A SECOND GONDWANAN DIPLODOCID DINOSAUR FROM THE UPPER JURASSIC TENDAGURU BEDS OF TANZANIA, EAST AFRICA

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Abstract: A new genus and species of diplodocid sauropod (Sauropoda, Diplodocoidea), *Australodocus bohetii*, is described. The type material from the Upper Jurassic (Tithonian) Tendaguru Beds of Tanzania, East Africa, consists of two successive mid-cervical vertebrae. These vertebrae do not show the extreme elongation of the cervical vertebrae that is diagnostic for *Tornieria*, and, apart from proportional differences, exhibit four autapomorphic characters not seen in other diplodocids: (1) pleurocoel weakly developed; (2) ridge posterolateral to the anterior condyle strongly posteroventrally orientated; (3) triangular pneumatic cavity ventral to the prezygapophysis, enclosed by the lateral ramus of the centroprezygapophyseal lamina and an anteriorly extended prezygodiapophyseal lamina; and (4) prominent prezygapophyseal process pointed, laterally keeled and surpassing the prezygapophysis anteriorly. *Australodocus bohetii* is the second diplodocid known from Tendaguru, and thereby the second diplodocid known from Gondwana. This impedes the customary reference of isolated East African diplodocid material to *Tornieria*, which can now only be assigned to Diplodocidae indet. The find supports previously proposed vicariance models of diplodocid palaeobiogeography.

Key words: Tendaguru, Sauropoda, Diplodocidae, Upper Jurassic.

THE Upper Jurassic Tendaguru beds of southern Tanzania, East Africa, are famous for their dinosaur diversity. The German Tendaguru Expedition (GTE) of 1909–13 explored these beds and shipped more than 250 tonnes of fossils back to Berlin, the majority of them sauropod bones (Maier 2003). Except for some recent finds in South America (Rauhut *et al.* 2005), Tendaguru currently is the only fossil site that has yielded an Upper Jurassic Gondwanan dinosaur fauna. Therefore, complete understanding of the Tendaguru fauna is essential for a comprehensive picture of dinosaur evolution in general.

In a recent revision of the Sauropoda (Upchurch *et al.* 2004*a*), species of five genera of Tendaguru sauropods were considered valid: the brachiosaurid *Brachiosaurus brancai*, the dicraeosaurids *Dicraeosaurus hansemanni* and *D. sattleri*, the basal titanosaur *Janenschia robusta*, the sauropod *incertae sedis Tendaguria tanzaniensis* and the diplodocid *Tornieria africana*. The last taxon is of special interest because, up to now, it is the only known representative of the Diplodocidae on the southern continents (Remes 2006), a group that is otherwise only known from the North American Morrison Formation (Kimmeridgian–Tithonian) and Upper Jurassic strata of western Eur-

ope (Upchurch *et al.* 2004*a*). In the course of revising material referred to *Tornieria* ('*Barosaurus*') *africana* (Remes 2004), I have found two successive cervical vertebrae in the collections of the Museum für Naturkunde in Berlin labelled '*Barosaurus africanus*' that have never been described or mentioned in the literature. These elements show several diplodocid and diplodocine characters. When compared with other diplodocids, including the well-known North American forms and *Tornieria africana* [the incomplete unnumbered MB specimen 'k 3' (Remes 2006), newly rediscovered posterior cervicals of 'skeleton k' (Remes in prep.), and the photograph of a relatively complete, but now destroyed cervical vertebra referred to that species by Janensch (1929*a*, pl. 8, fig. 2; field label 'dd 178')], major differences become evident, indicating that these elements represent a new species. The aim of this paper is to describe these elements, propose a name for the new taxon, and discuss the relevance of this finding for sauropod evolutionary and palaeobiogeographical history.

Institutional abbreviation. MB, Museum für Naturkunde der Humboldt-Universität zu Berlin.

Anatomical abbreviations used in the text-figures. ac, anterior condyle; acdl, anterior centrodiapophyseal lamina; apc, accessory pneumatic cavities; cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; di, diapophysis; epi, epipophysis; ls, ligament scars; mt, median tubercle; nc, neural canal; ns, neural spine (bifurcated); pa, parapophysis; pac, posterior articular cavity; pcdl, posterior centrodiapophyseal lamina; pleu, pleurocoel; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prsl, prespinal lamina; prz, prezygapophysis; przp, prezygapophyseal process; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tpol, interpostzygapophyseal lamina; tprl, interprezygapophyseal lamina; vc, ventral concavity.

GEOLOGICAL SETTING

The highly fossiliferous Tendaguru Beds were named after Tendaguru Hill (altitude 310 m) in south-east Tanzania, situated approximately 60 km north-west of the city of Lindi (Janensch 1914c; Hennig 1937). The succession is up to 110 m thick and consists of three terrestrial units (Lower, Middle and Upper Saurian Beds; Janensch 1914a, 1929b, c, 1935–36, 1961) that are separated by intercalated shallow marine sandstones (from oldest to youngest: *Nerinea* Beds, *Trigonia smeei* Beds and *Trigonia schwarzi* Beds; Heinrich 1999; Aberhan *et al.* 2002). The Saurian Beds are composed primarily of mudstones and fine sandstones, and yield amniote fossils, whereas the marine units consist of medium to coarse sandstones and are characterized by their mollusc (pelecypod) fauna. No dinosaur fossils are known from these marine sediments.

In the past, the exact age of the Tendaguru Beds has been a matter of debate. Fraas (1908) and Kitchin (1929) considered the complete succession to be of Early Cretaceous age, whereas the majority of authors have agreed that these sediments are Late Jurassic (Hennig 1914, 1937; Janensch 1914c; Schuchert 1918, 1934; Dietrich 1933; Aitken 1956, 1961; Kapilima 1984), with the exception of the uppermost *Trigonia schwarzi* Beds, which are thought to have been deposited on an erosional surface during the Early Cretaceous (Janensch 1914c; Lange 1914; Zwierzycki 1914; Dietrich 1933; Aitken 1961). In their recent re-examination of the Tendaguru biostratigraphy, Aberhan *et al.* (2002) concluded that the Upper Saurian Beds (which yielded the material described here) are definitely of Tithonian age.

In common with the age, there has been much debate over the palaeoenvironmental reconstruction of the Tendaguru deposits. The suggested models include shallow water lagoons under tidal influence (Janensch 1914b), swampy coastal plains proximal to a system of lagoons and estuaries (Dietrich 1933), salt marshes (Reck 1925), and a system of rivers and estuaries in a deltaic environ-ment (Fraas 1908; Schuchert 1918; Parkinson 1930; Colbert 1984). Russell *et al.* (1980) agreed with the interpretation of a near-shore environment and assumed that the sediments were deposited under a seasonal climate with periodic droughts. On the basis of their data, Aberhan *et al.* (2002) proposed an environment with shallow lagoons, vast tidal flats and coastal plains, and a hinterland covered with vegetation in a warm, strongly seasonal climate.

LOCALITY DATA

Most of the records of the German Tendaguru Expedition were lost during World War II, including taphonomic data for many of the excavation sites. What remains are the field catalogue (Janensch unpublished) that lists all elements found in any Tendaguru quarry, the published site maps (Janensch 1914c, 1925) and taphonomic data for a few sites that were reviewed by Heinrich (1999). However, the last work does not include data from Tendaguru site G, the origin of the material described here.

This site (Upper Saurian Beds) was situated adjacent to localities A (the type locality of *Tornieria africana*; Fraas 1908), e, F, and k (origin of the referred specimen of *T. africana*; Remes 2006), all about 400 m south of Tendaguru Hill (Text-fig. 1). Janensch (unpublished GTE field catalogue) noted that the work at site G commenced in July 1909 'southward not far from the old campground' (my translation). In total, 98 fossil bone elements from this site are listed in the GTE field catalogue, among them a posterior cervical vertebra and a partial caudal vertebral column of *Janenschia robusta* (Janensch 1929b; but see Bonaparte *et al.* 2000), a stegosaurian femur, a caudal vertebra of *Brachiosaurus*, and two small humeri referred to '*Barosaurus*' *africanus* (MB.R.2656 and 2709). Already, in his unpublished GTE field catalogue, Janensch presumed that 'another small animal' (my translation) was represented among the material from site G, but he did not make any further mention of this in his later publications. The historical list of material from the site is given in Table 1; unfortunately, many of these elements were destroyed during World War II (Maier 2003), including the remainder of the cervical series described here.

SYSTEMATIC PALAEONTOLOGY

SAURISCHIA Seeley, 1888
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
DIPLODOCOIDEA Marsh, 1884
FLAGELLICAUDATA Harris and Dodson, 2004

TABLE 1. List of material from site G, translated from Janensch (unpublished GTE field catalogue). Janensch's original caption reads as follows: 'Skeleton G. Southward, not far from old campground. July 1909. III. Stage (= Upper Saurian Beds)'. The series of cervical vertebrae that contains the type material of *Australodocus bohetii* gen. et sp. nov. is marked in bold type. The remaining vertebrae were destroyed during World War II.

Field no.	Element	Comments
G1	limb bone	another small animal?
G2	small rib	next to G1, another small animal?
G3	limb bone	another small animal?
G4	limb bone, fragment	another small animal?
G5	?small ilium?	another small animal?
G6	scapula	
G7	coracoid	
G8	multiple caudal vertebrae	
G9	multiple caudal vertebrae	
G10–32	caudal vertebrae	
G33–42	probably haemapophyses	listed by Boheti
G43–45	dorsal vertebrae	numbered from posterior to anterior, closely associated
G46–51	dorsal vertebrae	G46–48 approx. 1–1·5 m away
G52	rib	next to G45
G53–58	ribs and rib fragments	
G59–60	rib fragments	
G61–62	cervical ribs?	between G44 and G45
G63	pelvic bones	(ischium or pubis) 1 m east of G45
G64	humerus	
G65	scapula	west side of trench
G66–67	pelvic bones	G66 ischium?
G68–71	**cervical vertebrae**	
G72–73	cervical vertebrae?	
G74–75	cervical vertebrae	
G76	axis?	
G77	pelvic bone (ischium)	
G78	cervical vertebra	affiliation doubtful
G79	humerus	another animal!
G80	vertebral body	affiliation doubtful
G81	small humerus	another animal! east side
G82	small tibia	affiliation doubtful, east side
G83	small limb bone, plump radius	affiliation doubtful, east side
G84	caudal vertebral body	*Brachiosaurus*? east side
G85	small limb bone	
G86	small pubis?	affiliation to G74–78 doubtful
G87	coracoid?	affiliation to G74–78 doubtful
G88	?	affiliation to G74–78 doubtful
G89	stegosaurian femur	
G90	claw	
G91	small humerus	
G92–96	cervical vertebrae	
G97	small tibia	
G98	small claw	

DIPLODOCIDAE Marsh, 1884
DIPLODOCINAE Marsh, 1884

AUSTRALODOCUS gen. nov.

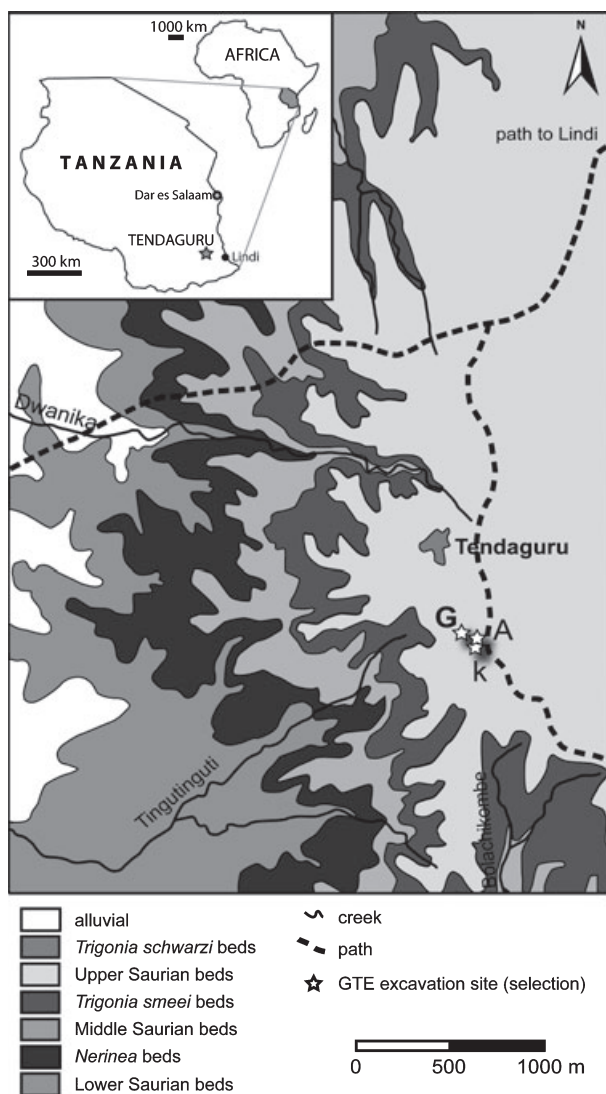*Derivation of name.* Latin, *australis*, southern, with reference to the Gondwanan provenance, and Greek, δοκος, beam, alluding to the close relationship of this genus to the North American *Diplodocus*.

Type species. Australodocus bohetii sp. nov.

Diagnosis. As for type species (see below).

TEXT-FIG. 1. Map of the type locality of *Australodocus bohetii*, Tendaguru site G, Upper Saurian Beds (Tithonian). Site A is the type locality of *Tornieria africana*, the other diplodocine species from Tendaguru; site k is where the referred skeleton of *T. africana* was found.

Australodocus bohetii sp. nov.
Text-figures 2–6, 7G

Derivation of name. After Boheti bin Amrani, the native African crew supervisor and chief preparator of the German Tendaguru Expedition, whose excellent work was essential for the success of the European researchers (Janensch 1914*b*).

Holotype. MB.R.2455 [G 70], mid-cervical vertebra (number ?6).

Paratype. MB.R.2454 [G 69], mid-cervical vertebra, in all probability of the same individual and successive to the holotype vertebra (number ?7).

Type horizon and locality. Upper Saurian Beds of the Tendaguru Beds, 400 m south of Tendaguru Hill, Tendaguru Plateau, District of Lindi, Tanzania, East Africa; Upper Jurassic, Tithonian (Aberhan *et al.* 2002).

Diagnosis. Diplodocid sauropod with cervical pleurocoel weakly developed; ridge posterolateral to anterior condyle strongly posteroventrally inclined; anteriorly facing triangular pneumatic cavity ventral to prezygapophysis, enclosed by the lateral ramus of the centroprezygapophyseal lamina and an anteriorly extended prezygodiapophyseal lamina; prominent prezygapophyseal process pointed, laterally keeled and reaching further anterior than the prezygapophysis. Additionally, *Australodocus* differs from other diplodocids in the combination of following traits: mid-cervical centra moderately elongate (Elongation Index < 4·1); pleurocentral lamina widened to form a shelf; parapophyses broad and robust; neural arch deep relative to centrum height; lateral ramus of centroprezygapophyseal lamina pillar-like.

Description. Additional to the consecutive field numbers that indicate close association when excavated, both vertebrae articulate perfectly and are therefore regarded as successive elements of one individual. The surface of the holotype vertebra MB.R.2455 [G 70] is better preserved than the paratype vertebra MB.R.2454 [G 69]. Its left side is slightly distorted, the parapophyses and diapophyses are broken off, and cervical ribs are missing (Text-fig. 2). The distal half of the ventral part of the centrum is distorted and partially broken away. The ventral part of the posterior articular facet is also broken off. In the paratype, the right parapophysis is better preserved, but both prezygapophyses are damaged and the right postzygapophysis is distorted. In their proportions, the vertebrae strongly resemble the sixth and seventh cervical vertebrae, respectively, of *Diplodocus*, but are about 30 per cent smaller. The neurocentral sutures are completely fused, indicating that the individual was a subadult or adult.

The following description is based on the holotype, not on the paratype vertebra unless mentioned explicitly. Anatomical terms favour anterior/posterior over cranial/caudal, to maintain compatibility with the standardized nomenclature of saurischian vertebral laminae established by Wilson (1999).

Centrum. The strongly opisthocoelous centrum is somewhat wider than high, and only moderately elongate, as indicated by an Elongation Index (EI, centrum length divided by posterior centrum width; Upchurch 1998) of < 4·1. This contrasts with the only other known Tendaguru diplodocid, *Tornieria africana*, which has an EI of 5·4 in the mid-cervical vertebrae (see 'Discussion' and Remes 2006). The EI value for *Australodocus* is even lower than for *Diplodocus*, the latter having an EI of 4·4 in the mid-cervical vertebrae (Text-fig. 7).

The well-developed anterior articular condyle is suboval in cross-section (Text-figs 2–3), being wider than high and anteroposteriorly elongate; in *Tornieria*, the condyle is more circular in outline (Remes 2006). Its diameter, relative to the width of the
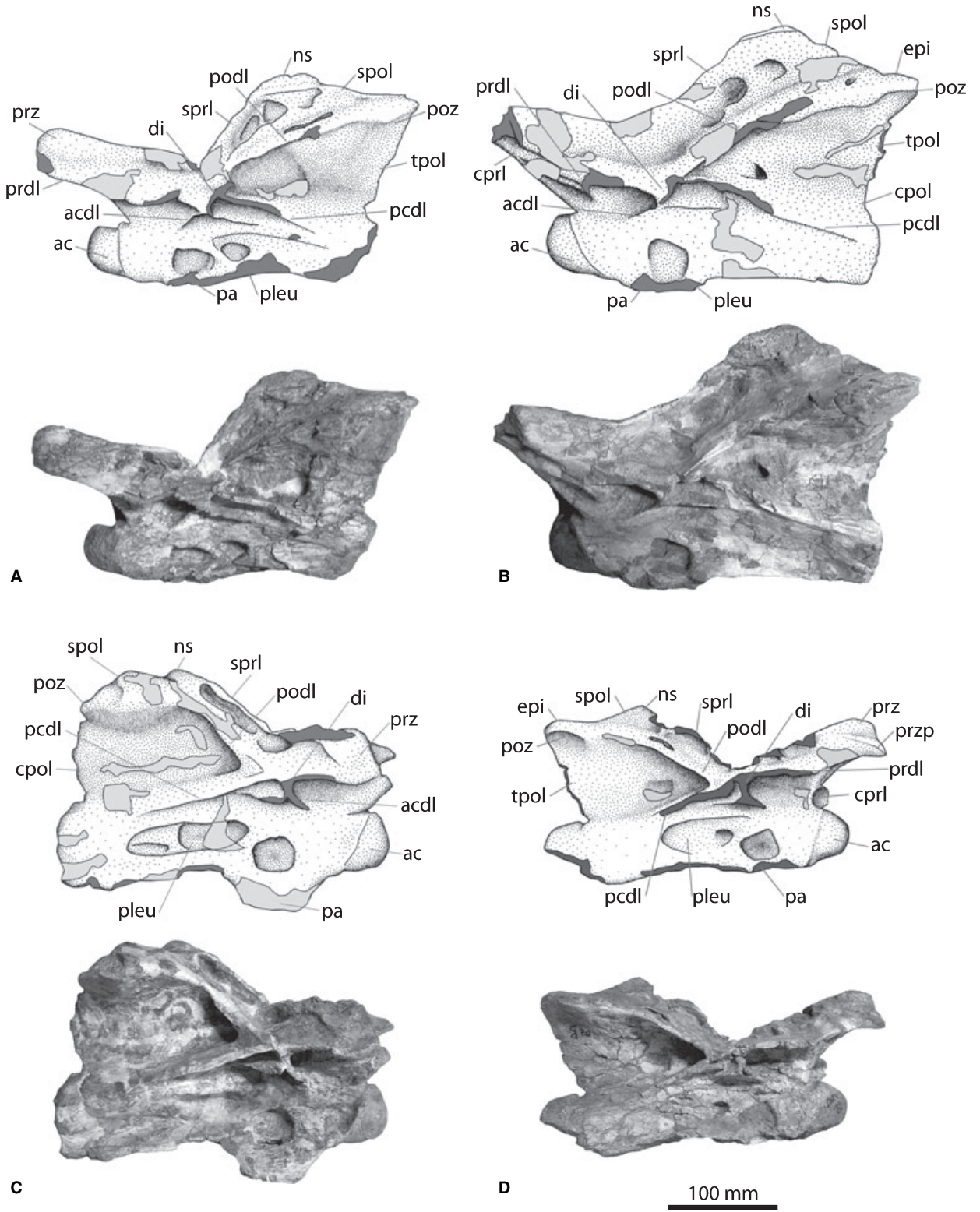
TEXT-FIG. 2. *Australodocus bohetii*, type vertebrae in A–B, left lateral, and C–D, right lateral views. A, D, MB.R.2455 [G 70], holotype, sixth (?) cervical vertebra. B–C, MB.R.2454 [G 69], paratype, seventh (?) cervical vertebra. Areas of dark shading are fractured surfaces; light shading indicates reconstruction.
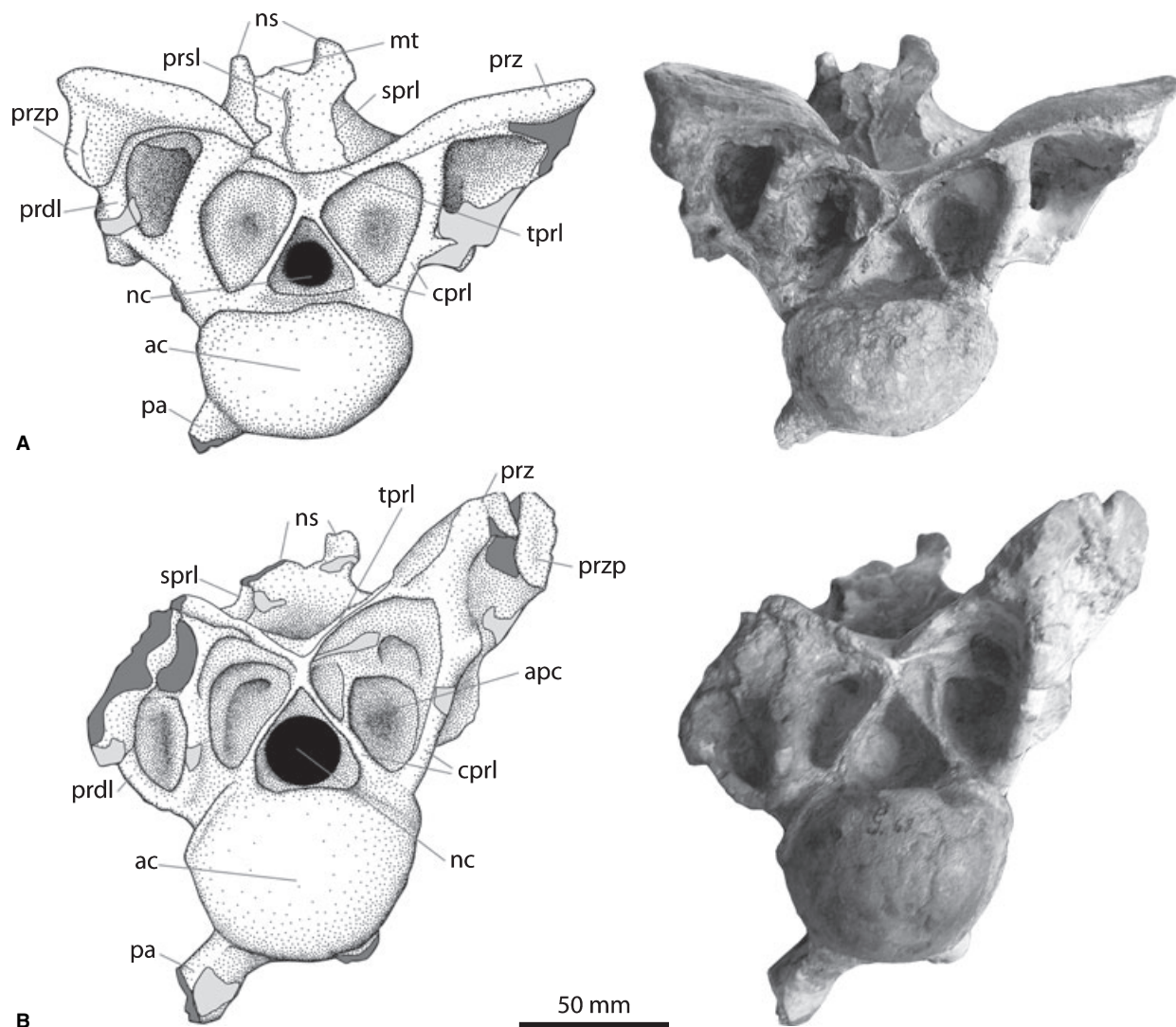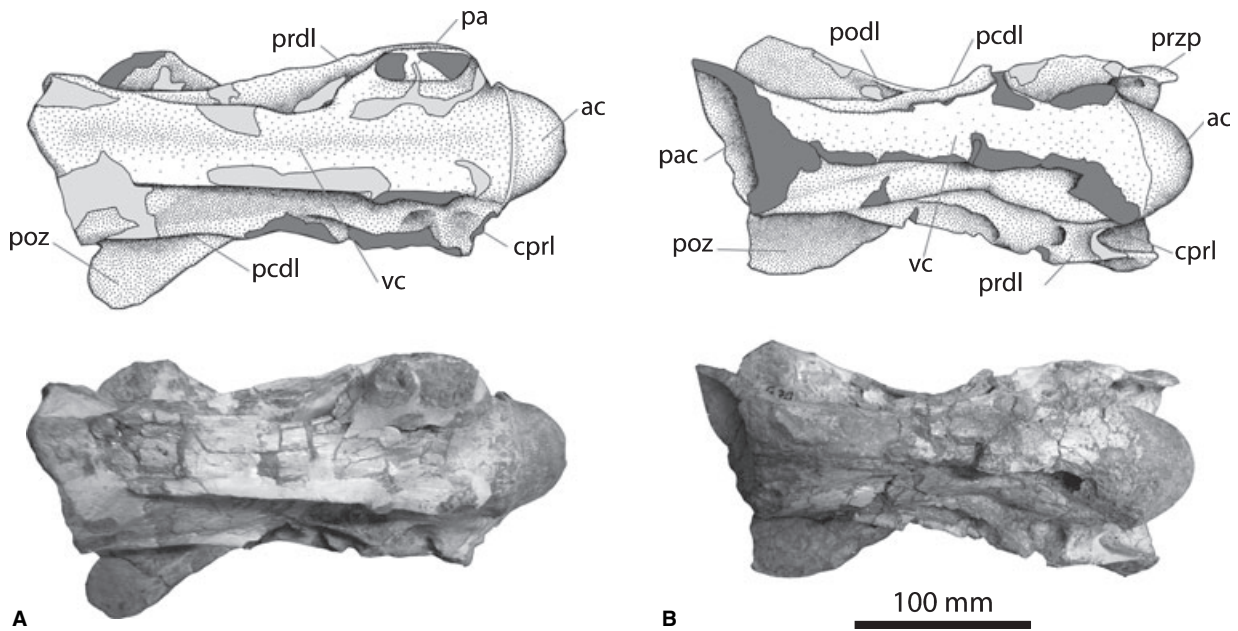
TEXT-FIG. 3. *Australodocus bohetii*, type vertebrae in anterior view. A, MB.R.2455 [G 70], holotype, sixth (?) cervical vertebra. B, MB.R.2454 [G 69], paratype, seventh (?) cervical vertebra. Areas of dark shading are fractured surfaces; light shading indicates reconstruction.

base of the neural arch, is similar to that of *Diplodocus* (Hatcher 1901), but smaller than in *Apatosaurus* (Gilmore 1936; Upchurch *et al*. 2004*b*) and greater than in *Suuwassea* (Harris and Dodson 2004) and *Barosaurus* (McIntosh 2005). The dorsal side of the condyle is flattened in the holotype vertebra, or bears a slight notch that forms the floor of the neural canal in the paratype.

On the lateral side (Text-fig. 2), a prominent rounded ridge, which probably supported intervertebral articular ligaments in the living animal, runs from the dorsal edge of the condyle posteroventrally. This ridge is more prominent in the paratype vertebra and has a backward inclination of 20 degrees relative to the vertical. This renders the centrum slightly chevron-shaped, implying a ventral curvature in this region of the cervical vertebral column. In *Diplodocus*, this angle is lower (Hatcher 1901), and in *Apatosaurus* (Gilmore 1936; Upchurch *et al*. 2004*b*),

Barosaurus (Lull 1919; McIntosh 2005) and *Tornieria* (Remes 2006) it is vertical. Uniquely in *Barosaurus*, the centra have a gentle, ventrally concave curvature (McIntosh 2005).

In *Australodocus*, the lateral side of the centrum is flattened, but bears a shallow pleurocoelous fossa that is divided by a broad shelf (rather than a true pleurocentral lamina) into a smaller anterior part and a larger posterior part. The anterior hollow is subquadrangular in outline with rounded corners, and placed directly above the parapophysis. The posterior depression is elongate, but shallow, tapers posteriorly, and has a small pneumatopore in its anterior edge. It ends well anterior to the posterior edge of the centrum. This comparatively weak development of the pleurocoel superficially resembles the condition in *Barosaurus* (where the pleurocoels are relatively small, but pointed both anteriorly and posteriorly; McIntosh 2005), but is unlike the extensive development of this feature in *Suuwassea*

TEXT-FIG. 4. *Australodocus bohetii*, type vertebrae in ventral view. A, MB.R.2454 [G 69], paratype, seventh (?) cervical vertebra. B, MB.R.2455 [G 70], holotype, sixth (?) cervical vertebra. Areas of dark shading are fractured surfaces; light shading indicates reconstruction.

(Harris and Dodson 2004), *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004b) or *Diplodocus* (Hatcher 1901). However, in *Barosaurus* there is an additional lamina laterally on the posterior centrum that borders an accessory cavity dorsally (McIntosh 2005); no such structure is present in *Australodocus*, leaving the posterior part of the centrum smooth and rounded laterally.

The parapophysis, best preserved on the right side of the paratype, is located upon the ventrolateral edge of the centrum, directly posterior to the first third of the centrum, and directly below the base of the diapophysis. It has a trapezoid shape in dorsal view and an elongate, subrectangular cross-section with rounded anterior and posterior margins, and is orientated steeply ventrolaterally. It is broader relative to other diplodocids; in *Barosaurus*, it has a triangular outline (McIntosh 2005). Ventrally, the centrum bears a shallow, transversely concave groove, extending posteriorly from the base of the anterior articular condyle (Text-fig. 4). The posterior articular cavity is subcircular in outline and bordered by a strong, rounded rim (Text-fig. 5).

Neural arch. The neural arch is high, making up more than two-thirds of the total height of the vertebra. As in other neosauropods (Wilson 1999), it is lightly but strongly constructed, having distinct bony laminae aligned to the major stress lines. The zygapophyses are also placed high relative to the height of the centrum, more so than in other diplodocids; their orientation is clearly angled to the long axis of the centrum, in contrast to *Barosaurus* (McIntosh 2005) and perhaps *Tornieria* (destroyed vertebra depicted by Janensch 1929a; Text-fig. 7E). The diapophysis is situated level with the parapophysis, as it is in *Barosaurus* (McIntosh 2005), whereas in other diplodocids the diapophysis is placed posterior to the parapophysis (Hatcher 1901; Gilmore 1936; Harris and Dodson 2004; Upchurch *et al.* 2004b).

In anterior view (Text-fig. 3), the dorsolateral edge of the centrum bears the origin of the centroprezygapophyseal lamina. The centroprezygapophyseal lamina divides into a thin medial ramus running to the dorsal margin of the neural canal, and a markedly robust, rounded lateral ramus that supports the prezygapophysis ventromedially. This divide is situated directly at the base of the centroprezygapophyseal lamina as in *Diplodocus* (Hatcher 1901), *Tornieria* (Remes 2006) and *Barosaurus* (McIntosh 2005), whereas in *Apatosaurus*, the lamina borders the ventral half of the neural canal before dividing (Gilmore 1936; Upchurch *et al.* 2004b). However, the marked robustness of the lateral ramus is similar only to *Barosaurus* (McIntosh 2005). In *Tornieria* the medial ramus is steeper (Remes 2006), and in *Suuwassea* the lateral ramus is even more robust, straight, and the medial ramus is only weakly developed (Harris and Dodson 2004).

The neural canal lies in a triangular depression, between the medial rami of the centroprezygapophyseal lamina, and is circular in outline. It has a relatively small diameter in comparison with *Diplodocus* (Hatcher 1901); in some specimens of *Apatosaurus* (Gilmore 1936) and in *Suuwassea* (Harris and Dodson 2004) it is oval. The interprezygapophyseal lamina contacts the dorsal end of the lateral ramus of the centroprezygapophyseal lamina and runs from the medial side of the prezygapophyses ventromedially. The left and right interprezygapophyseal laminae meet the midline and fuse to a single, median, dorsoventrally orientated lamina that contacts the medial rami of the centroprezygapophyseal lamina dorsolateral to the neural canal. This median lamina is relatively longer in *Tornieria* (Remes 2006).

The interprezygapophyseal laminae and both rami of the centroprezygapophyseal lamina enclose a deep, subtriangular pneumatic depression that is further subdivided by accessory
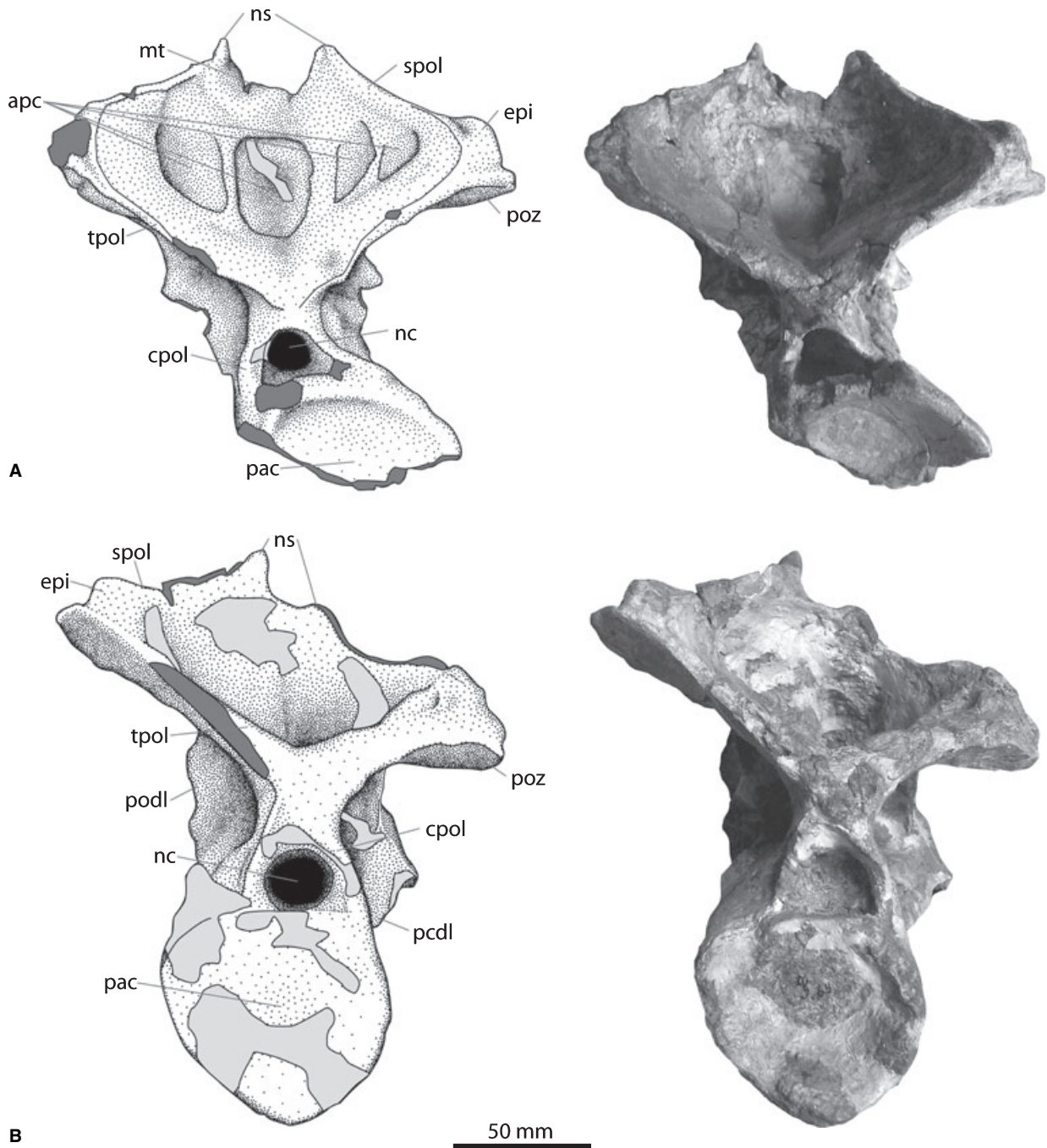
TEXT-FIG. 5. *Australodocus bohetii*, type vertebrae in posterior view. A, MB.R.2455 [G 70], holotype, sixth (?) cervical vertebra. B, MB.R.2454 [G 69], paratype, seventh (?) cervical vertebra. Areas of dark shading are fractured surfaces; light shading indicates reconstruction.

laminae in the larger, paratype vertebra. Immediately above its ventral third, the lateral ramus of the centroprezygapophyseal lamina contacts an anterior extension of the prezygodiapophyseal lamina that is also robust and rounded anteriorly. This extension of the prezygodiapophyseal lamina runs dorsally and supports the ventrolateral corner of the prezygapophysis. Together, both laminae make up the border of another deep, triangular pneumatic depression that lies ventral to the prezygapophysis, a condition unique among known diplodocids. There is no such cavity in *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*), *Barosaurus* (McIntosh 2005) or *Tornieria*, and in *Diplodocus* the prezygodiapophyseal lamina is much weaker and does not extend so far to the anterior, leaving the cavity open laterally (Hatcher 1901).

The ventrolateral margin of the prezygapophysis, anterolateral to the insertion of the prezygodiapophyseal lamina, carries a prominent, peg-shaped, anteroventrally orientated process that bears a sharp ridge on its lateral side (Text-fig. 2). This process extends far to the anterior, surpassing the anterior edge of the prezygapophysis. Similar prezygapophyseal processes are present in other diplodocids, e.g. *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Diplodocus* (Hatcher 1901), but not in *Barosaurus* (McIntosh 2005). However, the enlarged, laterally keeled, pointed and elongate condition is unique to *Australodocus*.

Posterior to this process, the prezygodiapophyseal lamina fuses laterally to the prezygapophysis and extends at a low angle (about 20 degrees relative to the horizontal) to the diapophysis (Text-fig. 2). This angle is higher than in *Barosaurus* (McIntosh 2005) and *Diplodocus* (Hatcher 1901), but lower than in *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Suuwassea* (Harris and Dodson 2004), and related to the relative vertebral elongation in these taxa (Text-fig. 7).

The transversely broad prezygapophysis is anterodorsally and slightly laterally directed. The articular surface of the prezygapophysis faces dorsally and slightly anteriorly, is suboval in outline, smooth and transversely convex (Text-figs 3, 6). In *Barosaurus* it is orientated more anteriorly (McIntosh 2005), whereas in *Suuwassea* it has a slightly sigmoidal curve, and is mediodorsally orientated (Harris and Dodson 2004). The articular facet is not stepped from the spinoprezygapophyseal lamina as in *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*), but a small ridge borders it posteriorly (Text-fig. 6). The lateral side of the prezygapophysis bears rough, anteroposteriorly orientated ligament scars, as does the dorsal side of the postzygapophysis (Text-fig. 6). As in *Diplodocus* (Hatcher 1901) and *Barosaurus* (McIntosh 2005), the prezygapophyses extend beyond the anterior condyle anteriorly, but they are wider and more robust in *Australodocus* than in these two genera.

The postzygodiapophyseal lamina runs from the diapophysis posterodorsally, curves slightly toward a subhorizontal orientation and then fuses to the lateral side of the postzygapophysis (Text-fig. 2). The dorsal side of the postzygodiapophyseal lamina bears a low, presumably pneumatic depression just anterior to the base of the neural spine (Text-fig. 6). The epiphysis (Text-fig. 5) is low in comparison with that of *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*), *Suuwassea* (Harris and Dodson 2004) and *Barosaurus* (McIntosh 2005), and resembles the condition in *Diplodocus* (Hatcher 1901). It does not extend beyond the postzygapophysis posteriorly as in *Suuwassea* (Harris and Dodson 2004). The short anterior centrodiapophyseal lamina extends from the diapophysis anteroventrally at an angle of approximately 50 degrees to the horizontal. The posterior centrodiapophyseal lamina also originates from the diapophysis, extends posteroventrally at a steep angle, and fuses to the centrum immediately prior to its posterior quarter. In *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Diplodocus* (Hatcher 1901) it is more prominent and associated with accessory pneumatizations either below (*Apatosaurus*) or above (*Diplodocus*) the lamina. Moreover, in *Apatosaurus* and *Barosaurus* (McIntosh 2005) it is orientated horizontally.

On the posterior side of the vertebra (Text-fig. 5), the curved centropostzygapophyseal lamina is undivided and encloses the neural canal. Dorsal to this canal, the left and right laminae fuse to each other and meet the rami of the interpostzygapophyseal lamina, as in other diplodocines. In *Tornieria*, the centropostzygapophyseal lamina is more robust and pillar-like; in *Apatosaurus* (Upchurch *et al.* 2004*b*), it is vertically orientated, but gives rise to a medial ramus that extends dorsomedially to meet the interpostzygapophyseal lamina above the neural canal (the resulting X-shape is autapomorphic for *Apatosaurus*; Wilson 2002; Upchurch *et al.* 2004*a*, *b*). In lateral view, the origin of the centropostzygapophyseal lamina is seen to be almost continuous with the posterior edge of the centrum; in *Apatosaurus* it is placed more anteriorly (Gilmore 1936; Upchurch *et al.* 2004*b*).

The postzygapophysis is ventrolaterally directed and has a pointed posterior edge (Text-fig. 6), whereas in *Apatosaurus* the posterior rim is convex (Gilmore 1936; Upchurch *et al.* 2004*b*). Its articular facet is flat, in contrast to the concave condition found in *Diplodocus* (Hatcher 1901). The interpostzygapophyseal lamina connects to the dorsolateral margin of the neural canal and to the postzygapophysis, while the spinopostzygapophyseal lamina extends from the postzygapophysis to the neural spine on each side. Together, these laminae border a deep, lozenge-shaped cavity that surpasses the posterior articular surface in size (Text-fig. 5). The angle between both rami of the interpostzygapophyseal lamina is somewhat steeper than in *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*), but as in that genus the rami are straight and not curved as in *Diplodocus* (Hatcher 1901), *Barosaurus* (McIntosh 2005) and *Tornieria*.

Anterodorsal to this cavity the bifid neural spines are thin, blade-like and low (about 20 mm deep). In lateral view they are continuous with the spinopostzygapophyseal lamina, in contrast to *Suuwassea* (Harris and Dodson 2004), *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Diplodocus* (Hatcher 1901), in which the robust neural spines are elevated relative to the lamina. Medioventrally between the neural spines there is a flattened, rugose tubercle (Text-fig. 6) for the insertion of a nuchal ligament (Janensch 1929*c*; Alexander 1985). It is not as prominent as, for example, in *Apatosaurus* (Upchurch *et al.* 2004*b*). The degree of bifurcation and transverse separation is also low in comparison with *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Diplodocus* (it corresponds to that of cervical vertebrae 3 and 4 in the latter genus; Hatcher 1901), and similar to that of *Suuwassea* (Harris and Dodson 2004) or *Barosaurus*, the latter having bifid neural spines that begin from the eighth cervical vertebra (McIntosh 2005).

On the anterior side of the spine the laterally orientated and markedly robust spinoprezygapophyseal lamina connects to the prezygapophysis (Text-fig. 6). The left and right spinoprezygapophyseal laminae enclose a wide, anteriorly directed medial groove that is situated level with their anteroposterior midlength. Originating from this groove, a weak prespinal lamina runs posterodorsally and connects to the median tubercle (Text-fig. 3). The prespinal lamina is reduced in most diplodocids, but comparatively robust in *Suuwassea* (Harris and Dodson 2004). In *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Suuwassea* (Harris and Dodson 2004) the left and right spinoprezygapophyseal laminae enclose a deep concavity that extends from the base of the neural spines anteriorly. This concavity has been interpreted as the elastic ligament fossa (Tsuihiji 2004). On the
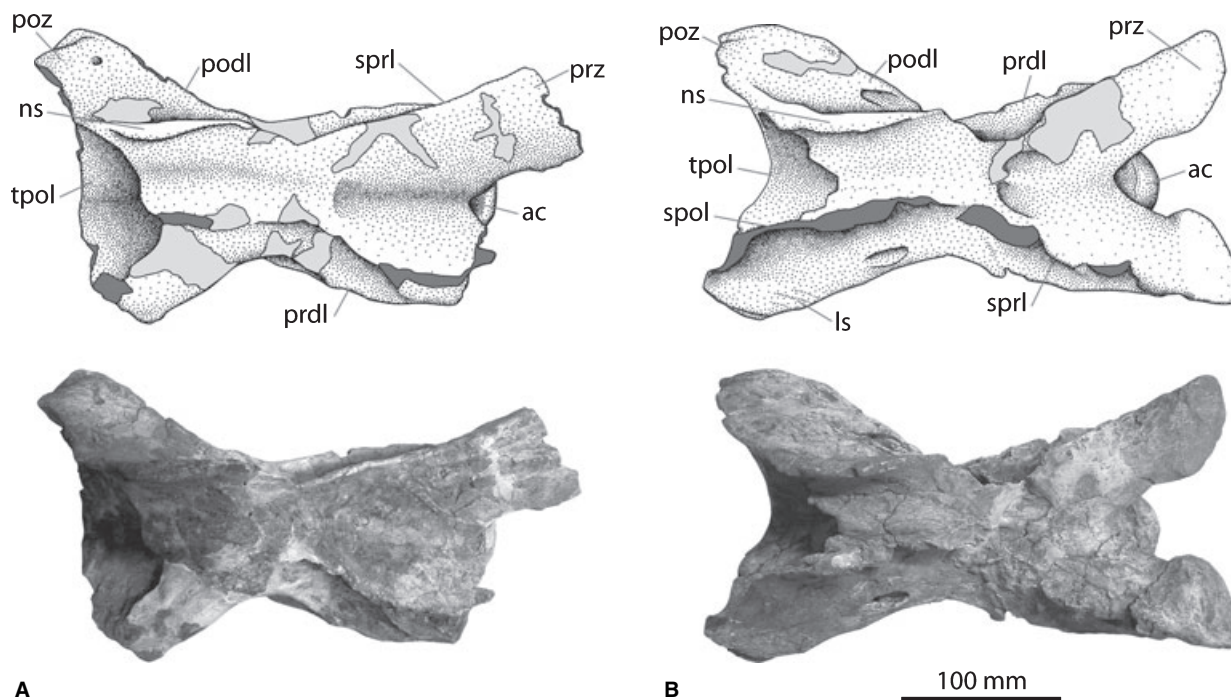
TEXT-FIG. 6. *Australodocus bohetii*, type vertebrae in dorsal view. A, MB.R.2454 [G 69], paratype, seventh (?) cervical vertebra. B, MB.R.2455 [G 70], holotype, sixth (?) cervical vertebra. Areas of dark shading are fractured surfaces; light shading indicates reconstruction.

lateral side, small accessory pneumatic cavities are placed directly below the spinoprezygapophyseal lamina (Text-fig. 2), a condition resembling that in *Barosaurus* (McIntosh 2005), but unlike that of *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004*b*) and *Diplodocus* (Hatcher 1901). As in other diplodocids, the spinoprezygapophyseal lamina is slightly curved in lateral view (Text-fig. 2), in contrast to the robust, hook-like shape in *Suuwassea* (Harris and Dodson 2004).

DISCUSSION

Taxonomy and phylogenetic relationships

Both vertebrae exhibit characters that permit an unambiguous phylogenetic classification of the new dinosaur. Bifurcated neural spines on the mid-cervical vertebrae, with a medial tubercle between them, and the concave ventral side of the centrum are synapomorphies of the Flagellicaudata (McIntosh 1990; Upchurch 1995, 1998; Wilson 2002; Harris and Dodson 2004; Upchurch *et al.* 2004*a*). A bifurcated centroprezygapophyseal lamina with a medial and a lateral ramus is diagnostic for the Diplodocidae (Wilson 2002; Upchurch *et al.* 2004*a*). Finally, transversely convex articular facets of the prezygapophyses, as well as elongate mid-cervical centra with an EI > 4·0 are synapomorphic for the Diplodocinae (Upchurch 1998; Wilson 2002; Upchurch *et al.* 2004*a*).

All known diplodocids have 25 presacral vertebrae including 15 cervical and ten dorsal vertebrae (Wilson 2005), the only exception being *Barosaurus* which has 16 cervical and nine dorsal vertebrae (McIntosh 2005). Because of the strong similarity in vertebral count in this group, it is likely that *Australodocus* also had 15 cervical vertebrae. Accordingly, and because of proportional similarities with *Diplodocus*, the two vertebrae described here are provisionally identified as cervical vertebrae 6 and 7.

The validity of *Australodocus bohetii* as a new taxon depends primarily on comparison with the other diplodocid from Tendaguru, *Tornieria africana*. Owing to their incompleteness and the loss of taphonomic data, both taxa can only be compared in terms of the cervical vertebrae. Although badly preserved, the sole cervical vertebra of *Tornieria* described by Remes (2006) is complete enough to demonstrate that these taxa are distinct. The posterior centrum width is only 3–5 per cent wider than in the paratype of *Australodocus*, but the centrum length is 55 per cent greater (Table 2). The minor difference in centrum width and the closed neurocentral sutures in the type material of *Australodocus* render ontogenetic explanations for that difference improbable, the more so as ontogenetic variation of cervical vertebral elongation in *Apatosaurus* (Carpenter and McIntosh 1994) and other diplodocids (Schwarz *et al.* in prep.) seems to be minimal. Another reason for differing elongation

indices may be different positions in the cervical vertebral column, but because the *Australodocus* vertebrae are mid-cervicals and elongation is greatest in this region of the neck in diplodocids (Hatcher 1901; Upchurch 1998; McIntosh 2005), this explanation can also be ruled out.
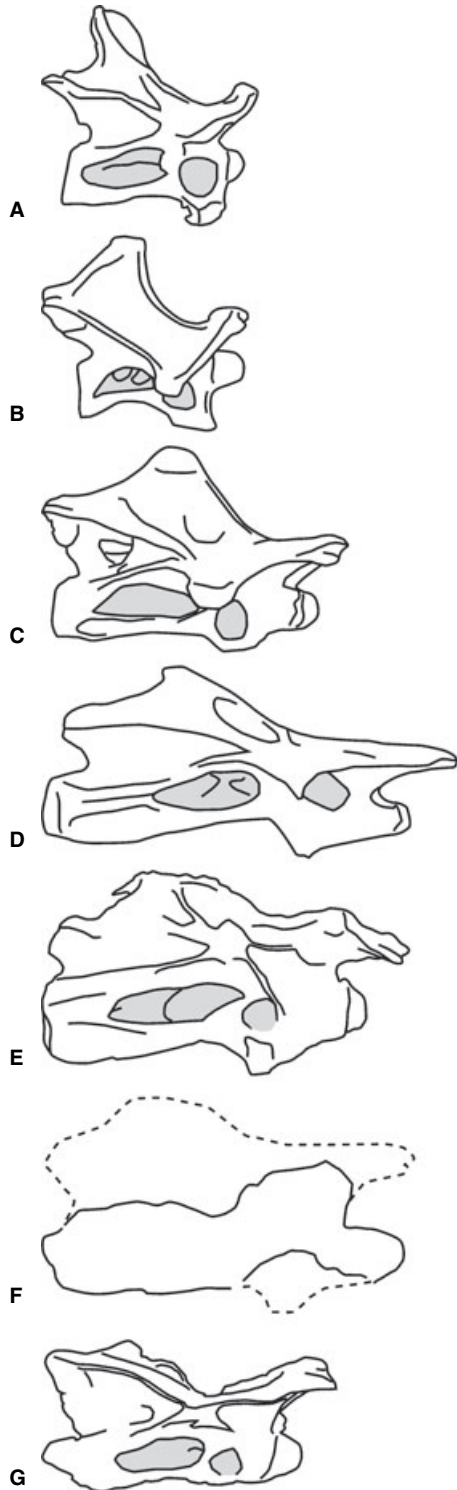
Even if it is assumed that the preserved cervical of *Tornieria* is the longest in the neck, there is no way to fit the vertebrae of *Australodocus* into a hypothetical neck of *Tornieria* without dismissing compatibility to complete diplodocids such as *Diplodocus* or *Apatosaurus*. *Tornieria*, unlike other diplodocids, either would have had elongate vertebrae only in the posterior region of the neck, while the anterior region would be rather plesiomorphic, or its vertebral elongation would be widely varying over the cervical vertebral column. Other differences between *Australodocus* and *Tornieria* (e.g. shape of the anterior condyle and angle of the medial ramus of the centro-prezygapophyseal lamina) may also result from distortion or differences in their positions in the cervical vertebral column. However, the high incongruence in vertebral elongation cannot be explained by serial, ontogenetic or diagenetic modifications.

Two recently rediscovered posterior cervical vertebrae of *Tornieria* (skeleton k) that were not described by Remes (2006) support this argument. These elements lack the autapomorphies of *Australodocus* listed above, but reveal additional differences. Most importantly, in contrast to *Australodocus*, they show no pneumatization of the dorsal side of the parapophysis, the neural spine summits are more anteriorly positioned, and the posterior centrodiapophyseal lamina is perfectly horizontally orientated and not inclined as in *Australodocus*. These vertebrae fully support the generic differentiation of *Tornieria* and *Australodocus*, but a full description and comparison will be published elsewhere.

In summary, with the data at hand there is no alternative explanation of how the vertebrae from Tendaguru site G may fit into *Tornieria*; as a result, a generic-level differentiation of the new sauropod from *Tornieria* is justified. An important consequence of this conclusion is that the customary reference of isolated, undiagnostic diplodocid material from Tendaguru and other Upper Jurassic East African sites to *Tornieria africana* is no longer valid. These elements may also belong to *Australodocus*, or even

TEXT-FIG. 7. Comparison of diplodocid mid-cervical vertebrae in right lateral view. Not to scale; the vertebrae are drawn to the same posterior centrum height to show differences in relative elongation. A, fifth cervical vertebra of the possible basal diplodocid *Suuwassea*, redrawn from Harris and Dodson (2004). B, seventh cervical vertebra of *Apatosaurus louisae*, redrawn from Gilmore (1936). C, seventh cervical vertebra of *Diplodocus longus*, redrawn from Hatcher (1901). D, eighth cervical vertebra of *Barosaurus lentus*, redrawn from McIntosh (2005). E, mid-cervical vertebra of *Tornieria* sp., redrawn from Janensch (1929a). F, mid-cervical centrum of *Tornieria africana* k 3. G, sixth (?) cervical vertebra of *Australodocus bohetii* MB.R.2455 [G 70].

TABLE 2. Measurements (in mm). MB.R.2455 [G 70] is the holotype vertebra, MB.R.2454 [G 69] the paratype vertebra of *Australodocus bohetii*; MB [k 3] comes from a referred partial skeleton of *Tornieria africana* (Remes 2006). Abbreviations: CL, centrum length; ACW, anterior centrum width; PCW, posterior centrum width; PCH, posterior centrum height; TL, total length; TH, total height. *Asterisks mark incomplete measurements due to breakage.

Specimen		CL	ACW	PCW	PCH	TL	TH
Australodocus bohetii	MB.R.2455	262	72	81	*55	334	195
	MB.R.2454	304	77	84	76	*342	246
Tornieria africana	MB [k 3]	472	80	87	81	*–	*–

another diplodocid, and should be classified as Diplodocidae indet. (Remes 2004).

The holotype and paratype material of *Australodocus* shows similarities to *Barosaurus* in some respects and to *Diplodocus* in other ways (e.g. in proportions), which is consistent with its identification as a diplodocine. However, the combination of a shelf-like pleurocentral lamina, a relatively low elongation index, broadened parapophyses, and a centroprezygapophyseal lamina with a markedly robust lateral ramus, has not been found in the mid-cervical vertebrae of any diplodocid described so far. A reduced pleurocoel, a strongly posteroventrally inclined ridge behind the anterior condyle, a prominent peg-like process on the ventral surface of the prezygapophysis that extends further anterior than the prezygapophysis itself, and an anteriorly open, triangular pneumatic cavity ventral to the prezygapophysis (which is enclosed by an extended prezygodiapophyseal lamina and the lateral ramus of the centroprezygapophyseal lamina) are characters not described or illustrated for any other member of the diplodocid clade, and are therefore regarded as autapomorphic for *Australodocus*. Interestingly, the pneumatization of the centrum is reduced, although the neural arch was invaded by several accessory air sacs, especially prominent in the paratype vertebra. In general, the mode of pneumatization of the neural arch seems to be different from *Apatosaurus*, *Barosaurus* and *Diplodocus* (Wedel 2003, 2005). This may hint at different adaptational pathways between Laurasian and Gondwanan diplodocids, but the data are still too sparse to draw any definite conclusions.

Palaeoecology and palaeobiogeography

The presence of a second diplodocid in the Tendaguru Beds is not surprising. Several sites in the contemporaneous North American Morrison Formation have yielded three or four diplodocids plus several other neosauropods (e.g. Foster 2001, 2003). Although the palaeoenvironments of the Morrison Formation and Tendaguru were different (see 'Geological setting'; Aberhan *et al.* 2002; Engelmann *et al.* 2004; Rees *et al.* 2004; Turner and

Peterson 2004), this high diversity shows that sauropods were able to specialize in several ecological niches instead of indiscriminately consuming any available foliage; otherwise the environment would probably not have been able to support a high number of giant herbivores. In this regard, one of the key feeding adaptations of the sauropods was their long neck (Upchurch and Barrett 2000; Wilson 2005). Presumably, its relative length, among other factors, played an important role in niche partitioning in this group (Calvo 1994; Barrett and Upchurch 1995, 2005; Stevens and Parrish 1999, 2005*a*, *b*; Christiansen 2000; Foster 2001; Christian 2002; Rauhut *et al.* 2005). *Tornieria* is very similar in body design to *Apatosaurus*, *Diplodocus* and *Barosaurus* (Remes 2006), and it is highly probable that *Australodocus* retained the general design of diplodocids, albeit with a relative neck length more similar to that of *Diplodocus* than to *Barosaurus* and *Tornieria*. In Tendaguru, high browsing (*Brachiosaurus*; Christian 2002) and low browsing (*Dicraeosaurus*; Janensch 1929*c*; Rauhut *et al.* 2005) sauropods are relatively well represented. The North American diplodocids have been interpreted, in terms of sauropod standards, as medium level browsers (Stevens and Parrish 1999, 2005*a*, *b*). Considering phylogenetic inference, the East African representatives of this clade possibly filled a similar ecological niche.

Finally, the recognition of a second Tendaguru diplodocid that is unknown from the Morrison Formation supports the idea of an early diversification of the Diplodocoidea prior to the separation of the northern and southern landmasses in the late Middle Jurassic, as proposed by Remes and Rauhut (2005). Palaeogeographical reconstructions (Smith *et al.* 1994; Golonka *et al.* 1996; Ford and Golonka 2003) and anatomical differences among known taxa (Paul 1988; Remes 2006) suggest that faunal exchanges in the Late Jurassic did not occur. The new Tendaguru diplodocine *Australodocus bohetii* indicates once more that Gondwanan diplodocids were distinct from their North American counterparts, and not Morrison fauna immigrants (Remes and Rauhut 2005; Remes 2006). Instead, it is probable that both faunas had a separate evolutionary history since the Callovian (Remes and Rauhut 2005; Remes 2006). This result

modifies somewhat the model of sauropod diversity over time calculated by Upchurch and Barrett (2005) and Barrett and Upchurch (2005) (who did not include palaeogeographical data), because it implies that most diplodocid lineages already existed in the Oxfordian. Consequently, the pattern found by Barrett and Upchurch (2005), a decline of sauropods in the Oxfordian followed by a radiation in the early Kimmeridgian, appears to have been less pronounced than previously supposed.

CONCLUSIONS

A second representative of the clade Diplodocidae is recognized in the sauropod material from Tendaguru. Although the material consists only of two successive mid-cervical vertebrae, it is diagnostic for the diplodocid subclade Diplodocinae and can be distinguished from all known diplodocids, including the other Tendaguru form *Tornieria africana*. The new form, *Australodocus bohetii*, is diagnosed by four autapomorphies: (1) a reduced pleurocoel, (2) a strongly posteroventral inclination of the ridge posterolateral to the anterior condyle, (3) an anteriorly facing triangular pneumatic cavity ventral to prezygapophysis that is enclosed by the lateral ramus of the centroprezygapophyseal lamina and an anteriorly extended prezygodiapophyseal lamina, and (4) a prominent, pointed, and laterally keeled prezygapophyseal process that extends further anterior than the prezygapophysis. Additionally, *Australodocus* exhibits a series of proportional differences compared with other diplodocids, including a broadened parapophysis and a centroprezygapophyseal lamina with a pillar-like lateral ramus. *Australodocus bohetii* is the second representative of diplodocids on Gondwana and although only fragmentary, it adds to our understanding of Tendaguru sauropod diversity and of the Jurassic evolution of sauropods on the southern continents in general.

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