and Salgado, 1995], have asymmetric neural canals, but in the opposite sense from R2095: they are circular anteriorly, and tall and arched posteriorly. Furthermore, the posterior arches of the neural canals in these taxa, composed of dorsomedially inclined CPOLs that meet below the zygapophyses, are very different from the anterior arch of R2095, which is composed of novel laminae that enclose the neural canal, laterally bound by the CPRLs.

Macronaria

The concave cotyle of R2095 in so posterior a dorsal suggests a macronarian identity (Salgado *et al.* 1997, p. 9). The concavity is sufficiently deep to rule out the possibility of the vertebra being amphicoelous, i.e. it must have had a convex condyle; this is also interpreted as a macronarian synapomorphy (Upchurch 1998, char. J6). However, the shallowness of the cotyle's curvature makes this only a weak indication, since in brachiosaurids, camarasaurids and titanosaurs, even the posterior dorsals are strongly opisthocoelous (Wilson and Sereno 1998, p. 51). Among macronarians, the dorsally arched ventral margin of the centrum in lateral view suggests either a brachiosaurid or camarasaurid identity rather than a titanosaurian one (Wilson and Sereno 1998, p. 51).

Camarasauridae

The name Camarasauridae has been widely used (e.g. Bonaparte 1986a; McIntosh 1990), even though its membership now seems to be restricted to *Camarasaurus* Cope, 1877. Other putative camarasaurid genera such as *Morosaurus* Marsh, 1878a and *Cathetosaurus* Jensen, 1988 are currently considered synonymous with *Camarasaurus* (Osborn and Mook 1921; McIntosh *et al.* 1996), although morphological differences between specimens suggest that the genus may have been over-lumped. Various other genera have been referred to Camarasauridae but most of these are no longer considered to be closely related to *Camarasaurus*: for example, *Opisthocoelicaudia* Borsuk-Bialynicka, 1977 was considered camarasaurid by its describer and by McIntosh (1990), but is now considered titanosaurian (Salgado and Coria 1993; Upchurch 1998); and *Euhelopus* is now considered either a mamenchisaurid (Upchurch 1995, 1998) or closely related to Titanosauria (Wilson and Sereno 1998; Wilson 2002). However,

remaining possible camarasaurids include *Janenschia* Wild, 1991, considered camarasaurid by Bonaparte *et al.* (2000) but titanosaurian by Wilson (2002, p. 248) and Upchurch *et al.* (2004, p. 310); the unnamed proximal fibula described by Moser *et al.* (2006, p. 46) as camarasaurid based on the shape of the tibial articular face; and *Datousaurus bashanensis* Dong and Tang, 1984 (Peng *et al.* 2005) and *Dashanpusaurus dongi* Peng, Ye, Gao, Shu and Jiang, 2005. Since *Camarasaurus* morphology differs so characteristically from that of other sauropods, it is useful to refer to 'camarasaurid' morphology, and to that end we provisionally use the name Camarasauridae to refer to the clade (*Camarasaurus supremus* Cope, 1877 not *Saltasaurus loricatus* Bonaparte and Powell, 1980), i.e. the clade of all organisms sharing more recent ancestry with *Camarasaurus* than with *Saltasaurus*.

The posterior dorsals of *Camarasaurus* have somewhat dorsoventrally elongated neural arches (Osborn and Mook 1921, pl. 70), and some posterior dorsal vertebrae of *Camarasaurus* have a tall infraprezygapophyseal vacuity similar in size to that of R2095 (e.g. Ostrom and McIntosh 1966, pls 23–25). However, the oval shape of this vacuity is very different, and there are no internal supporting laminae. The neural arches of camarasaurid dorsal vertebrae are typically very close to vertical, giving the vertebrae an 'upright' appearance very different from that of R2095 (Osborn and Mook 1921, fig. 37; McIntosh *et al.* 1996, pls 5, 9); and the small, subcircular, anteriorly placed lateral foramina of camarasaurids contrast with the medium-sized, anteroposteriorly elongate, centrally placed lateral foramen of R2095. Furthermore, camarasaurid centra are proportionally short, and their neural arches feature prominent infradiapophyseal laminae (Osborn and Mook 1921, pl. 70) that are absent in R2095. In summary, R2095 does not closely resemble *Camarasaurus*, and a camarasaurid identity may be confidently ruled out.

Instead, the length of the centrum relative to the cotyle height, with an EI of 1.25, suggests a titanosauriform identity for *X. proneneukos* (Upchurch 1998, char. K3). This is corroborated by the shape of the lateral foramen, which is an anteroposteriorly elongate oval (Salgado *et al.* 1997, pp. 18–19) with its posterior margin slightly more acute than its anterior margin (Upchurch 1998, char. M1).

Brachiosauridae

The long centrum particularly suggests a brachiosaurid identity, as *Brachiosaurus* Riggs, 1903 has the proportionally longest posterior dorsal centra of all sauropods. Brachiosaurids are the best represented sauropods in the Lower Cretaceous of England (e.g. the '*Eucamerotus*' co-type specimens BMNH R89/90, the unnamed cervical vertebra MIWG 7306 and the undescribed partial skeleton

MIWG BP001), so this identity is also supported on palaeobiogeographical grounds.

The cladistic analysis of Salgado *et al.* (1997) recovered a 'Brachiosauridae' that is paraphyletic with respect to Titanosauria, a finding that has been widely quoted (e.g. Wedel *et al.* 2000b; Naish *et al.* 2004). However, since only two putative brachiosaurids were included in the analysis (*Brachiosaurus brancai* Janensch, 1914 and *Chubutisaurus* Corro, 1975), this paraphyly amounts to the recovery of *Chubutisaurus* closer to titanosaurs than to *B. brancai*, which is not a particularly surprising result as its brachiosaurid affinity has only ever been tentatively proposed (McIntosh 1990, p. 384), with an alternative titanosaurian identity also mentioned. Furthermore, the (*Chubutisaurus* + Titanosauria) clade of Salgado *et al.* is supported only by a single synapomorphy, 'Distal end of tibia broader transversely than anteroposteriorly (reversal)'. That is, the distal end of the tibia of *Brachiosaurus brancai* is supposed to be longer than broad (Salgado *et al.* 1997, p. 26); but this seems to be contradicted by Salgado *et al.*'s own figure 11. In order to demonstrate that Brachiosauridae as traditionally conceived is paraphyletic, it would be necessary to perform an analysis that includes many putative brachiosaurids, such as *B. altithorax*, *B. brancai*, *Cedarosaurus weiskopfae* Tidwell, Carpenter and Brooks, 1999; *Atlasaurus imelakei* Monbaron, Russell and Taquet, 1999; *Sauroposeidon proteles*, the French '*Bothriospondylus*' material, the '*Eucamerotus*' cotype specimens BMNH R89/90, *Pleurocoelus* Marsh, 1888, the Texan '*Pleurocoelus*' material, *Lapparentosaurus madagascariensis* Bonaparte, 1986a and the unnamed Argentinian brachiosaurid MPEF PV 3098/9 (Rauhut 2006). Such an analysis would most likely indicate that some of these taxa are indeed not in the clade Brachiosauridae *sensu* Wilson and Sereno (1998) = (*Brachiosaurus* not *Saltasaurus*), but that a core remains. So far, the analysis that has included most putative brachiosaurids is that of Upchurch *et al.* (2004), which recovered a *Brachiosaurus-Cedarosaurus* clade, *Atlasaurus* as a basal macronarian and *Lapparentosaurus* as an indeterminate titanosauriform. Pending restudy of this group, we assess likely membership of Brachiosauridae primarily by morphological similarity to the two *Brachiosaurus* species.

While the overall proportions of R2095 are a good match for those of brachiosaurid dorsals, its lateral excavations are not characteristic of brachiosaurids. In this specimen, a deep foramen is located within a large, shallow fossa, a character usually associated with titanosaurs (Bonaparte and Coria 1993, p. 272), and not found in the *Brachiosaurus altithorax* holotype FMNH P25107 (Riggs 1904, pl. 72; MPT, pers. obs. 2005). Only two dorsal vertebrae belonging to *Brachiosaurus brancai* can be interpreted as having this feature: dorsal 7 of the *B. brancai* holotype HMN SII appears to have its lateral foramina

located within slightly broader fossae, but its centrum is so reconstructed that this apparent morphology cannot be trusted; and the isolated dorsal vertebra HMN AR1 has a complex divided excavation that could be interpreted in this way, but this vertebra is different from the other *B. brancai* material in several ways and may have been incorrectly referred (MPT, pers. obs. 2005). R2095 also differs from brachiosaurid dorsal vertebrae in the dorsal placement of its foramina and its lack of infradiapophyseal laminae.

Titanosauria

Although the lateral fossae and contained foramina of R2095 are a good match for those of titanosaurs (Bonaparte and Coria 1993, p. 272), the specimen is in most other respects incompatible with a titanosaurian identification. The neural spines of titanosaurs are posteriorly inclined by as much as 45 degrees and although the neural spine of R2095 is not preserved, the 35 degree anterior inclination of the neural arch makes such a posterior slope of the spine very unlikely. What remains of the neural arch does not have the 'inflated' appearance characteristic of titanosaurs: the laminae are gracile and clearly delineated, whereas those of titanosaurs are more robust and tend to merge into the wall of the neural arch. The sharp-edged, vertical ACPL of R2095, for example, does not at all resemble the more robust and posteroventrally orientated centroparapophyseal lamina of titanosaurs (Salgado *et al.* 1997, p. 19, fig. 2). *Xenoposeidon proneneukos* also lacks the thick, ventrally forked infradiapophyseal laminae of titanosaurs (Salgado *et al.* 1997, p. 19). Finally, the camerate internal structure of the centrum does not resemble the 'spongy' somphospondylous structure characteristic of titanosaurs, although Wedel (2003, p. 351) pointed out that there are exceptions such as *Gondwanatitan* Kellner and Azevedo, 1999, a seemingly camerate titanosaur. The overall evidence contradicts a titanosaurian identity for R2095.

The origin of titanosaurs has traditionally been interpreted as a vicariance event precipitated by the Late Jurassic break-up of Pangaea into the northern supercontinent of Laurasia and the southern supercontinent of Gondwana (e.g. Lydekker 1893b, p. 3; Bonaparte 1984, 1999c; Bonaparte and Kielan-Jaworowska 1987; Le Loeuff 1993). Wilson and Upchurch (2003, p. 156) rejected this model, in part on the basis that titanosaur fossils are known from before the Pangaeian break-up. However, the pre-Late Jurassic record of titanosaurs is dominated by trace fossils: 'wide-gauge' trackways (Santos *et al.* 1994; Day *et al.* 2002, 2004; see Wilson and Carrano 1999). Titanosaurian body fossils from this era are in short supply

TABLE 2. Character scores for *Xenoposeidon* in the matrix used for the phylogenetic analysis in this paper. Apart from the addition of *Xenoposeidon*, the matrix is identical to that of Harris (2006). *Xenoposeidon* is unscored for all characters except those listed. Conventional anatomical nomenclature is here used in place of the avian nomenclature of Harris.

Character	Score	
123 Lateral fossae in majority of dorsal centra	2	Present as deep excavations that ramify into centrum and into base of neural arch (leaving only thin septum in body midline)
124 Position of lateral foramina on dorsal centra	2	Set within lateral fossa
125 Anterior face of dorsal neural arches	1	Deeply excavated
127 Single midline lamina extending ventrally from hyposphene in dorsal vertebrae	0	Absent
134 Morphology of ventral surfaces of anterior dorsal centra	0	Ventrally convex [inferred from posterior dorsal]
137 Ratio of dorsoventral height of neural arch: dorsoventral height of dorsal centrum	1	> 1.0
139 Anterior centroparapophyseal lamina on middle and posterior dorsal neural arches	1	Present
140 Prezygaparapophyseal lamina on middle and posterior dorsal neural arches	1	Present
141 Posterior centroparapophyseal lamina on middle and posterior dorsal neural arches	1	Present [as the homologous accessory infrapapophyseal lamina]
149 Orientation of middle and posterior dorsal neural spines	0	Vertical [rather than posterodorsally inclined]
150 Morphology of articular face of posterior dorsal centra	1	Opisthocelous
151 Cross-sectional morphology of posterior dorsal centra	1	Dorsoventrally compressed
153 Position of diapophysis on posterior dorsal vertebrae	1	Dorsal to parapophysis

and very fragmentary: the earliest titanosaurian body-fossil known from adequate material is *Janenschia* from the Kimmeridgian Tendaguru Formation of Tanzania, Africa. We therefore have very little idea what the Middle Jurassic ur-titanosaur, or its Laurasian descendants, looked like. Good Cretaceous titanosaur body fossils are known from Laurasian continents (e.g. *Alamosaurus* Gilmore, 1922 from North America and *Opisthocoeleicaudia* from Mongolia), but only from the Maastrichtian, and these may be interpreted as end-Mesozoic immigrants from Gondwana. The body-fossil record of endemic Laurasian Early Cretaceous titanosaurs remains extremely poor, consisting only of suggestive scraps. In this context, it is possible that *Xenoposeidon proneneukos* may represent a titanosaur belonging to the hypothetical endemic Laurasian radiation, in which case it would be the first such known from presacral vertebral material.

In conclusion, while R2095 can be confidently identified as a member of Neosauropoda, its unusual combination of characters, its wholly unique characters and the paucity of comparable Wealden or other Early Cretaceous Laurasian material preclude assignment to any more specific group within that clade.

Phylogenetic analysis

In light of the uncertain result of group-by-group comparisons, and despite the fragmentary material, a preli-

minary phylogenetic analysis was performed in the hope of elucidating the phylogenetic position of *Xenoposeidon*. We used the data of Harris (2006) and added the new taxon, yielding a matrix of 31 taxa (29 ingroups and two outgroups) and 331 characters. Because of the paucity of material, *Xenoposeidon* could be scored for only 13 characters, 4 per cent of the total (Table 2). Following Harris (2006), PAUP* 4.0b10 (Swofford 2002) was used to perform a heuristic search using random stepwise addition with 50 replicates and with maximum trees = 500,000. The analysis yielded 1089 equally parsimonious trees with length = 785, consistency index (CI) = 0.5248, retention index (RI) = 0.6871, and rescaled consistency index (RC) = 0.3606.

The strict consensus tree (Text-fig. 6A) is poorly resolved, with Neosauropoda, Diplodocoidea and Macronaria all collapsing, and only Flagellicaudata and its subclades differentiated within Neosauropoda. This represents a dramatic loss of resolution compared to the results without *Xenoposeidon* (Harris 2006, fig. 5A), indicating the instability of the new taxon's position. In the 50 per cent majority rule tree (Text-fig. 6B) all the standard sauropod clades were recovered. This majority rule tree recovers *Xenoposeidon* as a non-brachiosaurid basal titanosauriform, the outgroup to the (*Euhelopus* + Titanosauria) clade. However, various most-parsimonious trees also recover *Xenoposeidon* in many other positions, including as a brachiosaurid, basal titanosaur, basal lithostrotian, saltasaurid and rebbachisaurid. In none of the

Although we are reluctant to inflict another vertebra-based taxon upon fellow sauropod workers, BMNH R2095 is highly distinctive and can be separated from other sauropods, and so formal systematic recognition is appropriate. Although some workers have preferred not to raise new names for specimens represented only by limited material, a better criterion is how autapomorphic the preserved portion of the specimen is; and R2095's suite of unique characters emphatically establishes it as distinct. In the light of its separation from all recognized major sauropod clades, failure to recognize it as a separate taxonomic entry would be misleading, as typically it is only named genera that participate in diversity surveys such as those of Holmes and Dodson (1997), Fastovsky *et al.* (2004) and Taylor (2006).

DISCUSSION

Historical taxonomy

While the specimen described here represents a diagnosable taxon, the possibility that it is referable to one of the named sauropod taxa from the Hastings Beds Group must be considered. Two named sauropods are known from the Hastings Beds Group. '*Pelorosaurus*' *becklesii* Mantell, 1852 is based on a humerus, ulna and radius with associated skin, discovered at Hastings. On the basis of the robustness of its limb bones, this taxon appears to be a titanosaur (Upchurch 1995, p. 380; Upchurch *et al.* 2004, p. 308), and one of the earliest reported members of that clade. BMNH R2095 therefore cannot be referred to it. [Since '*P.*' *becklesii* is not congeneric with the *Pelorosaurus* type species *P. conybeari* (see below) it should be given a new name, if it is sufficiently diagnostic. This decision falls outside the scope of the current work.]

The second taxon from the Hastings Beds Group has a complex nomenclatural history. Four proximal caudal vertebrae (BMNH R2544–2547) and three chevrons (BMNH R2548–2550) from the Hastings Beds Group of Cuckfield, together with specimens from Sandown Bay on the Isle of Wight, were named *Cetiosaurus brevis* Owen, 1842. This is the first named *Cetiosaurus* species that is not a *nomen dubium* and thus is technically the type species. However, because the name *Cetiosaurus* is historically associated with the Middle Jurassic Oxfordshire species *C. oxoniensis* Phillips, 1871. Upchurch and Martin (2003, p. 215) plan to petition the ICZN to make this the type species. *Cetiosaurus brevis* is clearly not congeneric with *C. oxoniensis*: accordingly, the former is referred to as '*C.*' *brevis* from here on. The Isle of Wight '*C.*' *brevis* material was demonstrated to be iguanodontian by Melville (1849) who went on to provide the new name '*C.*'

conybeari Melville, 1849 for the Cuckfield sauropod component of '*C.*' *brevis*. As has been widely recognized, Melville's (1849) course of action was inadmissible as '*C.*' *brevis* was still available for this material (Ostrom 1970; Steel 1970; Naish and Martill 2001; Upchurch and Martin 2003) and, accordingly, '*C.*' *conybeari* is a junior objective synonym of '*C.*' *brevis*.

Discovered adjacent to the Cuckfield '*C.*' *brevis* vertebrae and chevrons was a large humerus. Mantell (1850) referred this to Melville's (1849) name '*C.*' *conybeari*, but decided that the taxon was distinct enough for its own genus, *Pelorosaurus* Mantell, 1850. [As shown by Torrens (1999, p. 186), Mantell considered the name *Colossosaurus* for this humerus]. Though still discussed apart in most taxonomic reviews (e.g. Naish and Martill 2001; Upchurch and Martin 2003), it is therefore clear that *Pelorosaurus conybeari* and '*C.*' *brevis* are objective synonyms, with the latter having priority. As part of the previously mentioned ICZN petition, it is planned to suppress the latter name, and instead conserve the more widely used *Pelorosaurus conybeari*; for now, though, we continue to use '*C.*' *brevis*. The identity and validity of this material remains problematic. The humerus lacks autapomorphies and, though it is brachiosaurid-like and, hence, conventionally identified as representing a member of that group (e.g. McIntosh 1990), it differs in having a less prominent deltopectoral crest. Furthermore, the '*C.*' *brevis* caudal vertebrae are titanosaur-like in at least one feature, the absence of a hyposphenal ridge. On this basis, Upchurch and Martin (2003) proposed that the material be referred to Titanosauriformes *incertae sedis*. It can be seen to be distinct from '*Pelorosaurus*' *becklesii* as the humeri of both species are preserved.

Since R2095 is similar in age and geography to '*C.*' *brevis*, it is conceivable that it might belong to this species; indeed, Lydekker (1893a) assumed this to be the case, based on it being distinct from '*Eucamerotus*' ('*Hoplosaurus*' of his usage) and on the unjustified assumption that there were no more than two Wealden sauropods. However, this assignment cannot be supported owing to the lack of overlapping material.

To confuse matters further, during part of the nineteenth and twentieth centuries, '*C.*' *brevis* was referred to by the name *Morosaurus brevis*; and it is under this name that R2095 is catalogued. The description of *Morosaurus impar* Marsh, 1878a from the Morrison Formation of Como Bluff in Wyoming initiated the naming of several new *Morosaurus* species, and the referral to this genus of species previously classified elsewhere (Marsh 1878b, 1889). Marsh (1889) evidently thought that *Morosaurus* might occur in Europe, as '*Pelorosaurus*' *becklesii* was among the species he referred to it. Nicholson and Lydekker (1889), regarding '*P.*' *becklesii* as a junior synonym of '*Cetiosaurus*' *brevis* and agreeing with Marsh's referral of '*P.*' *becklesii* to *Morosaurus*, then incorrectly

used the new combination *Morosaurus brevis*. This name was now being used for assorted Lower Cretaceous English sauropods belonging to quite different taxa. Use of *M. brevis* was perpetuated by Lydekker (1890, 1893a) and Swinton (1934, 1936). However, Marsh's (1889) original referral of '*Pelorosaurus becklesii* to *Morosaurus* was unsubstantiated as no unique characters shared by the two were identified. The name *Morosaurus* was later shown to be a junior synonym of *Camarasaurus* (Osborn and Mook 1921), so this name is not available for R2095 because it is tied to a holotype now regarded as a junior subjective synonym.

In addition to the named taxa discussed above, a large sauropod metacarpal from Bexhill beach, derived from the Hastings Beds Group, has been identified as diplodocid (Anonymous 2005), an identification confirmed by Matthew F. Bonnan (pers. comm. 2006 to DN). If correctly identified, this specimen indicates the presence of at least three higher sauropod taxa in the Hastings Beds Group (diplodocids, basal titanosauriforms and titanosaurs) or four if *X. proneneukos* indeed represents a new group. The presence of these several different taxa in coeval or near-coeval sediments is not unexpected given the high genus-level sauropod diversity present in many other sauropod-bearing units (e.g. Morrison Formation, Tendaguru Formation).

Length and mass

Table 1 shows comparative measurements of R2095 and the dorsal vertebrae of other neosauropods. We can reach some conclusions about the probable size of *X. proneneukos* by comparing its measurements with those of a typical brachiosaurid and a typical diplodocid, reference taxa that bracket the known range of sauropod shapes.

The estimated total centrum length of R2095 including the missing condyle is 200 mm, compared with 330 mm for the seventh dorsal vertebra of *Brachiosaurus brancai* HMN SII (Janensch 1950, p. 44): about 60 per cent as long. If R2095 were built like a brachiosaurid, then it would be 60 per cent as long as HMN SII, yielding a length of 15 m based on Paul's (1988) estimate of 25 m for that specimen.

The average cotyle diameter of R2095 is 165 mm, compared with 270 mm for HMN SII: again, about 60 per cent. If the two animals were isometrically similar, R2095's mass would have been about $0.6^3 = 22$ per cent that of HMN SII. SII's mass has been variously estimated as 78,258 kg (Colbert 1962), 14,900 kg (Russell *et al.* 1980), 46,600 kg (Alexander 1985), 29,000 kg (Anderson *et al.* 1985), 31,500 kg (Paul 1988), 74,420 kg (Gunga *et al.* 1995), 37,400 kg (Christiansen 1997) and 25,789 kg (Henderson 2004). Of these estimates, those of Russell

et al. (1980) and Anderson *et al.* (1985) can be discarded, as they were extrapolated by limb-bone allometry rather than calculated from the volume of models. The estimates of Colbert (1962) and Gunga *et al.* (1995) can also be discarded, as they are based on obviously overweight models. The average of the remaining four estimates is 35,322 kg. Based on this figure, the mass of R2095 might have been in the region of 7600 kg, about the weight of a large African bush elephant (*Loxodonta africana*).

R2095 would have been longer and lighter if it were built like a diplodocid. Its centrum length and average cotyle diameter of 200 mm and 165 mm compare with measurements of 270 mm and 295 mm for corresponding vertebrae in *Diplodocus carnegii* CM 84. Therefore, if *X. proneneukos* were diplodocid-like it would be perhaps 74 per cent as long as a 27-m *Diplodocus*, i.e. 20 m. Its volume can be estimated as proportional to its centrum length multiplied by the square of its average cotyle diameter, under which assumption it would have been 23 per cent as heavy as *Diplodocus*: 2800 kg, based on Wedel's (2005) mass estimate of 12,000 kg for CM 84.

While R2095 represents an animal that is small by sauropod standards, neurocentral fusion is complete and the sutures completely obliterated, indicating that it belonged to an individual that was mostly or fully grown (Brochu 1996).

Sauropod diversity

Historically, Sauropoda has been considered a morphologically conservative group, showing less diversity in body shape than the other major dinosaurian groups, Theropoda and Ornithischia (e.g. Wilson and Curry Rogers 2005, pp. 1–2). For many decades, the basic division of sauropods into cetiosaurs, mamenchisaurs, diplodocoids, camarasaurids, brachiosaurs and titanosaurs seemed established, and as recently as 30 years ago, Coombs (1975, p. 1) could write that 'little information in the form of startling new specimens has been forthcoming for sauropods over the last 40 years'. Recent finds are changing this perception, with the discovery of previously unknown morphology in the square-jawed rebbachisaurid *Nigersaurus* Sereno, Beck, Dutheil, Larsson, Lyon, Moussa, Sadleir, Sidor, Varricchio, Wilson and Wilson 1999, the long-legged titanosaur *Isisaurus* Wilson and Upchurch, 2003 (originally '*Titanosaurus colberti* Jain and Bandyopadhyay 1997), the short-necked dicraeosaurid *Brachytrachelopan* Rauhut, Remes, Fechner, Cladera and Puerta, 2005, and the truly massive titanosaurs *Argentinosaurus* Bonaparte and Coria, 1993, *Paralititan* Smith, Lamanna, Lacovara, Dodson, Smith, Poole, Giegengack and Attia, 2001 and *Puertasaurus* Novas, Salgado, Calvo and Agnolin, 2005. During the same period, Rebbachisauridae has

emerged as an important group (Calvo and Salgado 1995; Pereda Suberbiola *et al.* 2003; Salgado *et al.* 2004).

Perhaps most interesting of all is the recent erection of two sauropod genera that arguably do not fit into any established group: *Agustinia* Bonaparte, 1999b and *Tendaguria* Bonaparte, Heinrich and Wild, 2000. Both of these genera are represented by specimens so different from other sauropods that they have been placed by their authors into new monogeneric 'families', Agustiniidae and Tendaguriidae. Together with *X. proneneukos*, these taxa emphasize just how much remains to be discovered about the Sauropoda and how little of the full sauropod diversity we presently understand. It is hoped that the discovery of new specimens will allow the anatomy and relationships of these enigmatic new sauropods to be elucidated.

CONCLUSIONS

BMNH R2095 is a highly distinctive dorsal vertebra with several features unique within Sauropoda, and as such warrants a formal name, *Xenoposeidon proneneukos*. It does not seem to belong to any established sauropod group more specific than Neosauropoda, and may represent a new 'family'. *Xenoposeidon* adds to a growing understanding of the richness of sauropod diversity, both within the Hastings Beds Group of the Wealden, and globally.

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