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Europe's largest dinosaur? A giant brachiosaurid cervical vertebra from the Wessex Formation (Early Cretaceous) of southern England

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Abstract

A single brachiosaurid sauropod cervical vertebra from the Wessex Formation (Barremian, Early Cretaceous) of the Isle of Wight is remarkable for its size. With a partial centrum length (i.e., excluding evidence of the anterior condyle) of 745 mm it represents the largest sauropod cervical reported from Europe and is close in size to cervical vertebrae of the giant brachiosaurid *Brachiosaurus brancai* from Late Jurassic Tanzania. The complete animal probably exceeded 20 m in total length. The specimen shares important morphological characters with *Sauroposeidon proteles* from Early Cretaceous USA, including extensive lateral fossae and well-developed posterior centroparapophyseal laminae, indicating that it is part of a *Brachiosaurus–Sauroposeidon* clade, and in some characters is intermediate between the two. Owing to the complexities of Isle of Wight sauropod taxonomy the specimen is not attributed to a named taxon.

Keywords: Dinosauria; Sauropoda; Brachiosauridae; *Brachiosaurus*; *Sauroposeidon*; Early Cretaceous; Isle of Wight; England

1. Introduction

Sauropod dinosaurs, the long-necked giants of the Mesozoic, are well represented in the fossil record of Europe. Examples of most major sauropod groups are known from the European Triassic, Jurassic and Cretaceous, including basal sauropods, basal eusauropods, diplodocoids and titanosauriforms (McIntosh, 1990; Weishampel, 1990; Hunt et al., 1994; Upchurch, 1998; Godefroit and Knoll, 2003). The stratigraphic range of sauropods in Europe is extensive and ranges from the Rhaetian to the Maastrichtian (Hunt et al., 1994; Godefroit and Knoll, 2003).

The Wessex Formation (Barremian, Early Cretaceous) of the Isle of Wight, southern England, is well known for its diverse dinosaur fauna (Benton and Spencer, 1995; Hutt et al., 2001; Martill and Naish, 2001), among which are several sauropod taxa (Naish and Martill, 2001). These include a possible diplodocoid and camarasaurid, several taxa traditionally regarded as brachiosaurids, a titanosaur and a number of indeterminate forms. Though as many as ten species-level names are attached to these remains, the holotypes are largely non-diagnostic and based on specimens that do not overlap with other UK Early Cretaceous sauropod holotypes (see Naish and Martill, 2001 for a review). Consequently, the majority of Isle of Wight sauropod genera and species are nomina dubia and none can presently be shown to be referable to the same species.

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Isolated sauropod elements, though in some cases referable to higher clades, cannot be reliably referred to a genus or species.

Here we report a large, isolated sauropod cervical vertebra collected from the foreshore in 1992 by Mr. Gavin Leng of the Isle of Wight. The specimen is notable for its size and also because it exhibits morphological features elsewhere seen only in the giant brachiosaurids *Brachiosaurus brancai* from the Upper Jurassic Tendaguru Formation of Tanzania (Janensch, 1950) and *Sauroposeidon proteles* from the Lower Cretaceous Antlers Formation of Oklahoma, USA (Wedel et al., 2000a,b).

2. Locality and stratigraphy

The new specimen, Isle of Wight Museum no. MIWG.7306, was found on the foreshore between Chilton Chine (Ordnance Survey grid reference 52 408821) and Sudmoor Point (OS grid ref. 57 392827) (Fig. 1). The specimen was enclosed in matrix heavily overgrown by calcareous algae and other marine organisms. The matrix comprises a beige sideritic mudstone with fragments of plant debris and mud clasts and equates to plant debris bed L1 of Stewart (1978). This unit crops out in the cliffs at this locality directly above the Sudmoor Point Sandstone Member (SS2 of Stewart, 1978) of the Wessex Formation. A second, incomplete sauropod vertebra, IWCMS: 2003.28, similar in overall form to MIWG.7306 but consisting only of an eroded centrum 640 mm long, has been collected from the same locality and we suspect that a disarticulated skeleton is being eroded from the cliff over time.

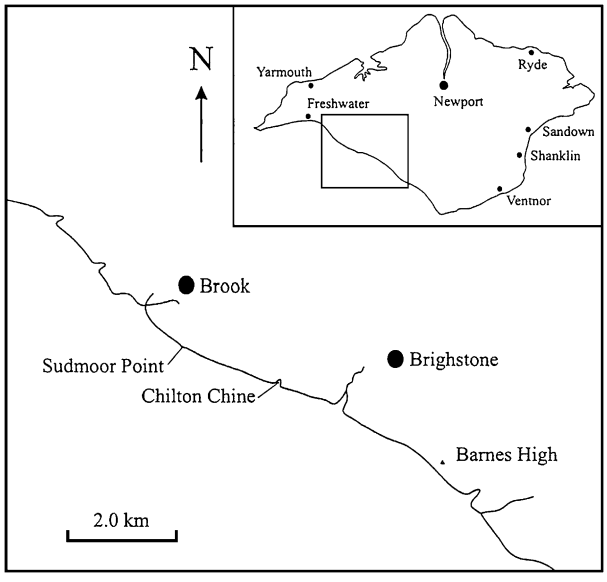

Fig. 1. Sketch map of the Isle of Wight showing the locality at which the new specimen was discovered.

3. Systematic palaeontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Titanosauriformes Salgado et al., 1997
Brachiosauridae Riggs, 1904

Gen. et sp. indet.
Figs. 2–4

Material. MIWG.7306, a cervical vertebra (possibly C6) 745 mm long. Relatively complete though crushed obliquely and missing most of the anterior condyle, the left prezygapophyis, the right diapophysis, most of the laminae associated with the neural arch and most of the left posterior centroparapophyseal lamina. A fragment of neural spine may be represented but cannot be attached to the rest of the specimen. The bone surface is highly brecciated and cemented by white calcite (Fig. 2A). The specimen has previously been figured by Martill and Naish (2001) and is currently on display at the Dinosaur Isle Visitor Centre, Sandown, Isle of Wight.

Abbreviations and terminology. The description here follows Upchurch (1998) in use of the abbreviation EI. We employ Wilson's (1999) terminology for sauropod vertebral laminae and we also follow his system of abbreviations. Hence: EI, elongation index (total length of centrum divided by width of cotyle); Cpol, centropostzygapophyseal lamina; Pcdl, posterior centrodiapophyseal lamina; Pcpl, posterior centroparapophyseal lamina; Podl, postzygodiapophyseal lamina; Prdl, prezygodiapophyseal lamina; Tpol, intrapostzygapophyseal lamina.

Description. MIWG.7306 is broken into two main pieces and examination of its interior shows that it is of camellate morphology. The internal cavities visible at the break are variable in size and shape and recall the cross-sectional view of a *Brachiosaurus* cervical centrum figured by Janensch (1947, fig. 71). The majority of cavities visible toward the dorsal surface of the centrum are taller than they are wide while the majority visible toward the ventral surface of the centrum are wider than they are tall. Most of the cavities are not measurable without ambiguity. Two measurable cavities located ventral to the level of the neural arch differ markedly in size. The smaller is 15 mm tall and 12 mm wide and the

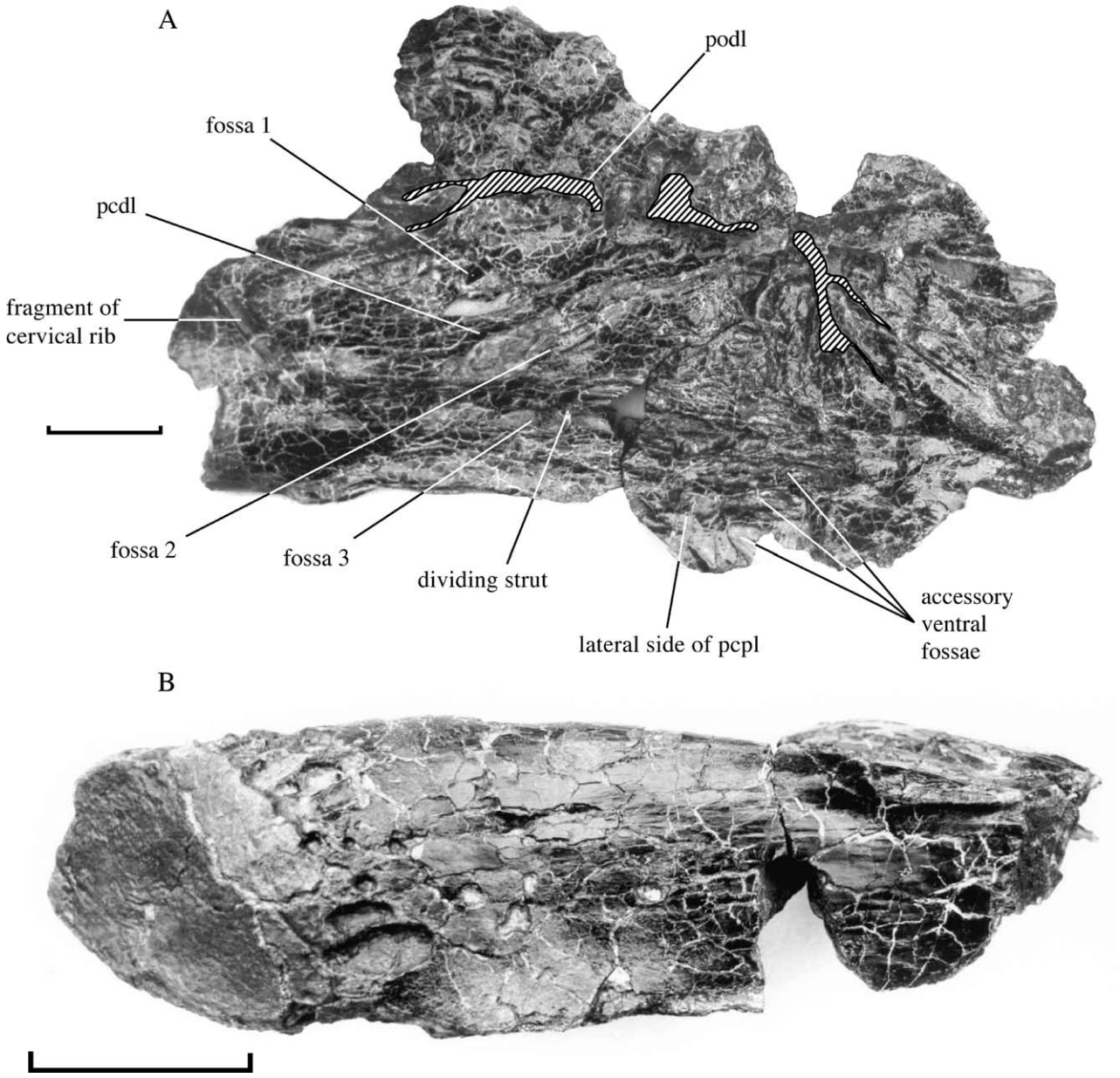

Fig. 2. A, MIWG.7306 in right lateral view. B, right prezygapophysis in dorsal view. Note the reniform articulatory facet and the rounded depressions on the dorsal surface. For abbreviations, see text. Scale bar represents 100 mm.

larger is 45 mm tall and 20 mm wide. The largest measurable cavity located close to the ventral surface of the centrum is 55 mm wide and 40 mm tall.

The centrum is elongate with extensive, complex lateral fossae. The posterior articulatory face is concave and, although somewhat deformed, approximately 195 mm wide and 160 mm tall. Given that the total length is 745 mm, the EI sensu Upchurch (1998) is 3.8. In MIWG.7306, the centrum length divided by the height of the cotyle, a value used by Wilson and Sereno (1998), is 4.7. What remains of the anterior condyle in MIWG.7306 indicates that it was clearly bulbous and convex.

The neural canal is subcircular, 50 mm wide and 40 mm tall. Posteriorly, and arising dorsolateral to the neural canal, distinct cpol extend to the ventromedial surface of the postzygapophyseal facet. A vertical strut extends dorsal to the neural canal to the base of the tpol which itself forms the ventral floor to the postspinous fossa (see Wilson, 1999, p. 647). On both sides, the cpol, tpol and vertical strut enclose deep, triangular pedunclular fossae on the posterior surface of the postzygapophysis (Fig. 3).

On the lateral side of the centrum there are a complex series of fossae. The most dorsal of these is a posteriorly located subtriangle pointing anteriorly (fossa 1 in

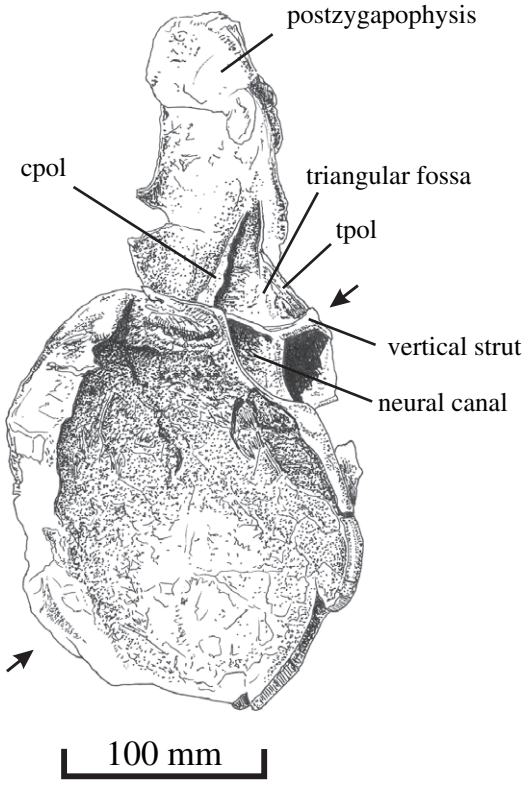

Fig. 3. MIWG.7306 in posterior view. The arrows represent the original dorsoventral midline of the specimen. For abbreviations, see text.

Fig. 2A; see also Fig. 4), bordered dorsally by the podl and ventrally by the pcdl. Similarly shaped and positioned dorsal fossae are seen in *Sauroposeidon proteles* and *Brachiosaurus brancai* (Janensch, 1950; Wedel et al., 2000a,b) (Fig. 5). This dorsal fossa is shallow compared to parts of the more ventral fossae and contains bony struts and smaller, shallow, rounded fossae on its medial bony wall.

Ventral to the pcdl, another subtriangular fossa (fossa 2 in Fig. 2A) extends much further anteriorly than the dorsal fossa but does not extend as far posteriorly. Unlike the dorsal fossa, it widens anteriorly. An anteroventrally descending ridge ventral to this fossa then forms the dorsal border to a subrectangular ventral fossa. The ventral fossa (fossa 3 in Fig. 2A) is complex and descends ventrally towards its anterior end. On the left side, an oblique, posteroventrally directed bony strut (Fig. 4) divides the fossa into anterior and posterior portions and the fossa becomes shallower and pointed anteriorly. On the right side the dividing strut has an anteroventral inclination and the fossa is rectangular anteriorly. Ventral to the anterior part of the ventral fossa is a rectangular accessory fossa, bound dorsally and ventrally by prominent ridges. Within this fossa, ridges on the medial bony wall form a series of smaller rectangular fossae. There are two additional fossae on the anteroventral part of the centrum (labelled accessory ventral fossae in Fig. 2A), the most ventral of which excavates the lateral surface of the pcpl.

As in *B. brancai* (Janensch, 1950), there is a small, shallow elliptical fossa on the anterior end of the ventral surface. There is no midline keel on the ventral surface of the centrum and the ventral surface of the centrum is gently concave. Beginning at a point ventral to the most ventral fossa on the lateral side of the centrum, the pcpl begin posteriorly as small ridges. On the right side, the pcpl originates further posteriorly than it does on the left side. This apparent asymmetry is a result of deformation due to compaction. Ventral to the anterior part of the ventral fossa, the pcpl expands ventrally to a marked degree, though on the left side the anteroventral part of the lamina is missing. The anteroventral extension of the pcpl of the right side is a very thin, sharp-edged plate of bone that is broken ventrally such that the parapophysis is missing (Fig. 2A).

The right prezygapophysis is well preserved and broken from the rest of the vertebra. The prezygapophyseal facet is a flat oval, being 75 mm wide and 105 mm long, and with a rugose ridge marking the facet's ventral edge. On the medial surface just posterior to the prezygapophyseal facet there is a series of oval and rounded fossae. These do not appear to be features of the original osteology and may be of pathological origin or may represent bite marks or post-mortem borings (Fig. 2B). On the lateral side of the prezygapophysis, a prominent prdl extends posteriorly from the anterior end of the prezygapophysis. This lamina overhangs a concave area that is delimited ventrally by a sharp, posteroventrally curving ridge. The left prezygapophysis is missing.

The postzygapophyseal facets are flat and reniform with the longest axis aligned mediolaterally (Fig. 4). There are several pneumatic fossae on the dorsal surface of the postzygapophyses, the number and position of which differ between the left and right postzygapophyses.

What is interpreted here as the left diapophysis (it is unattached to the rest of the specimen) is missing its margins and is still attached to the proximal part of its cervical rib. The diapophysis is broad anteroposteriorly compared with those of *B. brancai* and *S. proteles* and, unlike the diapophyses of these species, possesses a rhomboidal fossa on the body of the diapophysis near its posterior margin. These features may be autapomorphies of whichever taxon MIWG.7306 belongs to. On its lateral side, the diapophysis is flat but on its medial side it bears a prominent median vertical lamina to which are connected a series of parallel subhorizontal bony bars.

Cervical rib shafts are not preserved adjacent to the centrum but a fragment of cervical rib, 120 mm long, lies attached to the posterolateral surface of the centrum. This fragment has parallel dorsal and ventral margins

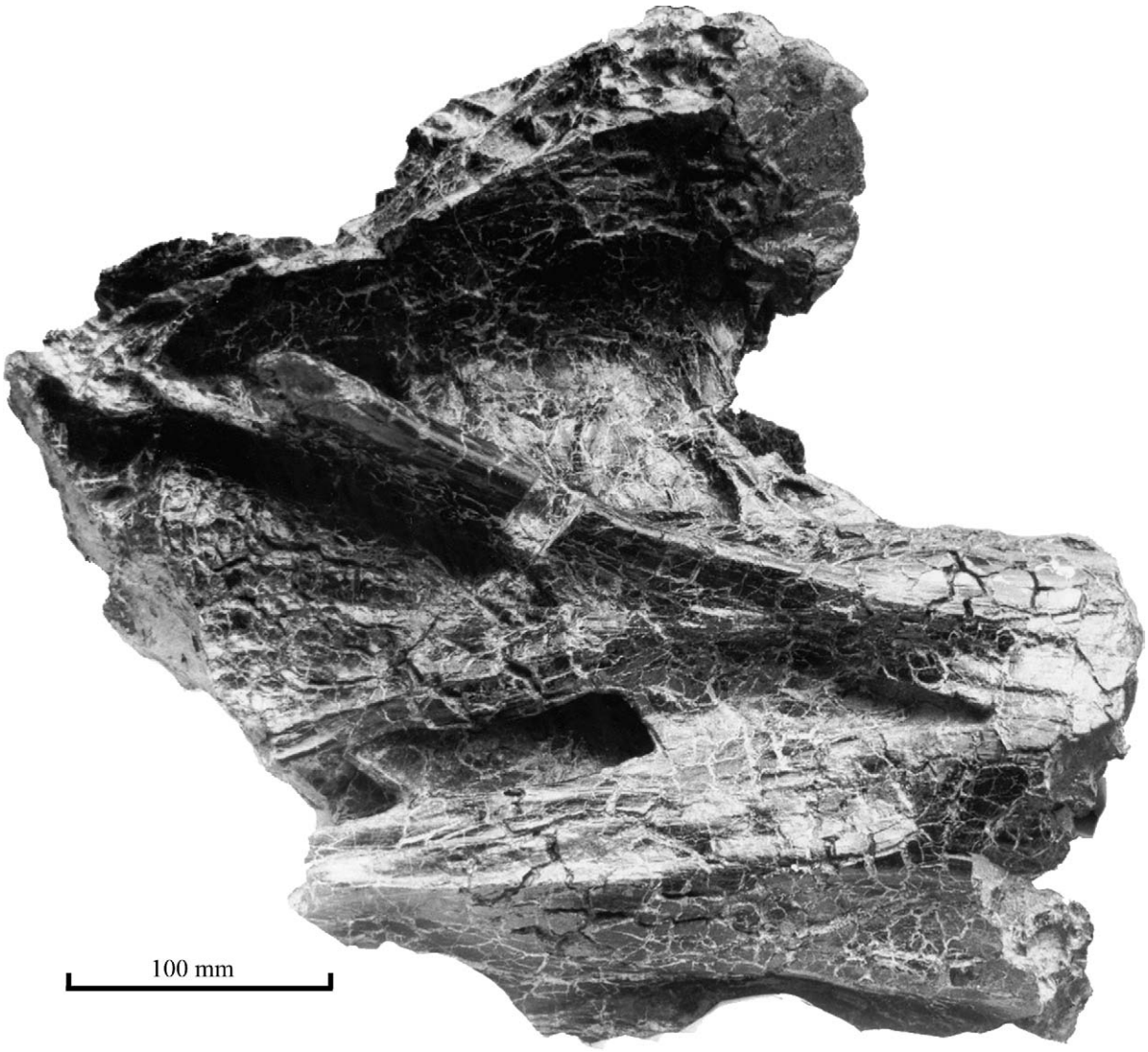

Fig. 4. Posterior part of MIWG.7306 in left lateral view showing (from top to bottom) fossa 1 and the posterior parts of fossae 2 and 3. The dividing strut of fossa 3 is visible at its anterior end.

and is a mediolaterally compressed ovoid in cross-section.

4. Comparisons and phylogenetic affinities

New phylogenetic schemes for Sauropoda have recently been proposed by Upchurch (1995, 1998), Calvo and Salgado (1995), Salgado et al. (1997), Wilson and Sereno (1998) and Wilson (2002). While the position of some sauropod taxa remains controversial, there is now a broad consensus on the affinities of all major sauropod clades. We examined MIWG.7306 within the larger context of sauropod phylogeny.

The marked opisthocoely, high length:width ratio (3.8:1), extensive lateral fossae and complex system of bony laminae of MIWG.7306 demonstrate its sauropod identity. The presence of extensive invasive pneumatic depressions on the sides of the centrum, and of bony septa dividing some of these depressions, indicate that it is a member of the *Omeisaurus* + Neosauropoda clade of Wilson and Sereno (1998). Furthermore, because the laminae associated with the neural arch do not appear to be rudimentary in MIWG.7306, it is excluded from Wilson and Sereno's (1998) clade Somphospondyli (*Euhelopus* + Titanosauria).

The presence in MIWG.7306 of camellate internal morphology invite comparison with *Mamenchisaurus* and members of Titanosauriformes, the only sauropods to exhibit this morphology (Upchurch, 1998; Wedel et al., 2000b; Wilson 2002). Furthermore, the centrum length/cotyle height value of 4.7 in MIWG.7306 is informative as values higher than 4 are only seen in *Omeisaurus*, *Mamenchisaurus*, some diplodocoids and

Brachiosauridae (Wilson, 2002). Combined with the distribution of characters outlined above, the presence of an elongate centrum and deep lateral depressions in MIWG.7306 indicate that it is from a brachiosaurid sensu Wilson and Sereno (1998). Possible affinities with the other taxa mentioned here can be excluded on the basis of the absence of camellate morphology (*Omeisaurus* and diplodocoids) or absence of deep lateral cavities (*Mamenchisaurus*).

Though monophyly of Brachiosauridae is controversial (see below), Wilson and Sereno (1998) regarded the group as a clade characterised by a subrectangular muzzle, humerus subequal in length to the femur and with a prominent deltopectoral crest, and elongate cervical centra with deep accessory depressions. Salgado et al. (1997) argued that Brachiosauridae and *Brachiosaurus* were paraphyletic and that *B. brancai* was closer to Titanosauria than to *B. altithorax*. However, *Brachiosaurus* shares a number of characters with *S. proteles* including elongate cervical centra and ribs, prezygapophyses extensively overhanging the condyle, and a transition point in the neural spine height of the mid-cervical vertebrae (Wedel et al., 2000a,b). As these shared characters are not seen in other titanosauriforms we recognise a restricted monophyletic Brachiosauridae for *Brachiosaurus* and *S. proteles*. It may be that other taxa traditionally regarded as brachiosaurids, including *Cedarosaurus*, *Eucamerotus*, *Ornithopsis*, *Pelorosaurus* and *Sonorasaurus*, also belong to this clade (McIntosh, 1990; Blows, 1995; Tidwell et al., 1999; Naish and Martill, 2001).

Notably, MIWG.7306 is reminiscent of *S. proteles* in exhibiting pcpl that begin in a relatively posteroventral position on the centrum, though they are not as hypertrophied as those of *S. proteles*. In this taxon the pcpl are evident as distinct ventrolateral laminae even at the posterior cotyle (Wedel et al., 2000b). These hypertrophied pcpl appear to be an autapomorphy of *S. proteles* as they are not present in other sauropods, including *B. brancai* (though Wilson, 2002 regarded *S. proteles* as referable to *Brachiosaurus*). In MIWG.7306, the pcpl begin ventral to the posterior half of the centrum and it therefore appears intermediate between other sauropods (including *B. brancai*) and *S. proteles*.

Significantly, the lateral fossae of MIWG.7306 occupy more of the centrum's surface area than do those of *B. brancai* or other titanosauriforms (excepting *S. proteles*). We estimate that ca. 40% of the lateral surface of C6 in *B. brancai* is excavated by pneumatic depressions. In *S. proteles*, this value for C6 is ca. 80% or more and in MIWG.7306 it is between 50 and 60%. These values were obtained by drawing the vertebrae of these dinosaurs on graph paper and estimating the total area of the lateral side of the centrum occupied by pneumatic fossae. The calculation of these values is somewhat subjective. However, only in *S. proteles* is the area occupied by lateral fossae more extensive than that in MIWG.7306. We therefore interpret MIWG.7306 as intermediate in this character between *B. brancai* and *S. proteles*.

We suggest that pcpl which originate ventral to the posterior half of the centrum and extensive lateral excavations that occupy more than ca. 50% of the lateral surface of the centrum are derived characters that unite MIWG.7306 and *S. proteles* within a restricted Brachiosauridae (Fig. 6).

5. Discussion

Determining the position in the cervical series of MIWG.7306 is difficult because of its incompleteness but in shape and the position of the parapophyses it appears to correspond most closely with C6 of *S. proteles* and *B. brancai*. It therefore may not have been the longest vertebra in the series, or the centrum with the highest EI. The presence of possible autapomorphies in MIWG.7306 (an anteroposteriorly broad diapophysis and a rhomboidal fossa near the posterior margin of the diapophysis) indicates that it represents a diagnosable taxon. It is likely, however, that the specimen is referable to one of the named Isle of Wight sauropod taxa, though this cannot be demonstrated at present due to the absence of overlapping material. A cervical vertebra from the Lower Cretaceous of Croatia is similar in several important respects to MIWG.7306 and probably represent a closely related taxon (Dalla Vecchia, 1998), albeit one that did not reach an adult body size comparable with that probably achieved by MIWG.7306 (the centrum of the Croatian vertebra is 350 mm and closure of the neurocentral sutures indicates that its owner was adult).

With a centrum length of 745 mm MIWG.7306 is the largest sauropod cervical vertebra reported from Europe, and one of the biggest known. In *B. brancai* the longest centra in the cervical series (C10 and C11 of HM SII) are 870 mm while C9 is 850 mm, C8 is 860 mm, C7 is 820 mm and C6 is 780 mm (Janensch, 1950). In *S. proteles*, the longest vertebra (C8) has a centrum length of 1250 mm while C6 has a centrum length of 1220 mm (Wedel et al., 2000b). *B. brancai* has been estimated to have obtained a total length of 25 m (Paul, 1988). *S. proteles* was presumably somewhat larger, though as noted by Wedel et al. (2000a,b) it is possible

Fig. 5. Cervical vertebrae 5, 6 and 7 (from top to bottom) of *Brachiosaurus brancai* specimen SI for comparison. MIWG.7306 is not identical to any of these vertebrae but is closest in proportions and morphological details to C6. Combined centrum and anterior condyle lengths are as follows: C5, 560 mm, C6, 691 mm, C7, 705 mm. Photograph courtesy of Prof. Chris McGowan.

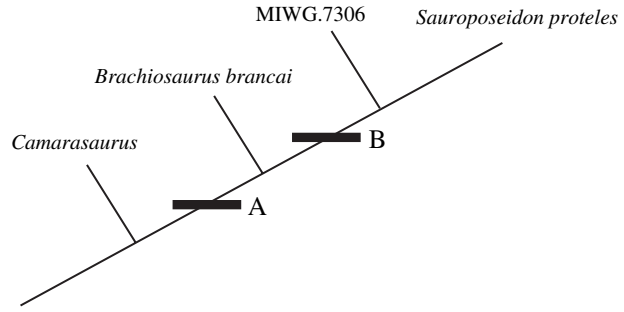

Fig. 6. Proposed phylogenetic relationships of MIWG.7306 to other sauropods. Group A is characterised by the presence of centrum length/cotyle height value > 4 and prezygapophyses extensively overhanging condyle. Group B is characterised by the presence of hypertrophied posterior centroparapophyseal laminae that originate ventral to the posterior half of the centrum and > ca. 50% of lateral surface of centrum excavated by pneumatic depressions.

that it was similar in size, or perhaps smaller. Similarly, MIWG.7306 may have differed in proportions from *B. brancai* and thus any estimate of its total length is speculative. We suggest, however, that the live animal exceeded 20 m in total length and may have been comparable in size to *B. brancai*.

Other titanosauriform elements from the Wessex Formation suggesting the presence of *B. brancai*-sized giants, though rare, are present. The tooth BMNH R964, the holotype of *Oplosaurus armatus* (see Naish and Martill, 2001), is 85 mm long (this length includes only the base of the root) and comparable in size to *B. brancai* teeth. However, Canudo et al. (2002) have recently suggested that this tooth may belong to a sauropod more closely related to *Camarasaurus* than *Brachiosaurus*. While the majority of Isle of Wight titanosauriforms were 'medium-sized', reaching approximately 15 m in length (Naish and Martill, 2001), MIWG.7306 is evidence that at least some of Europe's Early Cretaceous sauropods were giants and among the largest of known dinosaurs.

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References

Benton, M.J., Spencer, P.S., 1995. Fossil Reptiles of Great Britain. Chapman & Hall, London, 386 pp.

Blows, W.T., 1995. The early Cretaceous brachiosaurid dinosaurs *Ornithopsis* and *Eucamerotus* from the Isle of Wight, England. Palaeontology 38, 187–197.

Calvo, J.O., Salgado, L., 1995. *Rebbachisaurus tessonei* sp. nov. A new Sauropoda from the Albian–Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. Gaia 11, 13–33.

Canudo, J.I., Ruiz-Omeñaca, J.I., Barco, J.L., Royo Torres, R., 2002. Saurópodos asiáticos en el Barremiense inferior (Cretácico Inferior) de España? Ameghiniana 39, 443–452.

Dalla Vecchia, F.M., 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (upper Hauterivian/lower Barremian) limestones of SW Istria (Croatia). Geologia Croatica 51, 105–134.

Godefroit, P., Knoll, F., 2003. Late Triassic dinosaur teeth from southern Belgium. Comptes Rendus Palevol 2, 3–11.

Hunt, A.P., Lockley, M.G., Lucas, S.G., Meyer, C.A., 1994. The global sauropod fossil record. Gaia 10, 261–279.

Hutt, S., Naish, D., Martill, D.M., Barker, M.J., Newbery, P., 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. Cretaceous Research 22, 227–242.

Janensch, W., 1947. Pneumatizität bei Wirbeln von Sauropoden und anderen Saurischiern. Palaeontographica 3 (Supplement 7), 1–25.

Janensch, W., 1950. Die Wirbelsaule von *Brachiosaurus brancai*. Palaeontographica 3 (Supplement 7), 27–93.

Martill, D.M., Naish, D. (Eds.), 2001. Dinosaurs of the Isle of Wight. In: Field Guides to Fossils, 10. The Palaeontological Association, London, 433 pp.

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

Naish, D., Martill, D.M., 2001. Saurischian dinosaurs 1: Sauropods. In: Martill, D.M., Naish, D. (Eds.), Dinosaurs of the Isle of Wight. Field Guides to Fossils 10, The Palaeontological Association, London, pp. 185–241.

Paul, G.S., 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the world's largest dinosaurs. Hunteria 2 (3), 1–14.

Salgado, L., Coria, R.A., Calvo, J.O., 1997. Evolution of the titanosaurid sauropods I: Phylogenetic analysis based on the postcranial evidence. Ameghiniana 34, 3–32.

Stewart, D.J., 1978. The sedimentology and palaeoenvironment of the Wealden Group of the Isle of Wight, southern England. Unpublished PhD thesis, University of Portsmouth, 347 pp.

Tidwell, V., Carpenter, K., Brooks, W., 1999. New sauropod from the Lower Cretaceous of Utah. Oryctos 2, 21–37.

Upchurch, P., 1995. The evolutionary history of sauropod dinosaurs. Philosophical Transactions of the Royal Society of London, Series B 349, 365–390.

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

Wedel, M.J., Cifelli, R.L., Sanders, R.K., 2000a. *Sauroposeidon proteles*, a new sauropod from the early Cretaceous of Oklahoma. Journal of Vertebrate Paleontology 20, 109–114.

Wedel, M.J., Cifelli, R.L., Sanders, R.K., 2000b. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon proteles*. Acta Palaeontologica Polonica 45, 343–388.

Weishampel, D.B., 1990. Dinosaurian distribution. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, pp. 63–139.

Wilson, J.A., 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19, 639–653.

Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society 136, 217–276.

Wilson, J.A., Sereno, P.C., 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Journal of Vertebrate Paleontology, Memoir 5, 1–68.