

SEISMOSAURUS HALLORUM: OSTEOLOGICAL RECONSTRUCTION FROM THE HOLOTYPEMATTHEW C. HERNE¹ AND SPENCER G. LUCAS²¹School of Physics, University of Western Australia, Crawley, Western Australia 6009, mat_herne@hotmail.com; ²New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, New Mexico 87104-1375

Abstract—The Late Jurassic sauropod dinosaur, *Seismosaurus hallorum*, from the Morrison Formation of New Mexico, is reconstructed as a full-scale replica using casts of the holotype. We document the osteology of prepared elements from the thoracic, pelvic and caudal regions in comparison to related diplodocids. The thoracic vertebrae are described pending further preparation. A sauropod femur, collected with this material and believed to have been from the same individual, is also described. Using osteo-morphological comparisons with closely related diplodocids, previous axial length estimates of 39-52 meters for *Seismosaurus hallorum* are questioned, and the overall length is reinterpreted to have been approximately 33 meters.

INTRODUCTION

The sauropod dinosaur *Seismosaurus hallorum* is the only endemic sauropod taxon described from the Upper Jurassic Morrison Formation in New Mexico and has been considered by some the longest known dinosaur (e.g., Gillette, 1991, 1994). For the purposes of museum exhibits in Japan and New Mexico, reconstruction of *S. hallorum* was undertaken using fossils of the holotype and osteological information from closely related diplodocids. Mounted replicas (Fig. 1) were produced by the Canadian-based company, Prehistoric Animal Structures Inc., in conjunction with the New Mexico Museum of Natural History and Science. The first is on display in the Kitakyushu Museum of Natural History, Japan and the second at the New Mexico Museum of Natural History and Science.

Several mid-caudal vertebrae, chevrons, the right pubis and the distal right ischium of *Seismosaurus hallorum* were described by Gillette (1991), however, the thoracic, sacral and proximal caudal vertebrae were not fully prepared or formally described. Further preparation of these elements exposed key osteological details for description and allowed reconstruction to proceed with reasonable accuracy. To date, no cranial material, cervical vertebrae, terminal caudal vertebrae, scapulae or limbs elements (other than an incomplete femur) have been recovered. Hence, size and length estimates of *Seismosaurus hallorum* have been speculative.

Seismosaurus hallorum is distinctly diplodocid with elements remarkably similar to the known species of *Diplodocus* (Paul, 1988; Gillette, 1991, 1994; Lucas, 1993; Curtice, 1996); hence, comparisons of length, morphological character and osteological proportions used in this reconstruction centered on *Diplodocus*. Several workers have questioned the validity of the genus, *Seismosaurus hallorum* (Paul, 1988; Lucas, 1993; Curtice, 1996; Lucas et al., 2004), due to the close similarity of osteo-morphological characters in the caudal vertebrae with those of *Diplodocus*. The ischium of *Seismosaurus hallorum*, with its dorsally projecting distal expansion, long appeared to be the only autapomorphic character of the genus (Gillette, 1991; Upchurch et al., 2004). However, recent complete preparation of the ischium revealed the hook-like process to be part of a neural spine, so the validity of *Seismosaurus* is questionable (see Lucas et al., this volume).

The relatively high ratio of caudal, sacral and thoracic neural spine height to centra length for *Seismosaurus hallorum*, and the upright character of the caudal neural spines are not necessarily autapomorphic characters, when compared with other diplodocids (contrary to Gillette, 1991, 1994). Neural spine height and inclination are known to be variable within archosaur taxa, such as sexually dimorphic crocodylians, and it is not a reliable character for the separation of genera (Curtice, 1996, p. 26-27). Similarly, Gilmore (1932) noted that the neural spines of *Diplodocus longus* mounted in the United States National Museum are variably erect to backwardly inclined and thus were not a reliable character for separation of species of *Diplodocus*. Further, Curtice (1996, p. 26) notes that erect

neural spines are typical of diplodocids.

Regardless of the generic status of *Seismosaurus*, the recovered elements are those of a very large diplodocid. Here, we document in detail the skeletal reconstruction of *Seismosaurus* and reassess its axial length.

Institutional Abbreviations—American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Field Museum (FM); New Mexico Museum of Natural History and Science (NMMNH); National Museum of Natural History (NMNH); Prehistoric Animal Structures (PAST); Science Museum of Minnesota (SMM); Utah Museum of Natural History (UMNH); Wyoming Geological Museum (UWGM).

MATERIALS AND METHODS

Prepared and semi-prepared elements of the type specimen of *Seismosaurus hallorum* (NMMNH P-3690) and the femur catalogued separately (NMMNH P-25079) were photographed, measured and illustrated. Other than the elements described by Gillette (1991), recovered material also included four incomplete dorsal ribs, the partial right ilium in articulation with the sacrum, proximal caudal vertebrae Ca1 to Ca8 and thoracic vertebrae T3 to T10. In this work we refer to the detailed synopsis of Wilson (1999) for nomenclature of vertebral lamina relevant to Sauropoda.

For the physical reconstruction (replica construction), all elements of the holotype were molded and cast in fiberglass where possible. All missing elements were sculpted using polyurethane foam with plaster texturing and modeling clay. Fiberglass casts were produced by PAST for all elements and articulated over a steel structure to produce mounted replicas. The image of the mount (Fig. 1) was produced using large format slides of the first mounted replica.

OSTEOLOGICAL RECONSTRUCTION**Skull**

Despite the extensive and sophisticated search methods employed in the field by Gillette's team, no cranial or complete cervical vertebrae were located. The skull of *Seismosaurus* was modeled using *Diplodocus* morphology and the detailed description of Holland (1934). The dorsoventral depth was increased slightly (with artistic license), to reflect the higher comparative ratio of neural spine height to centrum length evident in the thoracic and caudal vertebrae of *Seismosaurus hallorum*.

Cervical Vertebrae

Very fragmented remains of two vertebrae (unprepared) and an intact isolated rib are questionably from the cervical region, but these are currently thought to be of cranial thoracic location. As no cervical vertebrae are known, reconstructed cervical vertebrae were modeled completely on *Diplodocus* morphology and were proportioned according to the relative dimensions of *Diplodocus* thoracic, sacral and caudal vertebrae



FIGURE 1. *Seismosaurus hallorum*, NMMNH P-3690, right lateral view of the mounted replica. Total axial length equals 33 meters; vertical height to dorsal extremity of the sacral neural spines equals 4.95 meters.

(Table 1).

Articulation of the cervical series and skull depicted in Figure 1 follows the gentle “S” curvature often illustrated for sauropods. The NMMNH mount incorporates a more elongated neck and obtusely-angled articulation of the skull. Support for this manner of cervical articulation can be found in Frey and Martin (1997), who discuss the biomechanical limits of bracing systems, and Stevens and Parrish (1999), who detail cervical articulation and flexion in both *Apatosaurus* and *Diplodocus*, based on digital reconstructions of the limits imposed on the cervical articulating surfaces.

Thoracic Vertebrae

Thoracic vertebrae T1 and T2 are in degraded condition. Vertebra T3 is mostly prepared, although the caudal surface remains unprepared. Vertebrae T4 to T10 are contained in one large block, which is partially prepared on the left side and ventrally. The thoracic vertebrae of *Seismosaurus hallorum* are strikingly similar in their general morphological character to those described for *Diplodocus carnegii* (CM 84) by Hatcher (1901, p. 25-30) and *Diplodocus longus* (USNM 10865) by Osborn (1899, p. 193-199). In their current state of preparation, several characters of note can be reported for the thoracic vertebrae *Seismosaurus hallorum*, T3 to T10. These include:

1. The neural arches are highly elevated, as they are in *Diplodocus*.
2. Centra T3, T4 (Figs. 2A-B) and possibly T5 have hemispherical cranial condyles and concave cotyles (opisthocoelous). These centra are transversely constricted mid-centra to form keels on their ventral surfaces. The medioventral constriction is greatest in T4 and corresponds with the description for *Diplodocus carnegii* by Hatcher (1901, p. 28). The overall transverse width of centrum T4 is small, in comparison with *Diplodocus carnegii* (Table 1) and other diplodocids. Similarly, the centrum T5 appears limited in transverse size, although only the cranial portion is preserved. The remarkably reduced size of centra T4 and T5 within the thoracic series seems at odds with the large overall proportions of *Seismosaurus hallorum*.
3. The middle and caudal thoracic vertebrae, from T6 to T10, are convexly shallow at their cranial articulating surfaces and are concave on their caudal surfaces (amphiplatyan). The centra are gently convex in mid-transverse section, with the centrum size of the thoracics caudal to T5 markedly increasing in overall transverse width and depth. The cranio-caudal lengths of these vertebral centra do not increase and become shortest in T9 and T10 (Table 1). The widths of the caudal thoracic vertebrae from T6 exceed their lengths (Table 1), which is a characteristic of *Diplodocus* and *Apatosaurus*.
4. Pleurocentral openings (pc [pleurocoels]) are seen in all centra, T3 to T10, where prepared. These can be seen in Figure 2 for T3, T4 and T8, which show varying architecture in the openings. Pleurocoels of T3 appear as fossae, or shallow excavations (Fig. 2A). The pleurocoels of

T4 are far more developed as two deep lateral foramina or openings into the centrum (Fig. 2B). The anteroventral foramina of T4 extend into the rim of the vertebral condyle (Fig. 2B). Although T5 is partially preserved, the cranial end is attached to T4 and shows a single small pleurocentral opening in the same lateral line as the ventral-most pleurocoel in the centrum of T4. The left pleurocoel of T8 is indicative of the caudal thoracics; it is ovular at the parasagittal surface, subtriangular at the lateral surface, which extends onto the neural arch, and is displaced slightly cranially.

5. Open cancellous structure is exposed within the condyles of centra T3, T4 and T5 (Fig. 2A-B).

6. The caudal centroparapophyseal lamina (pcpl) (the oblique lamina in Hatcher, 1901), which project caudoventrally from the parapophyses (pp) to the caudal neurocentral junction, are well developed in the middle to caudal thoracics from T5, T7, T8 (Fig. 2C) and T9. This is at odds with Wilson (1999), who reports that the pcpl are not generally well developed in sauropods. In these vertebrae the pcpl converges with the caudal centrodiapophyseal lamina (pcdl) (the inferior diapophyseal lamina in Hatcher, 1901), in a manner similar to that seen in *Diplodocus* (Hatcher, 1901, p. 29), on the midlateral surface of the neural arch between the diapophyses (dp) and the neurocentral junction. In *Apatosaurus louisae*, pcpl and pcdl of T6 cross (Gilmore, 1936, pl. 25), with the pcdl terminating at the cranial dorsolateral junction of the centrum. The pcdl of T6 in *Seismosaurus hallorum* appears to continue to the caudal neurocentral junction, similar to *Diplodocus*, although further preparation is needed to verify this condition.

7. Similar to *Diplodocus longus*, the transverse processes and diapophyses of T5 to T10 and especially T8 (Fig. 2B) and T9 are more highly elevated above the level of the zygapophyses than in *Diplodocus carnegii* and *Apatosaurus*. The transverse processes of T3 are lower than the prezygapophyses (prz) and postzygapophyses (poz) and are more robust than the caudal thoracics. The diapophyses of T3 face ventrolaterally. In shape, the diapophyseal articulating surfaces of T3 are triangular and dorsoventrally elongated (Fig. 2A-C). The transverse processes of T4 are transitional between the condition of T3 and the caudal thoracics (Fig. 2B) The articulating surfaces of the middle to caudal diapophyses are small, subtriangular in shape and project slightly ventrolaterally. The parapophyses are similarly small and are connected to the prezygapophyses by the paradiapophyseal lamina (prpl). These characters are seen in T8 (Fig. 2C)

8. The postzygodiapophyseal lamina (podl), which extends between the diapophyses and the post-zygapophyses of T8 (Fig. 2C) and T9, are paired with the superior (upper) lamina emanating from the transversely oriented, sheet-like spinodiapophyseal lamina (spdl). A similar condition is seen in *Diplodocus carnegii*.

9. The prezygodiapophyseal lamina (prdl) that extend between the diapophyses and the prezygapophyses are well developed wing-like sheets of bone in T5 to T10. The paradiapophyseal laminae (ppdl) that extend

TABLE 1. *Seismosaurus hallorum* NMMNH P 3690, *Diplodocus carnegii* CM 84, *Apatosaurus louisae* CM 3018 and *A. excelsus* FM 7163, ratios of total vertebral height to centrum total lengths.

Vertebrae	Ratios of vertebral height to centrum length			
	P-3690	CM 84	CM 3018	FM 7163
T3	3.37	2.21	2.85	1.76
T4	3.00	3.21	3.83	2.48
T5	3.60	3.45	4.08	3.03
T6	3.59	3.11	4.72	3.79
T7	3.32		5.15	4.62
T8	4.20	3.08	4.91	4.30
T9	4.38	4.20		5.24
T10	4.64	3.69		5.36
CA1	6.30	5.73	5.21	5.89
CA2	5.81		5.46	4.59
CA3			4.74	4.00
CA4	4.58	3.32	4.84	3.78
CA5	3.64	3.11	4.37	3.45
CA6	3.85	3.14	4.37	3.24
CA7	3.44	2.91	3.55	3.15
CA8		2.74	3.38	2.65
CA9		2.41	3.11	2.65
CA10		2.27	2.79	2.50
CA11		2.27		
CA12	2.23	1.95	2.63	2.74
CA13			2.38	2.35
CA14	2.39		2.41	2.35
CA15	1.99			2.00
CA16	1.88			1.86
CA17	1.89			1.73
CA18	1.86			1.64
CA19	1.41			1.00

between the parapophyses and the diapophyses (or from the pcdl in some caudal thoracics) in *Diplodocus* and *Apatosaurus* are not well developed in *Seismosaurus hallorum*. Paradiapophyseal laminae are evident in T8 (Fig. 2C) and T9, however, these structures are uncertain and are as likely to be small accessory lamina.

10. Hypantra are not evident on the prezygapophyses of T3, with the paired intraprezygapophyseal laminae (tprl) forming a broad concave sheet of bone between the left and right prezygapophyses. The caudal surface of T3 is unprepared and existence of a hyposphene cannot be determined at this stage. Figure 2A illustrates the probable layout of lamina on the caudolateral surface of the neural arch. Unfortunately, the prezygapophyseal region of T4 is eroded, and the presence of the hypantra cannot be determined. The postzygapophyses of T8 (Fig. 2C) are ventrolaterally and caudally oriented and are transversely concave in the manner reported for *Diplodocus* and *Barosaurus* by Upchurch et al. (2004). In *Seismosaurus hallorum*, the left and right post-zygapophyses of T8 coalesce

at their medioventral margins and appear to form a hyposphene (see Fig 2C), although this needs further examination.

11. The centropostzygapophyseal lamina (tpol) extends from the medioventral base of the postzygapophyses to the caudolateral neurocentral junction. This can be seen on T8 (Fig. 2C). The centropostzygapophyseal lamina (cpol) is also seen on T8, extending from the cranial dorsolateral edge of the postzygapophyses ventrally to the the podl, and projects cranioventrally to the midlateral neural arch. The cpol appears to continue cranioventrally as a poorly developed lamina that extends to the cranial neurocentral junction (Fig. 2C). The prezygapophyses of T9 (not illustrated) appear to extend to a hypantrum. A similar condition is likely for the other middle to caudal thoracics, but further preparation will be required to determine where the hypantrum-hyposphene articulation starts in the thoracic series.

12. In *Apatosaurus louisae*, the parapophyses migrate dorsally onto the neural arch at T3, and this continues to T10. With the migration of the parapophyses onto the neural arch, the cranial centroparapophyseal lamina (acdl), which extends between the diapophyses and the neurocentral junction above the parapophyseal facets of the cranial thoracic vertebrae, divides into two separate lamina: the cranial centroparapophyseal lamina (acpl), which projects ventrally from the parapophyses to the cranial neurocentral junction; and the ppdl, which extends dorsally or dorsoposteriorly from the dorsal parapophyses (Gilmore, 1936, pl. 25; Wilson, 1999). In *Seismosaurus hallorum*, however, and similar to *Diplodocus* (Hatcher, 1901), the parapophyses are located on the centrum of T3 and possibly at the neurocentral junction of T4 (Figs. 2A-B), thus maintaining the singular acdl condition at T4.

13. Neural spines from T3 to T5 are bifurcated, with the left and right spinoprezygapophyseal lamina (sprl), spinopostzygapophyseal lamina (spol) and the transversely-oriented spdl forming each spine. The middle to caudal thoracic neural spines, from T6, become decreasingly less bifurcated with the increased fusion of the left and right sprl, spol and spdl along the medial prespinal lamina (prsl) and postspinal lamina (posl). The dorso-lateral summits of these vertebrae form slightly outwardly-projecting horns, as can be seen at the neural spine summit of T8 (Fig. 2C). In the caudal thoracic vertebrae of *Seismosaurus hallorum*, the spol are apparent as two rami (Fig. 2C), one lateral (lat. spol) and the other medial (med. spol), and this is a condition common in the middle and caudal thoracics of sauropods (Wilson, 1999). In *Seismosaurus hallorum* the lateral spol of the cranial thoracic vertebrae are well developed, as they are in other diplodocids (Wilson, 1999). These are seen in T3 and especially T4 (Figs. 2A-B), where the lat. spol and spdl form deep fossae. In the middle and caudal thoracics, the fused lat. spol and spdl form a pronounced, laterally-projecting bump. On the cranial surface, a small accessory lamina is formed laterally between the inner edge of the bump and the prsl. These laterally-projecting bumps of the mid-lateral neural spines are seen in *Diplodocus* from T5 to T9 (Hatcher, 1901) and *Barosaurus* (Lull, 1919), however, they are not apparent in *Apatosaurus* (Gilmore, 1936, pl. 1V).

14. On the cranial surfaces of the middle to caudal neural spines, the sprl and the prespinal lamina (prsl) fuse to become broad medial bony plates that are capped by a rugose, bony thickening formed between the lateral "horns." The left and right med. spol in these vertebrae coalesce in the lower part of the neural spine with the posl, to form a narrow ridge to the summit of the spine and are similarly capped by a rugose bony thickening.

The ratio of vertebral height to centrum length (Table 1) indicates that *Seismosaurus hallorum* and *Diplodocus carnegii* are comparable in the preserved cranial thoracics, T3 and T4. The middle to caudal thoracics (T6 to T10) of *S. hallorum* are, however, approximately 20 percent longer than those of *D. carnegii* (Table 1). Total vertebral heights are comparable in *S. hallorum* and *Apatosaurus* (Table 2), although the middle to caudal thoracics of both *Apatosaurus louisae* and *Apatosaurus excelsus* are marginally higher for the vertebra represented. The ratio of vertebral height to centrum length (Table 1) indicates that *Seismosaurus hallorum* is generally similar to *Apatosaurus*, although possibly less in the middle to caudal thoracics T6 to T10.

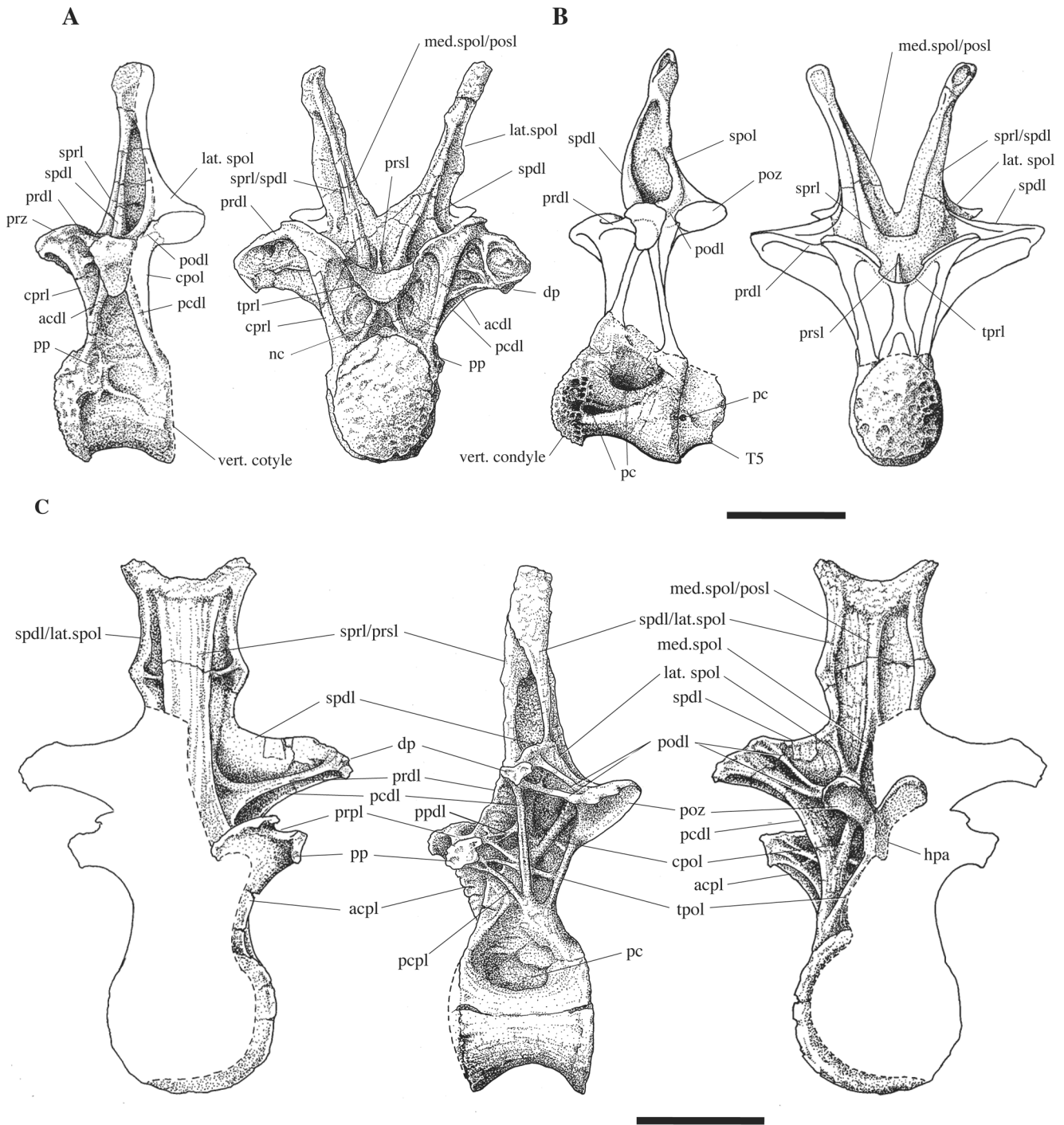


FIGURE 2. Thoracic vertebrae of *Seismosaurus hallorum*, NMMNH P-3690. **A**, T3 (right to left) cranial and left lateral views; **B**, T4 (right to left) cranial and left lateral views; **C**, T8 (left to right) cranial, left lateral and caudal views. For abbreviations see text; scale bar equals 300 mm.

Thoracic Ribs

Two rib heads and two partial ribs were recovered by Gillette's team. These elements are not described formally, but during reconstruction were positioned according to their appropriate morphological shape and size. These positions correspond to left thoracic 1, right thoracics 3 and 4 and left thoracic 8. Left thoracic 1 was positioned because of the small overall size compared with the other recovered ribs, with the shaft straight and triangular in cross section (description matching that of *Diplodocus carnegii*: Hatcher, 1901). The tuberculum is aligned linearly with the shaft, indicating a relatively perpendicular orientation visceral to the glenoid. The two rib heads, thoracic right 3 and 4, are partially prepared on one block of sandstone. Casts of these rib heads were used to locate their correct position on the thoracic vertebrae. These positions were matched by their sectional size, capitulum and tuberculum spacing and alignment on the vertebral apophyses and shaft alignment. Left thoracic rib 8 is proximally complete and was recovered overlying the sacral spines. This rib was similarly matched to T8. Left thoracic rib 1 has the appearance of an ossified tendonous mass, which is likely to be caused by exposure and erosion of the internal cancellous bone structure.

Sacrum

The sacrum of *Seismosaurus hallorum* is robust and has undergone little compression or distortion. Some oblique offset is evident sagittally between the left and right sides. The sacrum is prepared dorsally and clearly shows a radiating pattern of five sacral ribs in articulation with the right ilium and the neural spines; the third and broadest sacral rib measures 190 mm in parasagittal section. Estimated transverse widths between the sacricostal yoke are cranially ~1250 mm and caudally ~1100 mm (Table 2). Ventrally, the sacral centra, ribs and sacricostal yoke are unprepared. Due to erosion, there is some ambiguity as to the exact morphological character of the cranial and caudal surfaces of sacral ribs and centra 1 and 5, however, the estimated sacral axial length measures ~1100 mm.

In agreement with Gillette (1994), the sacrum of *Seismosaurus hallorum* is comparable in size and robustness to that of *Apatosaurus louisae*, although the former is broader transversely and craniocaudally shorter (Table 2). The first and fifth sacral spines are mostly unfused, although these may be fused at their summits. The fused sacral spines 2-3-4 measure approximately 680 mm, from the dorsalmost edge of the right ilium. The heights of the sacral spines are not available for *Apatosaurus louisae* (CM 3018), as they are not preserved (Gilmore, 1936). However, reconstruction of this height using *Apatosaurus excelsus* (CM 563; Gilmore, 1936, fig. 19) as a model indicates that the neural spine height for *Apatosaurus louisae* would have been approximately 600 mm and is therefore comparable with *Seismosaurus hallorum*. The maximum sacral spine height for *Seismosaurus hallorum* is 50% greater than *Diplodocus carnegii* (CM 84; Table 3).

Caudal Vertebrae

The cranial caudal series Ca1 to Ca7 of *Seismosaurus hallorum* is exposed in two sandstone blocks in a semi-prepared state. Preparation of the cranial caudal vertebrae shows: the zygapophyses in articulation; the neural arches and attachment surfaces for the separated, recovered neural spines of Ca2 and Ca4 to Ca7; and well-developed laminae of the laterally-projecting transverse processes and left, upper lateral surfaces of the centra in articulation. The ventral surfaces of these caudal centra remain unprepared. As the centrum of Ca1 is mostly eroded, it was reconstructed using caudal Ca2 and Ca3 as guides.

An isolated caudal vertebra was established as Ca8 (confirming the tentative placement of Gillette, 1991) due to the perfect articulation of the prezygapophyses with the postzygapophyses of Ca7. Centrum size, shape, the development of deep pleurocentral fossae and the degree of development of the transverse processes are consistent with direct articulation of the preceding vertebrae. Similar to *Diplodocus*, a dorsal cleft is present at the summits of the neural spines of the cranial caudal vertebrae, up to Ca7.

Although a cleft could not be established for the transversely-oriented spines of the more terminal vertebrae, it was included in the reconstructed spine of Ca8.

Some distal sections of the transverse processes are missing from cranial Ca2 to Ca8. However, intact sections show that these processes were pronounced and elaborately developed, as they are in *Diplodocus*. The transverse processes of the cranial caudals, up to Ca8, extend dorsolaterally and form pronounced shoulders. The rugose parasagittal margins of these transverse processes extend cranially beyond their centra from Ca1 to at least Ca4. Terminal to Ca4, the transverse processes do not appear to extend ventrally below the middle centrum and reduce rapidly in their lateral extent from Ca8. The transverse processes are reduced to bumps at Ca19. The cranial centrodiapophyseal laminae are well-developed in the first 15 caudal vertebrae, as noted for *Diplodocus* by Wilson (1999). In *Seismosaurus hallorum*, this lamina is weakly developed at Ca17 and absent from Ca18.

Since the publications of Gillette (1991, 1994), recent preparation of cranial caudal vertebrae Ca1, Ca2 and Ca4 to Ca7, with their intact neural spines, gives an accurate indication of spine height above the zygodiapophyseal lamina (the horizontal lamina that forms the dorsal margins of the transverse processes), as well as total vertebral height at these vertebral positions. Total vertebral heights are summarized in Table 2, together with comparative heights for closely-related diplodocids.

The missing neural spines for cranial vertebrae 3 and caudal 8 were reconstructed using the intact vertebrae with their sacral spines as a guide. A diagrammatically-imposed dorsal ridgeline following the progression of decrease in neural spine height from the sacrum across the recovered cranial caudal vertebrae Ca1 to Ca8 gave an indication of the likely placement of the preceding recovered vertebrae. This line indicated that Gillette's (1991) placement of the articulated series of eight caudal vertebrae, numbered Ca20 to Ca27, was inconsistent with the progression of decrease in the height of their neural spines. Thus, it was apparent these spines were untenably high at these caudal assignments. The curve of the dorsal ridgeline became consistent when this caudal series was assigned to positions Ca12 to Ca19.

Comparisons of caudal morphology with *Diplodocus* further indicate that more cranial caudal assignments for the above-mentioned articulated series of eight vertebrae is consistent with known diplodocid morphology and supports the views of Curtice (1996, p. 24-26), who states that in known diplodocids, caudal ribs are not known beyond caudal vertebrae Ca20, and as the second to the last caudal possesses caudal ribs, the caudal assigned position Ca26 by Gillette (1991), should be moved forward to approximately Ca18. Pneumatic fossae are evident in all recovered caudal vertebrae in the caudal series, including the second to the last caudal vertebra, which Gillette (1991) positioned as C26. As the caudal-most occurrence of pneumatic fossae in any previously described sauropod is on the nineteenth caudal, this vertebra is unlikely to have been located at assignment 26, and moving the caudals forward five or six positions places *Seismosaurus hallorum* in line with all known diplodocids.

In our reconstruction, the longest caudal, numbered by Gillette (1991) as Ca24, with a centrum length of 362 mm, is assigned position Ca16. The longest caudal in well known diplodocids is at Ca18, or adjacent to this number (Hatcher, 1901; Gilmore, 1932, 1936; Curtice, 1996). Our placement at caudal Ca16, although only marginally longer than the more cranially and terminally articulating caudals (Table 2), is congruent with neural spine height at this location.

Comparisons of the percentage decrease in succeeding caudal centra widths, using measurements from *Diplodocus longus* (from Osborn, 1899; Gilmore, 1932) and *Diplodocus carnegii* (from Hatcher, 1901), indicate that the widths of proximal to mid-caudal centra decrease at varying rates of between 2 and 12 percent, with an average of about 3 to 4 percent. Our suggested placements for the caudal vertebrae of *Seismosaurus hallorum* fall within this range.

The incomplete caudal described as Ca13 by Gillette (1991) was assigned position Ca11 in our reconstruction. Although the neural spine is

TABLE 2. *Seismosaurus hallorum* NMMNH P 3690, *Diplodocus carnegii* CM 84, *Apatosaurus louisae* CM 3018 and *A. excelsus* FM 7163, dimensions of T, thoracic and Ca, caudal vertebrae in mm.

Vertebrae	Centrum greatest length				Centrum greatest width at caudal end				Vertebrae total height			
	NMMNH P-3690	¹ CM 84	² CM 3018	² FM 7163	NMMNH P-3690	¹ CM 84	² CM 3018	² FM 7163	NMMNH P-3690	¹ CM 84	² CM 3018	² FM 7163
T1		*525	310	370		255	355	400		*680	845	490
T2		416	315	360		233	355	410		691	850	530
T3	300	326	310	330	300	311	350	410	1010	722	885	580
T4	340	*240	260	290	250	*330	315	400	1020	*770	995	720
T5	300	*245	260	290	300	300	335	410	1080	*845	1060	880
T6	320	255	270	280	380	280	335	400	1150	793	1275	1060
T7	340		260	260	390		335	410	1130		1340	1200
T8	300	275	275	300	400	309	350	410	1260	847	1350	1290
T9	290	*245	255	250	400	*310	315	410	1270	*1028		1310
T10	C. 280	*290	240	250	400	*325	365	400	C. 1300	*1070		1340
CA1	C. 200	183	240	192	C. 410	334	300	390	1260	1049	1250	1130
CA2	C. 220		205	220			290	380	1220	995	1120	1010
CA3			215	230		332	280	360		897	1020	920
CA4	C. 240	250	190	230	C. 380	330	280	350	1100	830	920	870
CA5	C. 280	250	190	220	C. 380	325	330	330	1020	777	830	760
CA6	C. 260	237	175	210	C. 360	309	250	310	1000	744	765	680
CA7	285	237	190	200	C. 360	317	260	300	C. 980	690	675	630
CA8	240	246	185	200		309	245	290		675	625	530
CA9		270	185	200		300	240	290		651	575	530
CA10		269	190	200		295	240	290		610	530	500
CA11	335	269			**332	285				610		
CA12	330	295	190	190	**285	272	235	280	790	576	500	520
CA13			200	200			220	260			475	470
CA14	310		195	200			215	250	740		470	470
CA15	360		200	210			190	220	715			420
CA16	365		200	220	**220		190	220	685			410
CA17	**350			220	210			210	660			380
CA18	**338		205	220	200		170	210	**630			360
CA19	320		200	330	200		170	200	C. 450			330

C. estimated; ¹dimensions from Hatcher (1901); ²dimensions from Gilmore (1936); *Peterson's dimensions from Lull (1919); **dimensions from Gillette (1991)

missing, morphological characters, such as centrum width, pleurocoel development and the height, inclination and projection of the prezygapophyses and postzygapophyses, are consistent with *Diplodocus longus* (Osborn, 1899). The oblique, ventrally projecting, cranial articulating surface of the centrum Ca11, illustrated by Gillette (1991, fig. 4), was not discernable by us on the fossil. Hence, the tail in our reconstruction (Fig. 1) was not kinked ventrally at this caudal position.

The number of caudal vertebrae is variable within and between sauropod species and may reach more than 80 for diplodocids (McIntosh, 1990). The recorded number of caudal vertebrae for *Apatosaurus louisae* is 83, with approximately 40 forming a so-called whiplash (Gilmore, 1936; McIntosh, 1990). In our reconstruction of *Seismosaurus hallorum*, the number of caudal vertebrae was kept at 75, with approximately 30 rod-like terminal vertebrae forming the characteristic diplodocid whiplash, in parity with the number assigned to *Diplodocus* composites (from Holland, 1906). If the number were 80, the tail length would not be significantly increased.

From the caudal series Ca1 to Ca19, the only vertebrae not accounted for in *Seismosaurus hallorum* are Ca9 and Ca10, a view supporting

Curtice (1996). Missing or partially missing vertebrae were sculpted with morphological reference to *Diplodocus carnegii*, while maintaining the upright neural spine condition evident in the preserved caudal vertebrae of *Seismosaurus hallorum*. A similar, upright neural spine condition is reported by Gilmore (1936) to be apparent in some caudal vertebrae of *Diplodocus longus* (USNM 10865).

Chevrons

Gillette (1991, figs. 9-11) identified three chevrons of *Seismosaurus hallorum*. Two of these are dorsoventrally elongated, with paddle-shaped ends. These chevrons were positioned as Ca2/Ca3 and Ca4/Ca5 and match the positions described in Gillette (1991). The other chevron is represented by one half of the pair, which is caudotermally elongated and asymmetrical. We believe this bone is part of a rib, not a chevron. Reconstruction of the missing chevrons used the recovered types as a guide, together with those of *Diplodocus*. The last sculpted chevron was at Ca24/Ca25.

Ilium, Pubis and Ischium

Only a partial right ilium was recovered during the NMMNH excavations. It is attached to the sacrum and is missing the cranial portion of the iliac blade and the distal extremity of the post-acetabular process. The lateral dimensions of the ilium are strikingly similar to those of *Apatosaurus louisae* CM 3018 (Gilmore, 1936, p. 229; for comparisons see Table 2).

The cranial transverse width between the left and right ilia of *Seismosaurus hallorum* is likely to have been broader than for *A. louisae* by approximately 28 percent (using estimates from *A. excelsus*, Gilmore, 1936, fig. 31; Table 2). The equivalent dimension for *Diplodocus carnegii* CM 84 is comparable to *Apatosaurus louisae* (based on transverse dimensions of CM 94 in Hatcher, 1901, fig. 9 and Gilmore, 1932, table 6). However, the sacral length and ilium lengths for *D. carnegii* are shorter than those of *A. louisae*. The sacroiliac proportions of *S. hallorum* are, therefore, more like *Diplodocus* than *Apatosaurus*, with broad transverse to short axial proportions (Table 2).

At 1010 mm, the pubic (dorsoventral) length for *Seismosaurus hallorum* is less than *Apatosaurus louisae*, which has a length of 1190 mm (Gilmore, 1936). The pubic length of *S. hallorum* is comparable with *Diplodocus carnegii*, which has a length of 1000 mm (Hatcher, 1901, and in agreement with the description of Gillette, 1991). Hence, the relative length of the pubis of *S. hallorum* against the proportions of the ilium and sacrum are comparatively less than the same proportions in *Apatosaurus* and *Diplodocus*. Accordingly, to articulate the relatively short pubes (the real right and the mirror-sculpted left) of *S. hallorum* at their medial symphyses, the pubes were acutely inclined medioventrally. Although the distal pubic peduncle of the recovered right ilium escaped preservation, the proximal portion does indicate this pronounced medioventral inclination. The iliac pubic peduncles of *Supersaurus vivianae* appear similarly inclined.

The distal portion of the right ischium and partial shaft were described by Gillette (1991). The missing proximal portion of the right ischium and complete left ischium were sculpted to correctly articulate with the pubes and the partially eroded ischiac peduncle of the right ilium. After reconstruction, the appearance of the proximal ischium was similar to *Supersaurus vivianae* (Jensen, 1985), with the iliac process of the ischium quite elongated. However, unlike the broad, uniform and upwardly curved ischial shaft of *Seismosaurus hallorum*, the shaft of *S. vivianae* is straight and narrows in midsection. The dorsolaterally projecting process of the distal ischium of *S. hallorum* is also evident on the distal ischium of *S. vivianae* (Jensen, 1985). However this process is more pronounced in *S. hallorum*.

Limbs, Pes, Manus and Pectoral Girdle

During our reconstruction, no elements of the limbs, pes, manus or scapulocoracoid had been recovered or attributed to the holotype, hence, from the recovered material, the pelvic elements provided the most usable dimensions for determining the hind limb proportions. From these measurements (Table 3) femur length was estimated first. The lengths of all other limb elements were calculated from femur length using ratios reported in McIntosh (1990); relative measurements from *Diplodocus carnegii* (Hatcher, 1901) and *Apatosaurus louisae* (Gilmore, 1936); and photographs of SMM P 84.15.8 (Table 3).

Compared with *Diplodocus carnegii*, the relative overall heights of *Seismosaurus hallorum* thoracic vertebrae are no greater than 30 percent taller; the sacral spines and ilia are approximately 50 percent taller, and the cranial caudal vertebrae about 35 percent taller; however, the pubis is comparable in length. Upon these dimensions, femur length was proportioned at about 24 percent greater than the femur length of *Diplodocus carnegii* CM 84 (Table 3), or 1900 mm long. This estimate of femoral length is comparable with lengths recorded for *Apatosaurus* (Gilmore, 1936) (Table 3). The total distance from the dorsal extremity of the sacral neural

spines, along the hind limb bones to the ground at the pes, measures 4.94 meters (Fig. 1)

During reconstruction of the mounted replicas, the partial femur NMMNH P-25079 (Fig. 3A-B) was not considered to have been an element of the holotype, NMMNH P-3906. This incomplete sauropod femur, found within 6 meters of the vertebral elements of *Seismosaurus hallorum*, was the only other dinosaur bone from the site not included in the holotype. Gillette (1991), however, does make mention of the recovery of this bone, and it is likely that a shortfall of time and resources sent this specimen into obscurity.

The femur is in three pieces, has eroded articular ends and is of the same preservation as the remaining bones of the holotype of *Seismosaurus hallorum*. We believe this femur is likely to belong to the same individual as the holotype specimen of *S. hallorum* due to the taphonomic nature of the site, close proximity, proportions when compared with the reconstructed estimate and morphological characteristics.

The fourth trochanter of the femur is eroded from the mediocaudal surface (Fig. 3A), although a prominent swelling is evident in lateral view just above midway on the shaft (Fig. 3B). The location of the fourth trochanter, the intercondylar groove and slight curvature of the shaft, indicate it is a right femur. The proximal and distal maximum widths are at least 380 mm and length is at least 1680 mm. The shape in caudal view (Fig. 3A), although generally similar to *Diplodocus*, appears more expanded about the medial deflection (Upchurch et al., 2004) of the femoral lateral edge (previously called the third trochanter), not unlike *Barosaurus lentus* (Lull, 1919, p. 36-37, fig. 9; McIntosh, 1990, p. 372, fig. 16.16).

The reconstructed length of this femur (Fig. 2C), with the articular ends added, is estimated at approximately 1800 mm and is compatible with the size range of the other elements of the holotype. The overall dimensions of the preserved shaft with reconstruction to the articulating ends (Fig. 3C) are similar to those of *Apatosaurus louisae* and *A. excelsus* (Table 3) and, congruently, the dimensions of the ilia, acetabular length and dorsoventral sacral dimensions of *Seismosaurus hallorum* and *A. louisae* are comparable.

Scapulae, coracoids, sternal plates, pes and manus were sculpted using *Diplodocus* data for reference. Dimensions of the recovered right scapulocoracoid of the diplodocid, *Supersaurus vivianae* (Jensen, 1985), which measures 2.7 meters in length, were similarly used as reference, as the size range of other *S. vivianae* elements, such as the pelvis and caudal vertebrae, appear comparable. From these dimensions, reconstruction of the scapulocoracoid for *Seismosaurus hallorum* was estimated at 2.4 meters in length and locates the distal end of the scapula over the fifth thoracic rib (Fig. 1).

AXIAL LENGTH

Estimates of length for *Seismosaurus hallorum* initially came from an article and the book “*Seismosaurus hallorum* The Earth Shaker” by Gillette (1991, 1994). In these publications, Gillette postulated the length of *Seismosaurus hallorum* to have been between 25 and 52 meters. However, Gillette favored the higher estimates of length, of between 39 to 52 meters, using comparative allometric inference from length-to-height data of vertebral and pelvic elements from *Diplodocus*.

In his estimates of the overall length of *Seismosaurus hallorum*, Gillette used three criteria in particular, relative to *Diplodocus*:

1. An expectation of protracted overall length, reasoning that the disproportionately extended heights of the caudal and sacral neural spines, relative to their centra lengths, the lengths of the cranial chevrons and the massive proportions of the pelvis, were indicative of an axial allometric increase in the tail and neck and thus in overall length.
2. An articulated series of eight mid-caudal vertebrae, positions Gillette assigned as 20 to 27, appeared disproportionately developed in their neural spine height and gross morphology (at relatively terminal positions) compared to known diplodocids and indicated a comparatively protracted tail length.
3. The pubis and elongated chevrons appeared relatively longer in

TABLE 3. *Seismosaurus hallorum* NMMNH P 3690, *Diplodocus carnegii* CM 84, CM 94, *Apatosaurus louisae* CM 3018, CM 563 and *A. excelsus* FM 7163, dimensions of ilia, sacra and femora in mm.

Character	NMMNH P-3690	¹ CM 84 (¹ CM 94)	² CM 3018
			(² CM 563) (² FM 7163))
Ilium overall length	C. 1400	1089	1460 (1280)
Width across ilia cranially	c. 1600	c. 1300 (1233)	
Width across ilia caudally	c. 1500	(940)	
Ilium superior border height above acetabulum	580		c. 570 (450)
Acetabulum length	460	355	c. 460 (445)
Sacral length	c. 1100	765	1325 (1183)
Sacral width cranially	c. 1400		c. 1080
Sacral width caudally	c. 1200		c. 970
Sacral spine height above superior iliac border	680	450	*600 (543)
Sacral spine height above superior acetabular border	1260	970	(c. 1000)
Greatest sacral vertebral height	c. 1300	1089	(1085)
Femur length	c. 1800	1542	1785 (1710) ((1830))
Femur shaft narrowest transverse width	c. 320		320 (260)
Femur transverse width at 3rd trochanter	c. 413		((310))
Femur proximal transverse width	c. 555	500	575 (543) ((570))
Femur distal transverse width	c. 515	412	565 (515) ((590))

c. estimated; * estimated size of CM 3018, based on a 14 percent size increase from CM 563; ¹ dimensions from Hatcher (1901); ² dimensions from Gilmore (1936)

axial lengths (presumably meaning antero-posterior lengths), which indicated, through allometric inference, that the tail and overall lengths were likely protracted.

The first and third criteria are essentially based on data of the dorsoventral lengths of elements, such as the neural spines, chevrons and pubis. These data were then extrapolated to give the anteroposterior estimate of lengths of vertebral elements, using allometric inference. In our opinion, using dorsoventral lengths of pelvic and caudal vertebral elements to give vertebral axial lengths, via allometric inference, is not viable.

With regard to the second criterion, our placement of the articulated series of eight mid-caudal vertebrae is consistent with more cranial assignments of these vertebrae (in agreement with Curtice, 1996) and at odds with the more terminal position assignments suggested by Gillette (1991, 1994). More cranial placement of these vertebrae effectively reduces the estimates of tail length. Paul (1988), Lucas (1993) and Curtice (1996) questioned the extreme length estimates suggested by Gillette (1991,

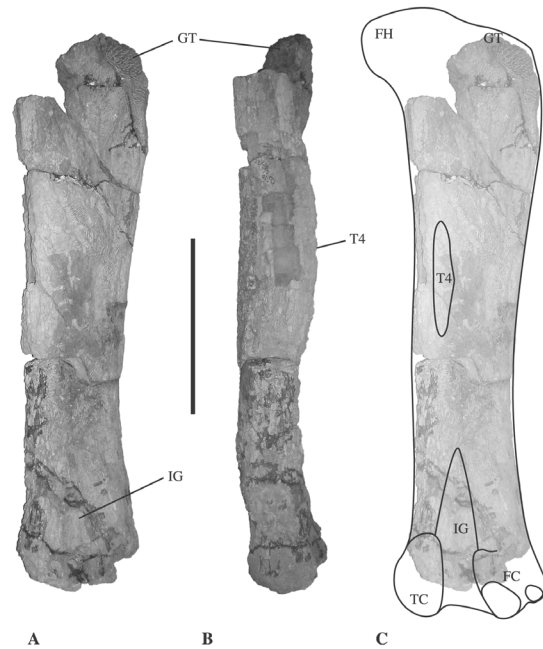


FIGURE 3. Right sauropod femur, NMMNH P-25079. A, caudal view; B, medial view; C, caudal view with the reconstructed outline of the articular ends. IG, intercondylae groove; 3T, 3rd trochanter; 4T, 4th trochanter; GT, greater trochanter; TC, tibial condyle; FC, fibular condyle; FH, femur head. Scale bar equals 0.5 meters.

1994). Lucas (1993) offered a more conservative estimate of around 30 meters.

Estimating the overall axial length for *Seismosaurus hallorum*, or any incomplete vertebral series, will always be constrained by the lack of necessary vertebral lengths, vertebral numbers and the unknown intervertebral distance between articulating centra. This intervertebral distance, which constitutes the cartilaginous disc or synovium forming the actual articulation, can be variable between procoelous, amphicoelous and opisthocoelous forms in extant reptiles (Hoffstetter and Gasc, 1969) and as likely, extinct reptiles. Research in this area is needed for sauropods. Over the approximately 105 articulated vertebrae for diplodocids, excluding the sacrum, every 10 mm error in the calculated intervertebral joint can change the overall length estimate by about a meter, which for discussion of the length of extremely long dinosaurs is not very significant. The intervertebral length for amphicoelous extant crocodiles, measured by Hoffstetter and Gasc (1969), is around 11.5 percent. This percentage translated to sauropod-sized vertebrae, indicates that for a caudal vertebrae of 300 mm, the intervertebral length is approximately 33 mm and for a cervical of 700 mm length, about 77 mm. In our reconstruction, the longer vertebrae were given an intervertebral spacing of about 40 mm to 70 mm and less for smaller (axially shorter) vertebrae.

Gillette (1994) suggested that relative to *Diplodocus*, the apparent allometry in the lengths of the sacral and caudal neural spines and chevrons, against axial measures of their centra lengths, indicated a protracted length in the tail and hence, a relative increase in axial length overall. This, of course, cannot be determined with certainty; Curtice (1996), however, argued that a relative increase in allometry in caudal neural spines could imply functions other than an increase in axial allometry. We argue further that the apparent allometric lengthening of dorsoventrally elongated elements, such as the neural spines and chevrons, are more likely to have a biomechanical basis related to the disproportionate increases in mass as the tail lengthens during growth.

Associated with a strictly proportional or isometric increase in the size of an object, such as the sauropod tail, there is a disproportionate relationship between increasing size to the resulting mass (Alexander,

1985; Wedel et al., 2000). Our calculations of volume for a typically shaped sauropod tail indicate that an isometric increase in tail size of 20 percent is accompanied by a disproportionate increase in mass of about 60 percent. With further increased axial allometry, the disparity between tail size and mass would be even greater. Due to the biomechanical constraints imposed by the relationship between ligament forces and ligament diameters, a disproportionate increase in tail mass to axial length would require a relative increase in the length of the leverage structure, such as the neural spines, which affect ligament suspension and bracing. Lever calculations for ligament forces of a suspended vertebral series show that these forces are reduced as neural spine height increases (Alexander, 1985, 1997). As such, an increase in the height of the sacral and caudal neural spines would be an adaptive response to counter increased tail mass during growth, in both the ontogenetic sense and phylogenetically.

In *Seismosaurus hallorum*, an increase in relative dorsoventral allometry of the sacral and caudal bones, with respect to an axial increase in tail length, supports this conclusion. Individual caudal centra of *S. hallorum* show axial length increases of between 10 to 25 percent, when compared with *Diplodocus carnegii* (CM 84; Gilmore, 1932). The heights of the sacral, cranial caudal and mid-caudal neural spines show relative increases of approximately 50 percent at the coalesced sacral spines, 32 percent at caudal vertebrae Ca5, Ca6 and Ca7 and less than 32 percent for the intact mid-caudal vertebrae from Ca11 to Ca19 (Table 2). The ratio of total vertebral height to centrum length (Table 1, up to Ca12) better illustrates the decreasing disparity, cranially to terminally, in relative caudal dimensions between *S. hallorum* and *D. carnegii*. Similarly, the ratio of total vertebral height to centrum length appears greater in *S. hallorum* than in *Apatosaurus* for the recovered caudal vertebrae, although the disparity is greater in the cranial caudals and increasingly less in caudals terminally. Increased axial allometry in the tail of *S. hallorum* may have occurred relative to *Diplodocus*, however, such allometry cannot be determined from the known material and is unlikely to have been to the degree suggested by Gillette (1991, 1994).

For *Seismosaurus hallorum*, the estimated length of the recovered caudal series from caudal 1 to 19 is approximately 5.76 m, with the complete caudal series of 75 vertebrae measuring 18.85 m; the total length of the five fused sacral vertebrae is estimated at 1.10 m; the total thoracic series of 10 vertebrae, including estimates for the length of 2 missing cranial thoracic vertebrae, measures 3.78 m; the reconstruction of the 15 cervical vertebrae measures 8.32 m and the skull 780 mm. The overall length is estimated at 32.83 (33) meters. With an added 10 percent error on the sculpted bones the total length would be 35 m and with negative 10 percent error the length would be 30.5 m.

CONCLUSIONS

Although only 30 percent of the skeleton of *Seismosaurus hallorum* was recovered by the NMMNH during the 1985 to 1990 excavations, the thoracic, pelvic and caudal elements gave adequate

osteological information and dimensions for comparisons with related diplodocids. The initial descriptions of caudal and ventral pelvic bones were published in Gillette (1991, 1994). However, subsequent preparation allowed further descriptive comparisons to be made and some re-interpretation. Production of a three-dimensional mount gave a rare opportunity to assess critically the reconstruction at full-scale, which, in so doing, has allowed reinterpretation of the overall length of the holotype.

The undescribed femur, NMMNH P-25079, which was recovered during the excavations of *Seismosaurus hallorum* within the quarry site, was formerly disregarded as an element of the holotype. Comparative dimensions of this femur with the femur of *Apatosaurus*, which also shares similar sized pelvic and thoracic dimensions, indicates that this femur is congruent with the holotype. Femur size estimates calculated during the reconstruction of *Seismosaurus hallorum* further support our proposed inclusion of the femur in the holotype.

The morphological similarities in the thoracic vertebrae of *Seismosaurus hallorum* and *Diplodocus*, such as their general proportions, development of their pleurocoels and overall layout of their vertebral lamina, reflects the undeniable taxonomic closeness of these two genera and begs the question: If the thoracic vertebrae had been found in isolation would assignment to the genus *Diplodocus* have been more appropriate?

The positions we assigned the middle caudal vertebrae were based first on the natural taper formed by the medial dorsal ridge of the recovered neural spines. Morphological similarities between comparative caudal vertebrae, although important, were considered secondarily. We considered placement of the intact mid-caudal vertebrae at the more terminal positions proposed by Gillette (1991, 1994) to be disproportionate.

With regard to axial length, we support the views of Paul (1988), Lucas (1993) and Curtice (1996) that the higher overall axial lengths proposed by Gillette (1991, 1994) of greater than 39 meters are an overestimation. Nevertheless, at 33 meters long, *Seismosaurus hallorum* remains among the longest terrestrial animals to have existed.

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REFERENCES

- Alexander, R. McN., 1985, Mechanics of posture and gait of some large dinosaurs: Zoological Journal of the Linnean Society of London, v. 83, p. 1-25.
- Alexander, R. McN., 1997, Biomechanics; in Currie, P. J. and Padian, K., eds., Encyclopedia of Dinosaurs: San Diego, Academic Press, p. 57-59.
- Curtice, B., 1996, Codex of diplodocid caudal vertebrae from the Dry Mesa Dinosaur Quarry [M. S. thesis]: Provo, Brigham Young University, 250 p.
- Frey, E. and Martin, J., 1997, Long necks of sauropods; in Currie, P. J. and Padian, K., eds., Encyclopedia of Dinosaurs: San Diego, Academic Press, p. 407-409.
- Gillette, D. D., 1991, *Seismosaurus halli*, gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico, USA: Journal of Vertebrate Paleontology, v. 11, p. 417-433.
- Gillette, D. D., 1994, *Seismosaurus*: The Earth Shaker. New York, Columbia University Press, 205 p.
- Gilmore, C. W., 1932, On a newly mounted skeleton of *Diplodocus* in the United States National Museum: Proceedings of the U.S. National Museum, v. 81, p. 1-2.
- Gilmore, C. W., 1936, Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum: Memoirs of the Carnegie Museum, v. 11, p. 175-300.
- Hatcher, J. B., 1901, *Diplodocus* Marsh, its osteology, taxonomy, and probable habits, with a restoration of the skeleton: Memoirs of the Carnegie Museum, v. 1, p. 1-63.
- Hoffstetter, R. and Gasc, J-P., 1969, Vertebrae and ribs of modern reptiles; in Gans, C., d'A. Bellairs, A. and Parsons, T. S., eds., Biology of the reptilia, volume 1: London and New York, Academic Press, p. 201-310
- Holland, W. J., 1906, The osteology of *Diplodocus* Marsh: Memoirs of the Carnegie Museum, v. 2, p. 225-264.

- Holland, W. J., 1934, The skull of *Diplodocus*: Memoirs of the Carnegie Museum, v. 9, p. 379-403.
- Jensen, J. A., 1985, Three new sauropod dinosaurs from the Upper Jurassic of Colorado: Great Basin Naturalist, v. 45, p. 697-709.
- Lucas, S. G., 1993, Dinosaurs of New Mexico. Albuquerque, New Mexico Academy of Science, 130 p.
- Lucas, S. G., Herne, M. C., Heckert, A. B., Hunt, A. P. and Sullivan, R. M., 2004, Reappraisal of *Seismosaurus*, a Late Jurassic sauropod dinosaur from New Mexico: Geological Society of America, Abstracts with Programs, v. 36, no. 5, p. 422.
- Lull, R. S., 1919, The sauropod dinosaur *Barosaurus* Marsh: Memoirs of the Connecticut Academy of Arts and Science, v. 6, p. 1-42.
- McIntosh, J. S., 1981, Annotated catalogue of the dinosaurs (Reptilia, Archosauria) in the collections of the Carnegie Museum of Natural History: Bulletin of the Carnegie Museum of Natural History, v. 18, p. 1-67.
- McIntosh, J. S., 1990, Sauropoda; in Weishampel, D. B., Dodson, P. and Osmólska, H., eds., The Dinosauria: Berkeley, University of California Press, p. 345-401.
- Osborn, H. F., 1899, A skeleton of *Diplodocus*: Memoirs of the American Museum of Natural History, v. 1, p. 191-214.
- 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, v. 2, no. 3, p. 1-14.
- Stevens, K. A. and Parrish, J. M., 1999, Neck posture and feeding habits of two Jurassic sauropod dinosaurs: Science, v. 284, p. 798-800.
- Upchurch, P., Barrett, P. M. and Dodson, P. 2004. Sauropoda; in Weishampel, D. B., Dodson, P. and Osmólska, H., eds., The Dinosauria: Berkeley, University of California Press, p. 259-322.
- Wilson, J. A., 1999, A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs: Journal of Vertebrate Paleontology, v. 19, p. 639-653.
- Wedel, M. J., Cifelli, R. L. and Sanders, R. K., 2000, Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*: Acta Palaeontologica Polonica, v. 45, p. 343-388.