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A new sauropod dinosaur from the Lower Cretaceous Cedar Mountain Formation, Utah, USA

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Brontomerus mcintoshi is a new genus and species of sauropod dinosaur from the Hotel Mesa Quarry in Grand County, Utah, USA, in the upper part of the Ruby Ranch Member (Aptian–Albian) of the Lower Cretaceous Cedar Mountain Formation. It is known from at least two fragmentary specimens of different sizes. The type specimen is OMNH 66430, the left ilium of a juvenile individual; tentatively referred specimens include a crushed presacral centrum, a complete and well-preserved mid-to-posterior caudal vertebra, the partial centrum of a distal caudal vertebra, a complete pneumatic anterior dorsal rib from the right side, the nearly complete left scapula of a much larger, presumably adult, individual, and two partial sternal plates. *Brontomerus* is diagnosed by five autapomorphies of the type specimen: preacetabular lobe 55% of total ilium length, longer than in any other sauropod; preacetabular lobe directed anterolaterally at 30° to the sagittal, but straight in dorsal view and vertically oriented; postacetabular lobe reduced to near absence; ischiadic peduncle reduced to very low bulge; ilium proportionally taller than in any other sauropod, 52% as high as long. In a phylogenetic analysis, *Brontomerus* was recovered as a camarasauromorph in all most parsimonious trees, but with uncertain position within that clade. The large preacetabular lobe of the ilium anchored powerful protractor and abductor muscles, but precise interpretation is impossible without functionally related elements such as femora and proximal caudal vertebrae. *Brontomerus* is the eighth sauropod genus named from the Early Cretaceous of North America, and more remain to be described: North American sauropod diversity did not decline catastrophically at the end of the Jurassic as often assumed. The most striking differences between Late Jurassic and Early Cretaceous sauropod faunas in North America is that the former are abundant and dominated by diplodocids, whereas the latter are comparatively scarce—though still diverse—and dominated by macronarians.

Key words: Dinosauria, Sauropoda, Camarasauromorpha, *Brontomerus*, *Brontomerus mcintoshi*, diversity, Early Cretaceous, North America.

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Introduction

The record of Early Cretaceous sauropod dinosaurs in North America was for many years poorly represented, with the only generic names in use being *Astrodon* Leidy, 1865 and *Pleurocoelus* Marsh, 1888, the former represented only by teeth and often considered synonymous with the latter (e.g., Hatcher 1903a; Gilmore 1921; Carpenter and Tidwell 2005). In recent years, this record has been greatly expanded and clarified by the discovery and description of *Sonorasaurus* Ratkevich, 1998; *Cedarosaurus* Tidwell, Carpenter, and Brooks, 1999; *Sauroposeidon* Wedel, Cifelli, and Sanders, 2000a; *Venenosaurus* Tidwell, Carpenter, and Meyer, 2001; *Paluxysaurus* Rose, 2007; and *Abydosaurus* Chure, Britt, Whitlock, and Wilson, 2010. Further material, representing yet more new sauropod taxa, is known and awaits description: for example, two new taxa from the Dalton Wells Quarry, a camarasaurid and a titanosaurian (Eberth et al. 2006: 220); and a titanosaurian from the Yellow Cat Member of the Cedar Mountain Formation represented by an articulated sequence of five presacral vertebrae (Tidwell and Carpenter 2007).

Here we describe a new sauropod taxon which further extends the record of Early Cretaceous North American sauropods. The ilium and scapula of this sauropod were figured, but not described, by Kirkland et al. (1997: 93), who considered them as "comparable to *Pleurocoelus*" (at that time the only known Early Cretaceous sauropod from North America).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; BMNH, the Natural His-

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tory Museum, London, UK; CCG, Chengdu College of Geology, Chengdu, China; CM, Carnegie Museum of Natural History, Pittsburgh, USA; DMNH, Denver Museum of Natural History, Denver, USA; DNM, Dinosaur National Monument, Dinosaur, USA; FMNH, Field Museum of Natural History, Chicago, USA; FWMSH, Fort Worth Museum of Science and History, Fort Worth, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; OMNH, Oklahoma Museum of Natural History, Norman, USA; ZDM, Zigong Dinosaur Museum, Zigong, China.

Anatomical nomenclature.—We follow Upchurch et al. (2004a) in describing scapulae as though oriented horizontally: the coracoid articular surface is designated anterior and the end commonly called "distal" is designated posterior. See Taylor (2009: 787) for a summary of other schemes that have been used. Names of clades are used as summarized in Table 1.

Geological and faunal context

The holotype and referred specimens described herein were collected at OMNH locality V857, known as the Hotel Mesa Quarry (Kirkland et al. 1997: 96–97, fig. 28). One of us (RLC), who had already been working in Lower Cretaceous rocks of the region, was notified about the site through the courtesy of James I. Kirkland, and was guided to it by Bill Hawes of Grand Junction, Colorado, in September 1994. Additional collecting at the site for OMNH was conducted by Randall L. Nydam and James I. Kirkland in March 1995.

OMNH V857 lies on the southwest flank of Hotel Mesa in easternmost Grand County, Utah (see Kirkland and Madsen 2007: fig. 2), about 1.3 km north-northeast of the junction of the Colorado and Dolores rivers (sec. 4, T23S R24E, Dewey 7.5' quadrangle, USGS provisional edition 1985; precise locality data are on file at OMNH and are available to qualified investigators upon request). This site had previously been worked by private collectors; the number, identity, condition, and disposition of the privately collected fossils cannot now be determined. However, given the density of bone still present and exposed, and the fact that the existing quarry was already some 5–6 m long and 3 m deep, it appears that a considerable number of elements were removed from the quarry and that the loss of valuable scientific information has unfortunately been considerable. Bones left exposed by these previous collectors were in various states of disrepair: some had been broken and their pieces used to hold down the remnants of a plastic tarpaulin. The material reported herein was recovered in the course of the two brief OMNH survey/salvage visits to this site.

Stratigraphically, OMNH V857 lies in a sequence of Lower Cretaceous rocks interposed between the Morrison Formation (Kimmeridgian) below and the Dakota Formation (Cenomanian) above. Westward, these rocks are recognized as the Cedar Mountain Formation; eastward, the Burro Canyon Formation. The arbitrary dividing line between these entities is generally placed at the Colorado River (Stokes 1952; Tschudy et al. 1984) which technically places OMNH V857 within the Burro Canyon Formation. However, we will refer to the locality as belonging to the more widely recognized Cedar Mountain Formation, as it is in this formation that comparable specimens are known, and the stratigraphy and sedimentology do not change across the arbitrary border. The most extensive recent applicable stratigraphic work is that of Kirkland et al. (1997, 1999), who recognized five members within the Cedar Mountain Formation (in ascending order): the Buckhorn Conglomerate, Yellow Cat, Poison Strip Sandstone, Ruby Ranch, and Mussentuchit members.

Table 1. Clade names used in this study and the definitions used. For simplicity, specifiers are indicated by genus rather than species; in each case, the type species of the genus is intended. Node-based clades are indicated by "+", branch-based clades by "not".

Clade name	As defined by	Definition
Sauropoda	Yates (2006: 12)	*Saltasaurus* not *Melanorosaurus*
Neosauropoda	Wilson and Sereno (1998: 46)	*Diplodocus* + *Saltasaurus*
Diplodocoidea	Wilson and Sereno (1998: 17)	*Diplodocus* not *Saltasaurus*
Diplodocimorpha	Calvo and Salgado (1995: 14)	*Diplodocus* + *Rebbachisaurus*
Rebbachisauridae	Salgado et al. (2004: 910)	*Rebbachisaurus* not *Diplodocus*
Diplodocidae	Sereno (1998: 63)	*Diplodocus* not *Dicraeosaurus*
Diplodocinae	Taylor and Naish (2005: 5)	*Diplodocus* not *Apatosaurus*
Macronaria	Wilson and Sereno (1998: 49)	*Saltasaurus* not *Diplodocus*
Camarasauromorpha	Upchurch et al. (2004a:306)	*Camarasaurus* + *Saltasaurus*
Camarasauridae	Taylor and Naish (2007: 1555)	*Camarasaurus* not *Saltasaurus*
Titanosauriformes	Wilson and Sereno (1998: 51)	*Brachiosaurus* + *Saltasaurus*
Brachiosauridae	Wilson and Sereno (1998: 20–21)	*Brachiosaurus* not *Saltasaurus*
Somphospondyli	Wilson and Sereno (1998: 53)	*Saltasaurus* not *Brachiosaurus*
Titanosauria	Wilson and Upchurch (2003: 156)	*Andesaurus* + *Saltasaurus*
Lithostrotia	Wilson and Upchurch (2003: 156)	*Malawisaurus* + *Saltasaurus*
Saltasauridae	Sereno (1998: 63)	*Saltasaurus* + *Opisthocoelicaudia*
Opisthocoelicaudiinae	Sereno (1998: 63)	*Opisthocoelicaudia* not *Saltasaurus*

(The Buckhorn Conglomerate Member has a non-overlapping geographic distribution with respect to the Yellow Cat and Poison Strip Sandstone members and may be a lateral equivalent of one or both; see Kirkland et al. 1999: figs. 1, 2) The existing paleontological record from these units is patchy, but there is evidence of three distinct dinosaur faunas from the Yellow Cat (Barremian or older), Poison Strip Sandstone plus Ruby Ranch (Aptian–Albian), and Mussentuchit (Albian–Cenomanian) members, respectively (Kirkland et al. 1997). While spanning a total of some 30 Ma, the faunal record from the Cedar Mountain Formation is punctuated by significant hiatuses (Sames et al. 2010), and fossil horizons that are stratigraphically close may therefore be widely separated in time.

Like most terrigenous Mesozoic units of the Western Interior (see for example Ostrom 1970: 14), the laterally equivalent Cedar Mountain and Burro Canyon formations are enormously variable. At Hotel Mesa, the lowest two (Buckhorn Conglomerate, Yellow Cat) and uppermost (Mussentuchit) members are absent, and only two members of the Cedar Mountain Formation may be recognized: the Poison Strip Sandstone (below) and Ruby Ranch (above) members. Stratigraphically, OMNH locality V857 lies within the Ruby Ranch Member, a few meters below the local contact with the Dakota Formation (see Kirkland et al. 1999: fig. 8). As a working hypothesis, we regard the fossils from the Hotel Mesa site as being Aptian–Albian, and therefore approximately equivalent in age to assemblages from the Cloverly Formation of Wyoming and Montana and the Trinity Group of Texas and Oklahoma (e.g., Ostrom 1970; Winkler et al. 1990; Jacobs et al. 1991; Brinkman et al. 1998; Davis et al. 2008). As elsewhere, the Ruby Ranch Member in this area is comprised predominantly of drab, pale green, and mauve mudstones with abundant carbonate nodules. The fossil horizon, which is mainly sandstone with some pebbles and intermittent, irregular mudstone stringers, is about 40–50 cm thick. Locally, these mudstones contain sparse microvertebrate fossils, often rounded or broken. About 100 kg of this matrix was collected and transported back to the OMNH for fossil extraction using underwater screen washing and associated concentration techniques (Cifelli et al. 1996).

Although the microvertebrate assemblage from Hotel Mesa is neither very diverse nor particularly well represented, it does merit attention as being the only such site of Aptian–Albian age within the Colorado Plateau. A faunal list is presented in Table 2. As is generally the case for such assemblages, a number of aquatic taxa are represented though no remains of Testudines have been recovered yet. Probably two chondrichthyans are present, a hybodontid (possibly *Hybodus*, which was listed in the Ruby Ranch fauna by Kirkland et al. 1999: table 2) and a polyacrodontid, perhaps *Polyacrodus*. The neoceratodontid form genus *Ceratodus*, widespread in Aptian–Albian faunas of North America (see review by Kirkland 1987), is represented by a poorly preserved tooth plate; two actinopterygians are present, one represented by teeth, and ganoid scales probably referable to Lepisosteidae. No mammalian or lissamphibian fossils have been recovered, and Reptilia is represented solely by archosaurians, of which crocodyliforms (three or four taxa, including a species of the widespread taxon *Bernissartia* and unidentified species of Goniopholididae and Atoposauridae) are most diverse. Megafossils of the Hotel Mesa Quarry mainly represent Sauropoda (including many unidentified fragmentary specimens in addition to those described herein); theropods are known by isolated teeth and rare, incomplete postcranial elements. The fauna includes an ornithopod represented by a single non-diagnostic tooth. Kirkland et al. (1999) mentioned the presence in the Ruby Ranch fauna of *Tenontosaurus*, otherwise known from the Cloverly Formation of Wyoming and Montana (Ostrom 1970) and the Trinity Group of Texas and Oklahoma (Langston 1974; Winkler et al. 1997b; Brinkman et al. 1998), based on specimens from an unidentified site on the western side of the San Rafael Swell, Utah. The ornithopod specimen from the Hotel Mesa Quarry, OMNH 27824, probably does

Table 2. Vertebrate fauna of the Hotel Mesa Quarry (OMNH V857), Ruby Ranch Member, Cedar Mountain Formation (?Aptian–Albian), Grand County, Utah.

- Chondrichthyes
  - Ctenacanthiformes
    - Hybodontidae
      - Gen. et sp. indet.
    - Polyacrodontidae
      - ?*Polyacrodus* sp.
- Osteichthyes
  - Order indet.
    - Family indet.
      - Gen. et sp. indet.
  - ?Lepisosteiformes
    - ?Lepisosteidae
      - Gen. et sp. indet.
  - Dipnoi
    - Neoceratodontidae
      - *Ceratodus* sp.
- Reptilia
  - Crocodyliformes
    - Family indet.
      - Gen. et sp. indet.
    - Bernissartiidae
      - *Bernissartia* sp.
    - Goniopholididae
      - Gen. et sp. indet.
    - Atoposauridae
      - Gen. et sp. indet.
  - Theropoda
    - Family indet.
      - Gen. et sp. indet.
  - Sauropoda
    - Camarasauromorpha family incertae sedis
      - *Brontomerus mcintoshi* gen. and sp. nov.
  - Ornithopoda
    - Family indet.
      - Gen. et sp. indet.

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not represent *Tenontosaurus*, but further identification cannot be firmly established at present.

Although the quarry has not been worked in several years, it is not exhausted and may contain additional relevant material (James Kirkland, personal communication, October 2007).

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Camarasauromorpha Salgado, Coria, and Calvo, 1997

Genus *Brontomerus* nov.

Type species: Brontomerus mcintoshi sp. nov., see below.

Etymology: From Greek *bronto,* thunder; Greek *mērós,* thigh; "thunder-thighs", in reference to the substantial femoral musculature implied by the morphology of the ilium. Intended English pronunciation: Bron-toe-MEER-us.

Diagnosis.—As for type and only species (see below).

Brontomerus mcintoshi sp. nov.

Figs. 1, 2, 5–8, 10, 12; Table 3.

Etymology: In honor of veteran sauropod worker John S. McIntosh, whose seminal paleontological work, done mostly unfunded and on his own time, has been an inspiration to all of us who follow.

Holotype: OMNH 66430, a left ilium.

Tentatively referred material: OMNH 66429, crushed presacral centrum; OMNH 61248, mid-to-posterior caudal vertebra; OMNH 27794, partial distal caudal centrum; OMNH 27766, anterior right dorsal rib; OMNH 27761, nearly complete left scapula missing anterior portion; OMNH 66431 and 66432, two partial sternal plates; other fragments as detailed in Table 3.

Type locality: Hotel Mesa Quarry (OMNH locality V857), Grand County, eastern Utah.

Type horizon: Top of the Ruby Ranch Member of the Cedar Mountain Formation (Lower Cretaceous, Aptian–Albian).

Diagnosis.—Preacetabular lobe 55% of total ilium length, longer than in any other sauropod; preacetabular lobe directed anterolaterally at 30° relative to the sagittal plane, but straight in dorsal view and vertically oriented; postacetabular lobe reduced to near absence; ischiadic peduncle reduced to very low bulge; ilium proportionally taller than in any other sauropod—height is 52% of total length, compared with a maximum of 45% in other sauropods. If the tentatively referred ele-

Table 3. Material referred to the camarasauromorph sauropod *Brontomerus mcintoshi* from the Lower Cretaceous Cedar Mountain Formation of Utah.

OMNH specimen number	Description	Length (cm)	Width (cm)	Thickness (cm)
27761	partial scapula, missing anterior part	98	55	?5
27762	large, flat rib shaft	101	7.5	2
27763	rib fragment	63	8	5
27764	rib fragment	60	2.5	2
27765	rib fragment	58	6	3
27766	complete pneumatic rib	76	12	4
27767	dorsal part of rib, flattened	26	17	2
27768	rib fragment	31	6	1.5
27769	fragment of ?ischium	10	5	2.5
27770	rib fragment	14	3.5	1
27771	rib fragment	17	3	2
27772	rib fragment (in two parts)	13	7	2
27773	rib fragment	13.5	4	2
27773	flat scrap	7	5	0.5
27773	flat scrap	11.5	9	1
27774–27783	fragments			
27784	collection of 21 fragments			
27785–27793	fragments			
27794	partial distal caudal centrum			
27795–27800	fragments			
61248	nearly complete mid-caudal vertebra	11	6	5.5
66429	crushed presacral centrum	14	14	3
66430	ilium	40.5	31	8
66430	dorsal fragment of ilium	14	3	1
66430	dorsal fragment of ilium	15.5	9	1
66431	incomplete sternal plate	15	7.5	1.5
66432	incomplete sternal plate	11.5	7	1

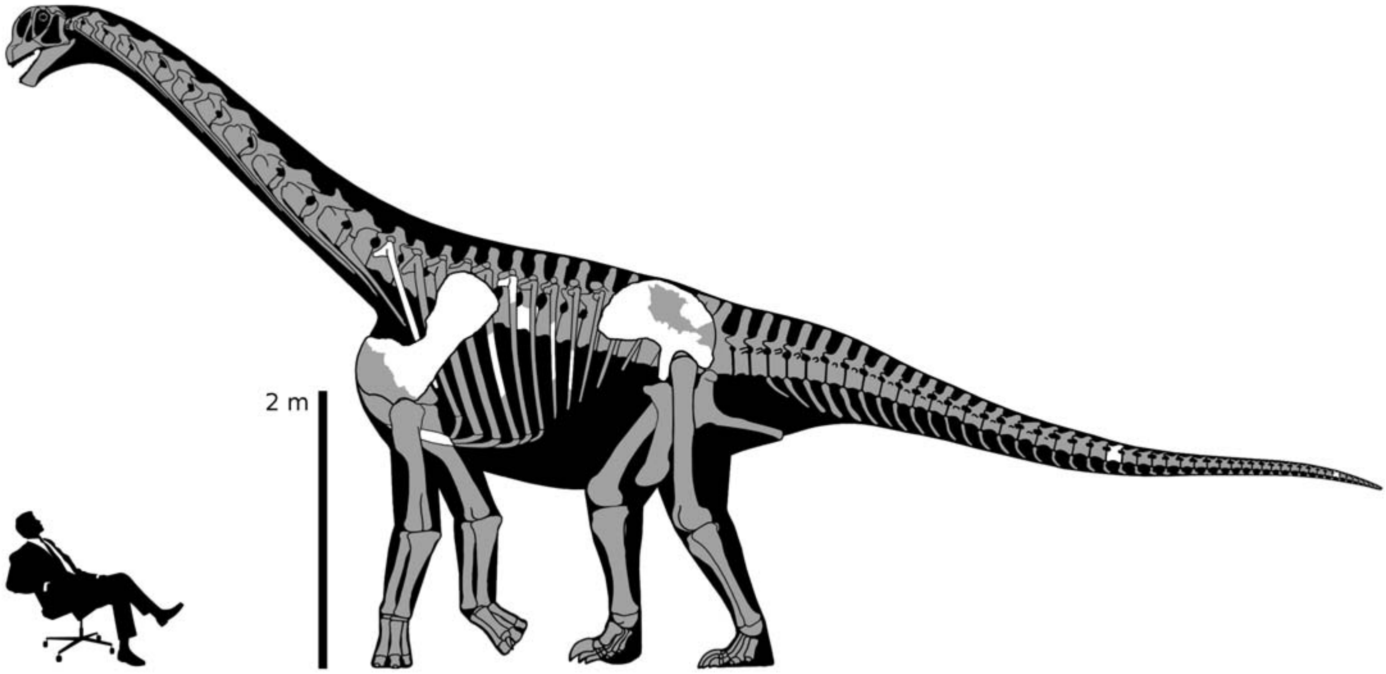

Fig. 1. Skeletal inventory of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, in left lateral view. Preserved elements are white, missing elements are reconstructed in gray. After a *Camarasaurus grandis* reconstruction kindly provided by Scott Hartman.

ments do belong to the same species as the holotype, then the following additional characters also diagnose the new taxon: presacral vertebrae camellate; mid-to-posterior caudal vertebrae with elongate pre- and postzygapophyseal rami, having the postzygapophyseal facets hanging below the level of the ramus; first dorsal rib with expanded, dorsally oriented articular facets, laterally curving shaft, and ventrally directed pneumatic foramen in head; acromion expansion of scapula pronounced and steep, but not forming acromion fossa; dorsal and ventral margins of scapular blade "stepped"; sternal plates crescentic, and three times as long as broad.

Unambiguous autapomorphies distinguishing *Brontomerus* from the root of the polytomy in which it is recovered in the strict consensus of most parsimonious trees in the phylogenetic analysis below: character 184, ratio of centrum length:height in middle caudal vertebrae ≥ 2.0; 185, sharp ridge on lateral surface of middle caudal centra at arch-body junction absent; 212, posterior end of scapular body racquet-shaped (dorsoventrally expanded); 261, in lateral view, the most anteroventral point on the iliac preacetabular lobe is also the most anterior point (preacetabular lobe is pointed); 264, projected line connecting articular surfaces of ischiadic and pubic peduncles of ilium passes ventral to ventral margin of postacetabular lobe of ilium.

Description

This taxon is based on a collection of elements all from the same quarry, all of them consistent with assignment to a single taxon (Fig. 1). However, the elements were not found articulated, and their differing sizes do not permit interpretation as belonging to a single individual. For example, the partial scapula is 98 cm long. Reconstruction after the scapula of *Giraffatitan brancai* (Janensch 1914) suggests that the complete element was about 121 cm long. In *Rapetosaurus* Curry Rogers and Forster, 2001, the scapula and ilium are about the same length (Curry Rogers and Forster 2001: fig. 3) but the ilium of *Brontomerus* is only one third the reconstructed length of the scapula. The quarry therefore contains at least two individuals of widely differing sizes. The smaller, providing the holotype ilium and the referred presacral centrum and sternal plates, is interpreted as a juvenile; the remaining elements probably belonged to the larger, mature individual.

Among the sauropod elements recovered from the Hotel Mesa site, at least three (the caudal vertebra, scapula and ilium) have characters not known in any other sauropod. Since it is not possible to conclusively demonstrate that all three elements belong to the same taxon (and size differences preclude their belonging to a single individual), it is therefore possible that the quarry contains as many as three new taxa. However, since all the informative elements have characters that indicate a titanosauriform identity, we conservatively consider it more likely that only a single new taxon is present. Groups of sauropods of mixed ages are known for several taxa (e.g., Bird 1985; Coria 1994; Bader 2003), so there is a precedent for finding adults and juveniles together. Although we diagnose the new taxon solely on the type ilium, we also tentatively refer the other elements to this taxon and note the additional characters that pertain if this referral is correct; we hope that subsequent work in the Hotel Mesa Quarry or elsewhere in the Cedar Mountain Formation will yield specimens that allow us to confirm or refute this referral.

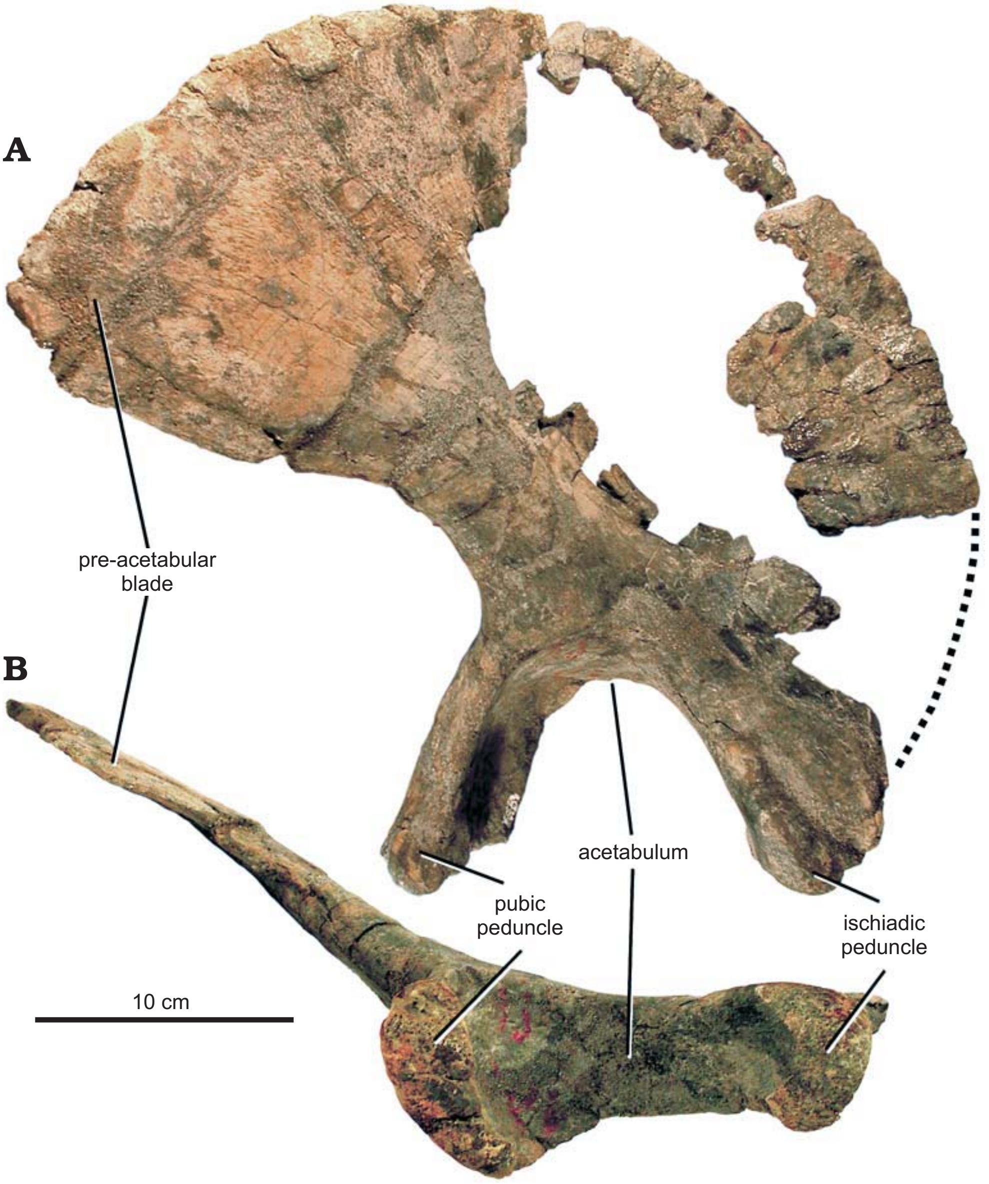

Fig. 2. Left ilium of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, type specimen OMNH 66430 in lateral view reconstructed from the three fragments (**A**), and ventral view (**B**).

The assignment of specimen numbers to the material described here is complex (Table 3). Specimen number OMNH 27773 comprises three elements; OMNH 27784 consists of 21 small fragments of bone, none of them informative; all other elements have their own specimen numbers, in the range 27761–27800 apart from the mid-caudal vertebra OMNH 61248 and the reassigned numbers 66429–66432, for elements extracted from OMNH 27773.

Ilium.—The most informative element is OMNH 66430, a left ilium (Fig. 2), which has therefore been selected as the holotype. The ilium was preserved complete, but lay hidden beneath the scapula, and so was damaged in the field (James Kirkland, personal communication, March 2008). The ilium is preserved in three parts: one provides most of the bone, including the well preserved preacetabular lobe, pubic and ischiadic peduncles and acetabular margin, and the other two provide most of the dorsal margin, giving a good indication of the degree of curvature. The relative positions and orientation of the two smaller fragments can not be definitely ascertained, but they appear to be parts of a single large fragment broken at the point where we have reconstructed them as touching; and if this interpretation is correct then the curvature of the pair indicates which side must be oriented laterally.

The ilium is remarkable in that the preacetabular lobe is relatively larger than in any other sauropod (Fig. 3, Table 4; measurement protocol is illustrated in Fig. 4), the postacetabular lobe is reduced almost to the point of absence, and the ilium is proportionally taller than in any other sauropod. The ischiadic peduncle is reduced to a very low ventral projection from almost the most posterior point of the ilium. The near absence of the ischiadic peduncle cannot be attributed to damage as the iliac articular surface is preserved. Immediately postero-

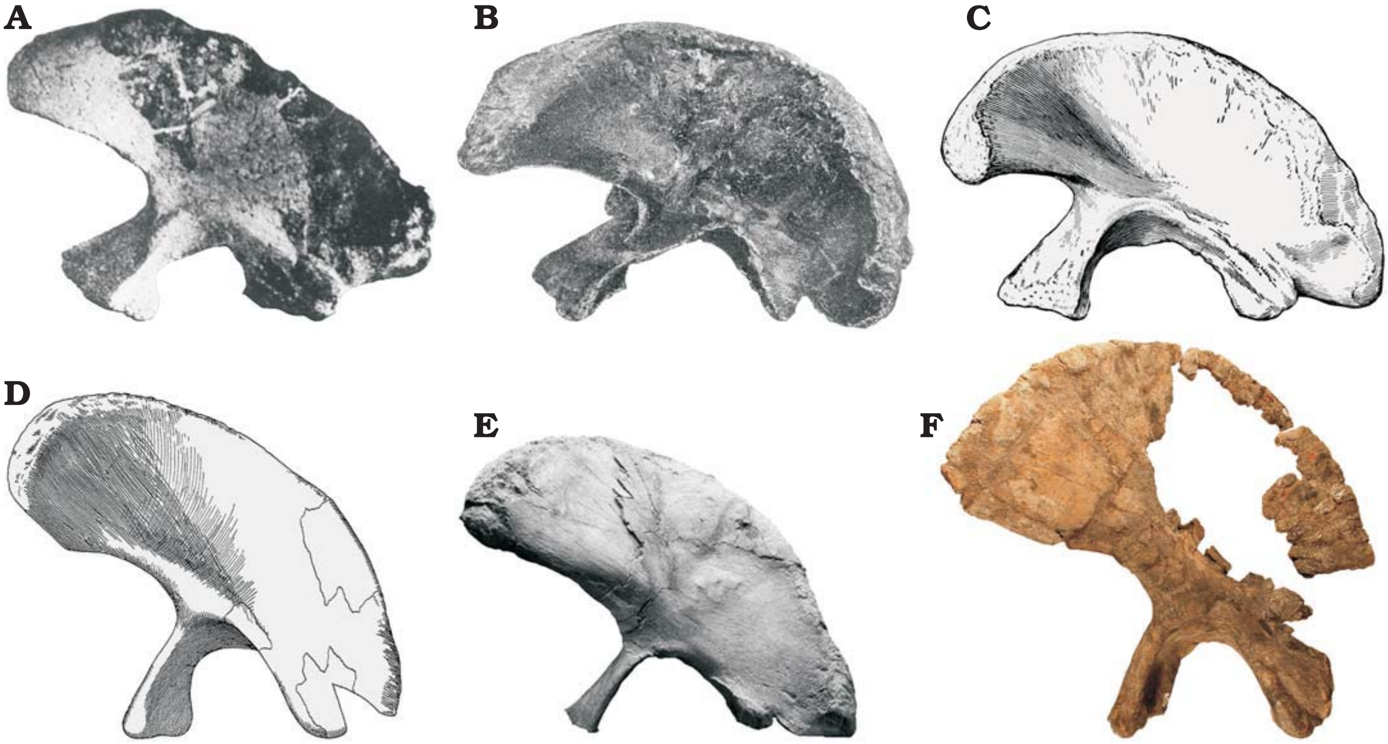

Fig. 3. Ilia of sauropod dinosaurs, scaled to same total length. **A**. *Mamenchisaurus hochuanensis* Young and Zhao, 1972, holotype CCG V 20401, right ilium reversed, modified from Young and Zhao (1972: pl. 6: 1a). **B**. *Diplodocus carnegii* Hatcher, 1901, CM 94, right ilium reversed, modified from Hatcher (1901: pl. 10: 1). **C**. *Camarasaurus supremus* Cope, 1877, AMNH 5761 Il. 1, left ilium, modified from Osborn and Mook (1921: fig. 87). **D**. *Giraffatitan brancai* (Janensch, 1914), HMN J1, left ilium, modified from Janensch (1961: pl. E: 2). **E**. *Rapetosaurus krausi* Curry Rogers and Forster, 2001, holotype FMNH PR 2209, left ilium, modified from Curry Rogers (2009: fig. 39B). **F**. *Brontomerus mcintoshi* gen. et sp. nov. holotype OMNH 66430, left ilium.

dorsal to this surface is a subtle notch between the peduncle and the very reduced postacetabular lobe. This notch and the areas either side of it are composed of finished bone, demonstrating that the great reduction of the postacetabular lobe, too, is a genuine osteological feature and not due to damage. In regard to the proportionally large preacetabular lobe, the ilium of *Brontomerus* resembles that of *Rapetosaurus* (Fig. 3E, Table 4). However, that taxon has a normal postacetabular lobe and is not proportionally tall. In overall proportions, the ilium of *Brontomerus* is more similar to the left ilium HMN J1 assigned to *Giraffatitan brancai* (Janensch 1961: pl. E: 2) which also has a reduced postacetabular lobe —see also Fig. 3D. However, the ilium of *Brontomerus* is proportionally taller than that of *G. brancai*, and its anterior margin comes to a point rather than being smoothly rounded as in that taxon. In *Brontomerus*, the maximum height of the ilium above the acetabular margin, when measured perpendicular to the longest axis, is 52%; in other sauropods examined this proportion does not exceed 45%, and averages 40% (Table 4).

As with many sauropods, the preacetabular lobe of the ilium flares laterally. However, in most sauropods this flaring is progressive, so that in dorsal or ventral view the most posterior part of the preacetabular lobe is nearly parallel with a line drawn between the pubic and ischiadic peduncles, and smooth lateral curvature inclines the more anterior parts increasingly laterally, so that the more anterior part is almost at right angles to this line and the ilium appears smoothly

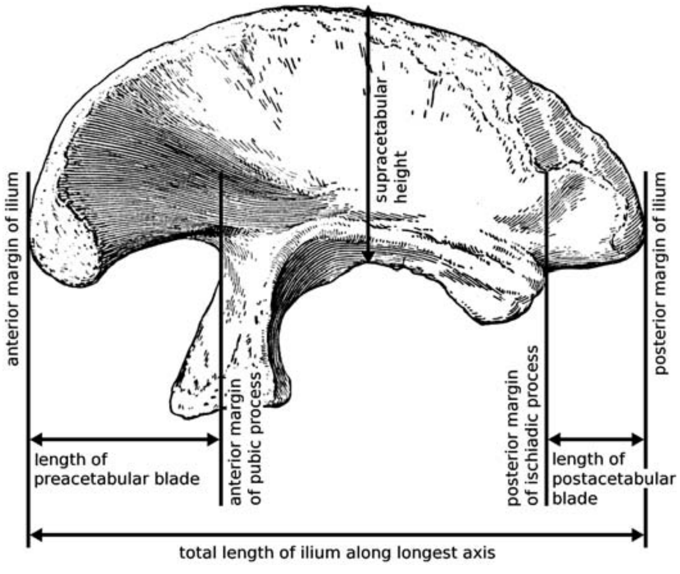

Fig. 4. Measurement protocol for sauropod ilia as illustrated in Fig. 3 and shown in Table 4. Total length is measured along the longest axis of the ilium; lengths of preacetabular and postacetabular lobes are measured parallel to this axis, and extend from the extremity of the lobe to the anterior margin of the pubic peduncle and posterior margin of the ischiadic peduncle respectively. Supracetabular height is measured perpendicular to the longest axis, and extends from the highest point of the acetabulum to the point level with the highest part of the ilium.

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Table 4. Relative measurements of ilia in sauropods. Measurement protocol is illustrated in Fig. 4.

Taxon	Specimen	Reference	Total length (cm)	Length of preacetabular lobe (cm; proportion of total length)		Length of postacetabular lobe (cm; proportion of total length)		Supracetabular height (cm; proportion of total length)	
Mamenchisaurus hochuanensis	CCG V 20401	Young and Zhao (1972: pl. 6: 1a)	102	39	38%	18	18%	41	40%
Diplodocus carnegii	CM 94	Hatcher (1901: pl. 10: 1)	109[1]	41	38%	20	18%	49	45%
Camarasaurus supremus	AMNH 5761 Il. 1	Osborn and Mook (1921: fig. 87)	115	36	31%	19	17%	48	42%
Giraffatitan brancai[2]	HMN Aa 13	Janensch (1961: pl. E: 1a)	119	47	39%	21	18%	46	39%
		Measured by Schwarz-Wings (personal communication, 2009)	114.3	53.5	47%	29.9	26%		
	HMN J1	Janensch (1961: pl. E: 2)	105.5	55	52%	16	15%	37	35%
		Measured by Schwarz-Wings (personal communication, 2009)	107.7	52.8	49%	13.5	13%		
Rapetosaurus krausi	FMNH PR 2209	Curry Rogers (2009: fig. 39)	42	20	48%	7	17%	16	38%
Brontomerus mcintoshi	OMNH 66430	(this study)	40.5	22.3	55%	0	0%	21	52%

[1] Hatcher (1901) did not state the length of the ilium of CM 94 and did not figure that of CM 84. We have assumed that the ilium of the figured specimen CM 94 is the same size as that of CM 84 (Hatcher 1901: 46) and calculated the proportions from the figured specimen.

[2] Janensch's (1961: pl. E) figures of the two ilia of *Giraffatitan brancai* are not executed from an orthogonal perspective: the ilium of HMN Aa 13 is illustrated from a slightly anterolateral position, foreshortening the preacetabular lobe, and that of HMN J 1 from a slight posterolateral position, foreshortening the postacetabular lobe. The true lengths of the two lobes are probably somewhere between the two percentages calculated from the figures: about 45% for the former, and 16% for the latter.

curved in dorsal or ventral view—for example, *Apatosaurus* Marsh, 1877 (Upchurch et al. 2004b: pl. 4: D, E), *Haplocanthosaurus* Hatcher, 1903b (Hatcher 1903a: pl. 5: 1) and *Saltasaurus* Bonaparte and Powell, 1980 (Powell 1992: fig. 17). In *Brontomerus*, by contrast, the blade of the ilium appears to be "hinged"—deflected laterally at a point directly anterior to the public peduncle—so that the preacetabular lobe is straight in dorsal or ventral view, and directed anterolaterally by an angle of about 30° to the sagittal. In this respect, it more closely resembles the ilium of *Camarasaurus* Cope, 1877 (Osborn and Mook 1921: fig. 49) although it differs in other respects.

The *Brontomerus* ilium is laterally compressed, and unlike most sauropod ilia the dorsal margin is not deflected laterally relative to the more ventral part, so that in ventral view it appears very thin (Fig. 2B). It is well established that the long bones of sauropods grow isometrically through ontogeny (Carpenter and McIntosh 1994; Wilhite 1999, 2003; Ikejiri et al. 2005; Tidwell and Wilhite 2005; Taylor 2009) while their vertebrae undergo significant changes in proportions, lamina-

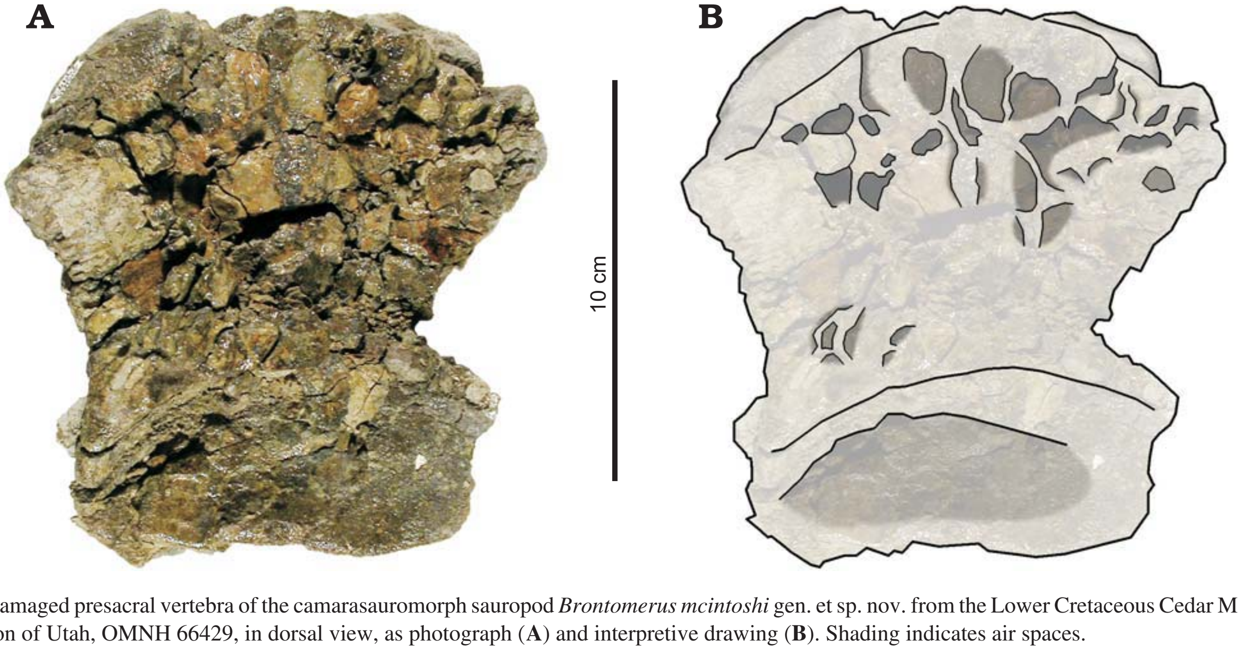

Fig. 5. Damaged presacral vertebra of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, OMNH 66429, in dorsal view, as photograph (**A**) and interpretive drawing (**B**). Shading indicates air spaces.

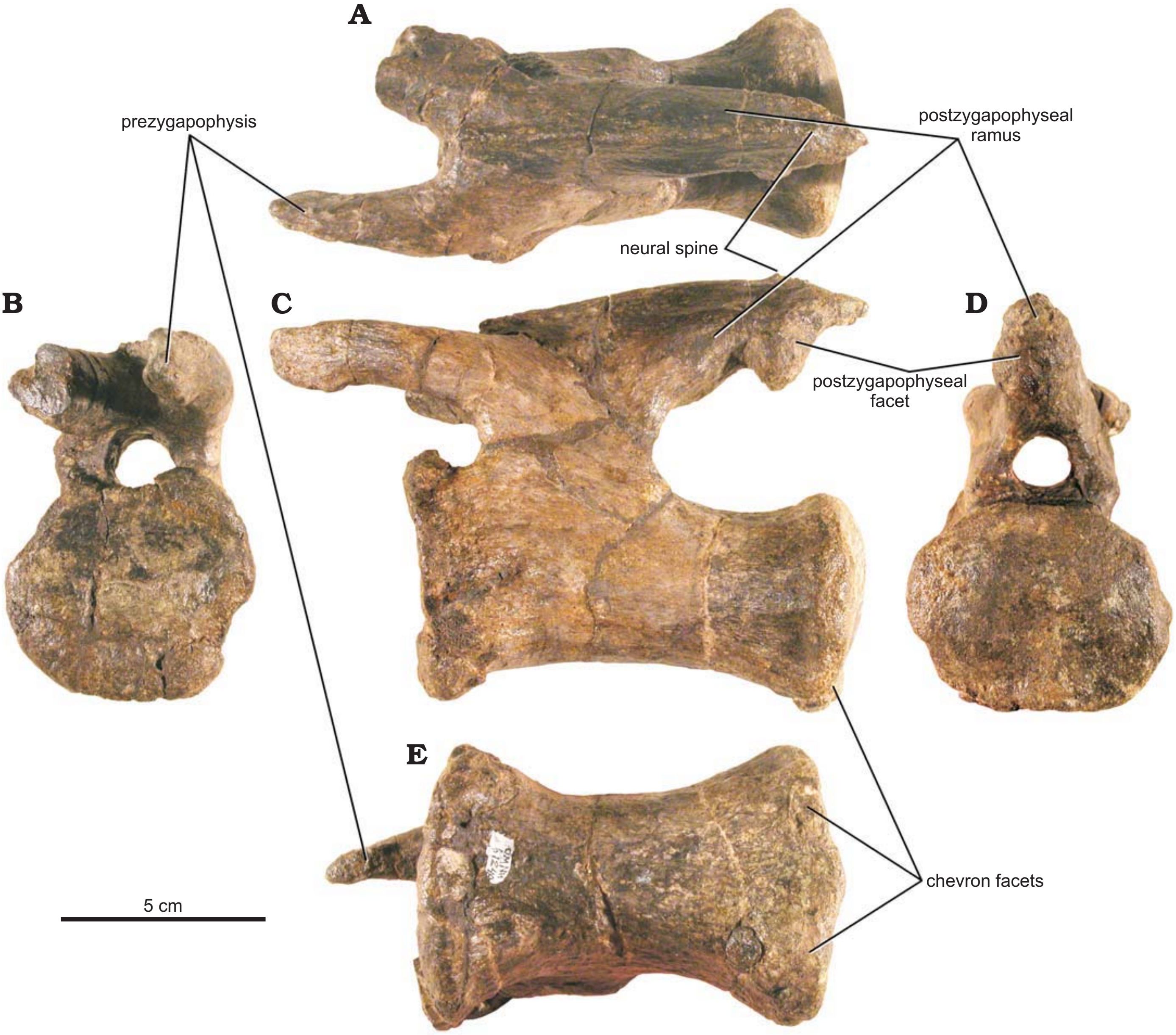

Fig. 6. Mid-caudal vertebra of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, OMNH 61248 in dorsal (**A**), anterior (**B**), left lateral (**C**), posterior (**D**), and ventral (**E**) views.

tion, pneumatic excavations, and neurocentral fusion (Wedel 2003a: 248, b: 352–354). Ontogenetic changes in limb-girdle elements such as the ilium are less well understood due to a paucity of sufficiently well preserved specimens (Ray Wilhite, personal communication, October 2007). Therefore the lateral compression of the *Brontomerus* ilium may be a juvenile character, with the ilium thickening through ontogeny to support the growing weight of the animal, or it may in fact be phylogenetically significant.

Presacral centrum.—A single presacral centrum, OMNH 66429, was recovered (Fig. 5). Unfortunately, preservation is very poor: the neural arch and all processes have been lost, and the centrum has been greatly crushed dorsoventrally so that the remaining part is essentially flat: the element is 14 cm in both anteroposterior length and transverse width, but no more than 3 cm in dorsoventral depth. The small size indicates that this element belonged to a juvenile. The internal structure of the centrum is visible, however, and consists of fine septa dividing a hollow internal space irregularly into many small camellae. This morphology is characteristic of titanosauriforms (Wedel 2003b: 354–355). Highly camellate internal structure has not previously been observed in juvenile sauropod vertebrae, but this may be due to sampling bias: so far, all juvenile sauropod vertebrae that have been studied for internal structure have been those of *Camarasaurus* and diplodocoids, which follow an ontogenetic trajectory in which large, shallow lateral fossae develop into camerae from which smaller accessory camerae and camellae de-

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velop (Wedel et al. 2000a: fig. 11; Wedel 2003b: 349). The Hotel Mesa presacral suggests that camellate vertebrae may have developed differently in titanosauriforms, possibly by in-situ formation of camellae during pneumatization, as occurs in the camellate vertebrae of birds (personal observation, MJW).

Caudal vertebrae.—OMNH 61248 is a distinctive caudal vertebra with elongated pre- and postzygapophyseal rami (Fig. 6). Apart from the tip of the right prezygapophysis, the element is complete and well preserved. While the centrum is only 11 cm in length, the distance from the prezygapophysis to postzygapophysis is 14.5 cm. The centrum is slightly broader than tall (6 cm compared with 5.5 cm anteriorly, 6.5 cm compared with 5 cm posteriorly) and gently waisted. The neural arch is set forward on the centrum but does not reach the anterior margin. The neural spine is so reduced and so strongly inclined posteriorly as to be all but indistinguishable, and is apparent only as a very low eminence above the postzygapophyses. The postzygapophyseal facets themselves are set on the posterolateral faces of a low process that hangs below the main postzygapophyseal ramus. Chevron facets are weakly present on the posterior margin of the ventral surface of the centrum, but not on the anterior margin. The elongation index of 2.2 indicates a mid-to-posterior position in the caudal sequence for this element, as similar centrum proportions do not appear until about caudal 30 in *Giraffatitan brancai* (Janensch 1950: pl. 3).

This vertebra most closely resembles the indeterminate sauropod vertebra BMNH 27500 from the Wessex Formation of the Isle of Wight, figured by Naish and Martill (2001: pl. 33). The Barremian age of that specimen places it about 15 Ma earlier than OMNH 61248. Its neural arch is less elevated than that of the Hotel Mesa specimen, its postzygapophyses project yet farther posteriorly and its prezygapophyses less far anteriorly, and it is very mildly biconvex rather than procoelous; but in other respects, including absolute size, it is a good match for the *Brontomerus* caudal.

Also included in the Hotel Mesa material is OMNH 27794, a partial distal caudal centrum figured by Wedel (2005: fig. 7.7). This centrum is approximately round in cross-section, about 4 cm in diameter, and internally consists of apneumatic cancellous bone.

Ribs.—The Hotel Mesa material contains several dorsal ribs in various states of preservation but no readily identifiable cervical ribs. The dorsal rib elements include the shaft of a large, flat rib (OMNH 27762), portions of several smaller rib shafts (OMNH 27763–27765, 27768, and others), a flattened rib head (OMNH 27767) and most informatively a small complete rib (OMNH 27766, Fig. 7). Despite its excellent preservation and apparent lack of distortion, this element is difficult to interpret. Its shaft is straight for almost its whole length and both articular facets are directed dorsally rather than being inclined medially. The tuberculum is directly in line with the main part of the shaft of the rib, and the capitulum is at an angle of about 30° to it. In these respects the rib resembles the most anterior dorsal rib of the *Diplodocus carnegii* holotype CM 84 (personal observation, MPT; this element was not figured by Hatcher [1901]). We therefore interpret this rib as having probably belonged to the right side of the first dorsal vertebra.

The rib is unusual in other respects, however, most notably that the ventral part of the shaft curves laterally rather than me-

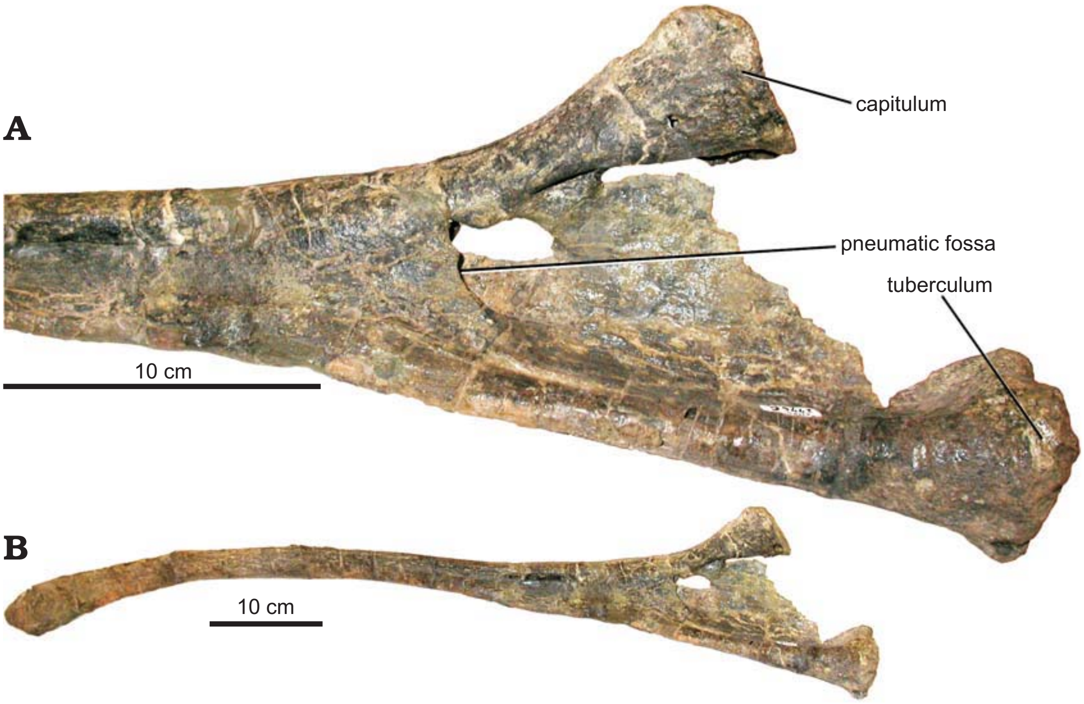

Fig. 7. First right dorsal rib of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, OMNH 27766 in posterior view: head of rib, showing pneumatic invasion of shaft (**A**) and complete rib, showing laterally directed curvature of shaft (**B**).

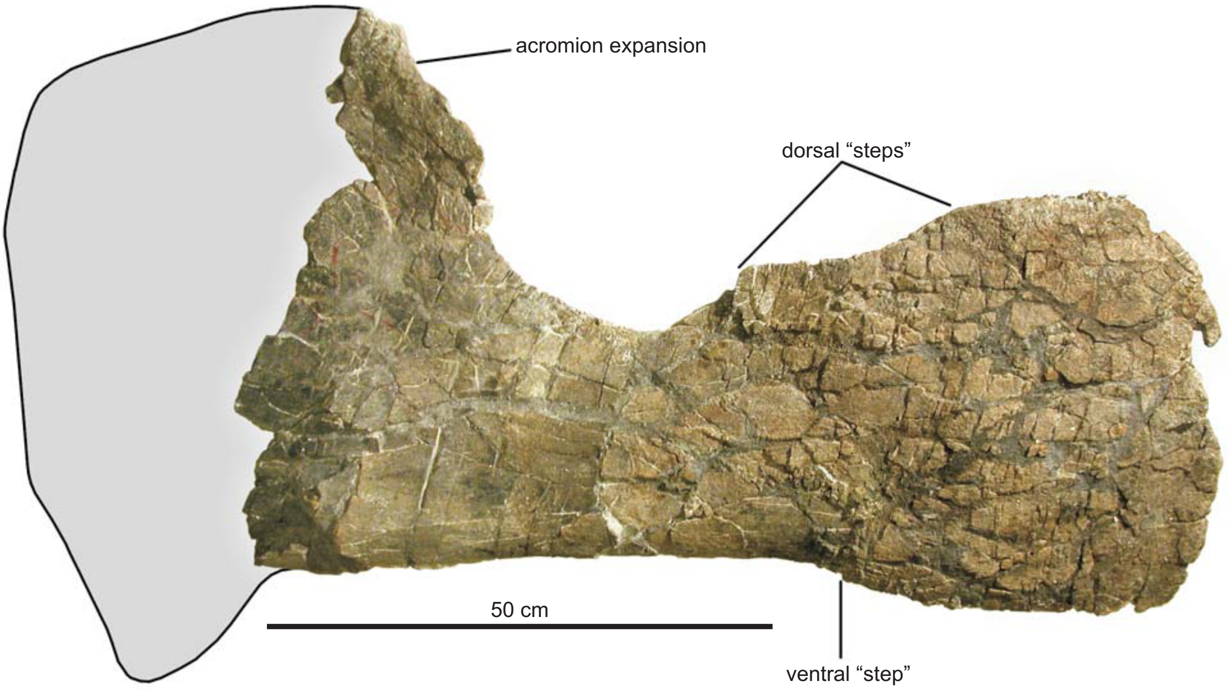

Fig. 8. Partial left scapula of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, OMNH 27761, in lateral view, tentatively reconstructed after *Giraffatitan brancai* HMN Sa 9 (Janensch 1961: pl. 15: 1).

dially. Careful inspection of the bone reveals no indication of distortion or of incorrect reconstruction. It may be possible that in life the thorax was transversely compressed so that the dorsal part of the rib shaft was directed ventromedially and the more ventral part was vertical. Both articular facets are subcircular in dorsal view, and significantly expanded compared with the rami that bear them. On the anterior face of the head, a low ridge arises just below the capitulum and extends down the medial edge of the rib for about 40% of its length.

The head of the rib is also unusual in that a thin sheet of bone connects the rami that support the articular facets, and this sheet extends much farther proximally than in most sauropod ribs. Its precise extent cannot be ascertained due to breakage. The sheet of bone is perforated close to the capitular ramus, and from this perforation a pneumatic cavity invades the shaft of the rib, extending ventrally from within a shallow fossa in the posterior face. Pneumatization of the dorsal ribs is a synapomorphy of Titanosauriformes (Wilson and Sereno 1998), although pneumatic dorsal ribs are also infrequently present in diplodocids (Gilmore 1936; Lovelace et al. 2003, 2008).

Pectoral girdle.—OMNH 27761 is a partial scapula, consisting of the blade and part of the anterior expansion, but missing the glenoid region and the remainder of the anterior expansion (Fig. 8). As preserved, the element is nearly flat; but this may be due to post-mortem distortion, and in any case the most strongly curved part of most sauropod scapulae is the anterior part that is missing from this specimen. The gentle curvature preserved in the posterior part of the blade indicates that the element was from the left side. The bone is surprisingly thin in all preserved parts, never exceeding a few cm, in contrast to for example the scapula of *Camarasaurus supremus*, which is thick even in mid-blade (Osborn and Mook 1921: fig. 74b). This suggests that the glenoid thickening and the acromial ridge may have been located some distance anterior to the preserved portion, and a reconstruction after the proportions of *Giraffatitan brancai* (Fig. 8) suggests that about 80% of the scapula's full length is preserved. The posterior part of the acromion expansion is preserved, however, and is sufficient to show that this expansion was pronounced, so that the maximum dorsoventral height of the scapula was more than two and half times its minimum height, at the midpoint of the blade. The dorsal margin slopes up towards the anterior expansion rather than forming a posteriorly directed "hook" or a distinct acromion fossa between the blade and the acromion process.

The posterior expansion of the scapula is distinctive. In some sauropods, the posterior part of the scapular blade is expanded not at all or only slightly: for example in *Omeisaurus* Young, 1939 (He et al. 1988: fig. 41), *Apatosaurus* (Upchurch et al. 2004b: fig. 4) and *Rapetosaurus* (Fig. 9E). In others, the ventral margin of the scapular blade is straight or nearly so while the dorsal margin is deflected dorsally to create an asymmetric expansion: for example in *Camarasaurus* (Fig. 9C) and *Giraffatitan brancai* (Fig. 9D). In a few sauropods, however, the ventral margin of the blade is also deflected ventrally, to form a "racquet-shaped" posterior expansion. This is seen in rebbachisaurids and some titanosaurians, e.g., some specimens of *Alamosaurus* Gilmore, 1922 (Gilmore 1946: fig. 6). In *Brontomerus*, the posterior part of the scapular blade is expanded in a characteristic manner: the ventral margin is straight except for a posteroventral

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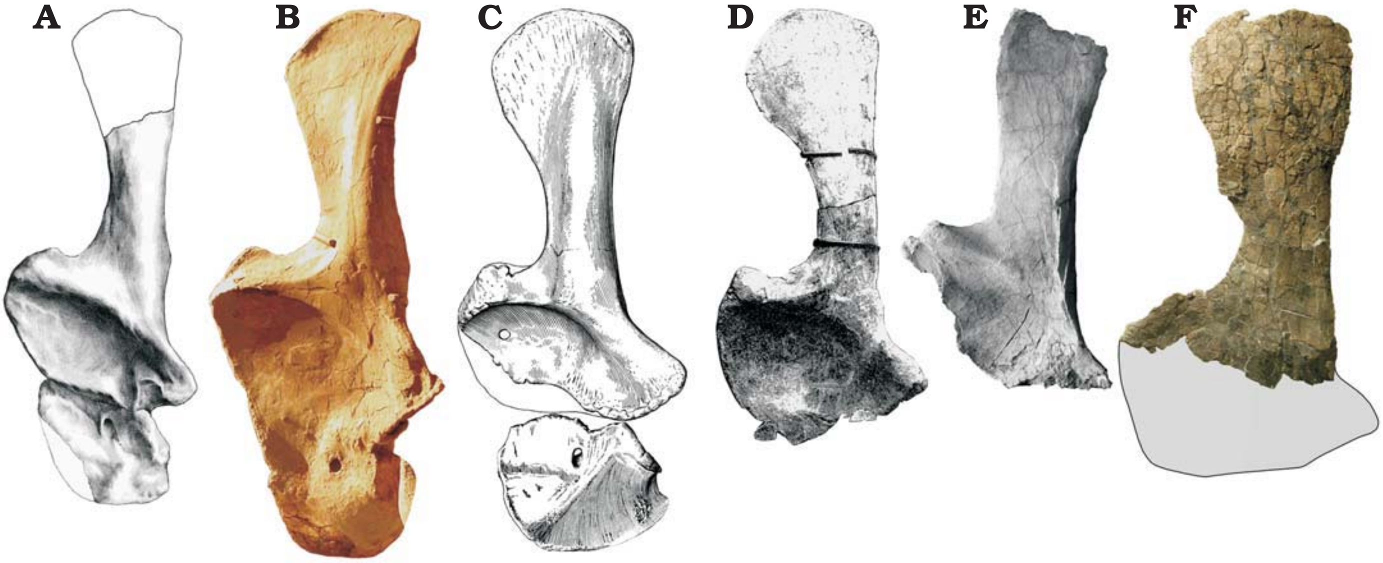

Fig. 9. Scapulocoracoids and scapulae of sauropod dinosaurs, scaled to same length of scapular blade from posterior point of glenoid to posterior margin of blade. **A**. *Mamenchisaurus youngi* Young and Zhao, 1972, holotype ZDM0083, left scapulocoracoid, modified from Ouyang and Ye (2002: fig. 22). **B**. *Diplodocus longus* Hatcher, 1901, USNM 10865, right scapulocoracoid reversed, photograph by MPT. **C**. *Camarasaurus supremus* Cope, 1877, AMNH 5761 Sc. 1, left scapula, and AMNH 5761 Cor. 1, left coracoid, probably associated, modified from Osborn and Mook (1921: figs. 75, 81a). **D**. *Giraffatitan brancai* (Janensch, 1914), HMN Sa 9, left scapula, modified from Janensch (1961: pl. 15: 1). **E**. *Rapetosaurus krausi* Curry Rogers and Forster, 2001, holotype FMNH PR 2209, right scapula reversed, modified from Curry Rogers (2009: fig. 32). **F**. *Brontomerus mcintoshi* gen. et sp. nov. OMNH 27761, left scapula, tentatively reconstructed after *Giraffatitan brancai*.

excursion two thirds of the way along the preserved portion, after which the margin continues parallel to its original trajectory, so that the excursion appears as a gentle "step". The dorsal margin is also "stepped" in this manner, though with two distinct steps rather than one, of which the more anterior is most strongly pronounced. The net result of these features is that the dorsal and ventral borders of the scapula are both straight near the posterior extremity, and that they are subparallel, diverging by only about five degrees in the region just anterior to the rounded end of the posterior expansion. The step in the ventral border is not known in any other sauropod; however, the scapula of *Neuquensaurus* Powell, 1992 has a stepped dorsal border similar to that of *Brontomerus* (Huene 1929 via Glut 1997: 275).

These characters of the scapula must be treated with some caution, however, since this bone appears subject to more variation than any other in the sauropod skeleton: see for example the range of shapes in scapulae of *Giraffatitan brancai* (Janensch 1961: pl. 15: 1–3) and in *Camarasaurus supremus* (Osborn and Mook 1921: figs. 74–80).

Two small, flat elements OMNH 66431 and 66432 are interpreted as partial sternal plates (Fig. 10). The medial edge of each is identifiable due to its rugose texture which formed the attachment site for cartilage joining the plates to each other and to the sternal ribs. The sternals are anteroposteriorly elongate and mediolaterally narrow: when complete, they were probably at least three times as long as broad, as in "*Saltasaurus*" *robustus* Huene, 1929 (Huene 1929 via McIntosh 1990: fig. 16.9L) and proportionally longer than in any other sauropod including *Saltasaurus loricatus* (McIntosh 1990: fig. 16.9; Powell 1992: fig. 30). The sternals are crescentic in shape, the anterior and posterior extremities curving laterally away from the midline. This state was considered a titanosaurian synapomorphy by Wilson (2002: 268) but its distribution is more complex in the current analysis, being synapomorphic for Neosauropoda with losses in Flagellicaudata and *Camarasaurus*.

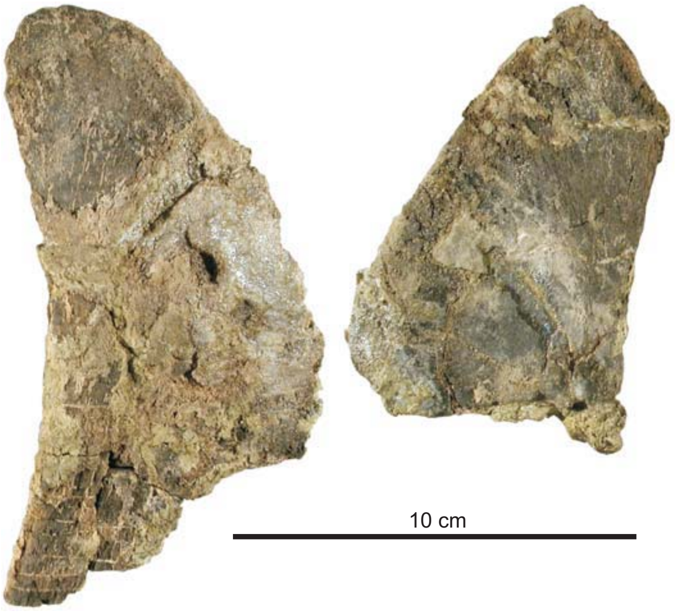

Fig. 10. Partial paired sternal plates of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, OMNH 66431 and 66432, in ?ventral view.

Comparison with other Early Cretaceous North American sauropods

Brontomerus cannot be directly compared with *Astrodon*/*Pleurocoelus*, *Sonorasaurus*, or *Sauroposeidon* due to the absence of overlapping material between these genera, nor with *Abydosaurus* as the overlapping elements have not yet been adequately described (Carpenter and Tidwell 2005; Ratkevich 1998; Wedel et al. 2000b; Chure et al. 2010). Two other sauropod dinosaurs are already known from the Cedar Mountain Formation: *Cedarosaurus* from the Yellow Cat Member and *Venenosaurus* from the Poison Strip Member. *Brontomerus* is from the stratigraphically higher Ruby Ranch Member, and can be distinguished from both of these taxa as discussed below. Since the Yellow Cat Member is Barremian in age, the Poison Strip Member is Aptian, and the upper part of the Ruby Ranch Member (where the Hotel Mesa Quarry is located) is Aptian–Albian, these three sauropods together probably span the last three ages of the Early Cretaceous. *Brontomerus* is also distinct from *Paluxysaurus*, as shown below.

Cedarosaurus.—*Cedarosaurus* is known from a single partial, semi-disarticulated skeleton, DMNH 39045, described by Tidwell et al. (1999). Although much of the skeleton is preserved, relatively few elements overlap with the material of *Brontomerus* described above: only dorsal vertebrae, mid-to-posterior caudal vertebrae, dorsal ribs, partial scapulae, and sternal plates are in common. The single crushed presacral centrum of *Brontomerus* cannot be usefully compared with the dorsal vertebrae of *Cedarosaurus* beyond the observation that the presacral bone texture described by Tidwell et al. (1999: 23) as "numerous matrix filled chambers which are separated by thin walls of bone" is a good match. Tidwell et al. (1999) did not figure either the ribs or sternal plates of *Cedarosaurus*, but photographs supplied by Virginia Tidwell show that its sternals are generally similar in shape to those of *Brontomerus*, though much larger and somewhat less elongate. Tidwell et al. (1999: 25) noted the absence of pneumatic foramina in the two preserved rib heads while recognizing the possibility that anterior ribs might be pneumatic while posterior ribs of the same individual lack this feature. Photographs of a rib head were supplied by Virginia Tidwell and show little resemblance to that of *Brontomerus*, but damage to both articular facets hinders comparison. The preserved portions of *Cedarosaurus* scapulae are from the anterior end and therefore do not greatly overlap with the more posterior preserved portion of the *Brontomerus* scapula; however, the mid scapular region of *Cedarosaurus* differs in the possession of a more pronounced acromion process, less straight ventral border and relatively narrower scapular shaft. Finally, the mid-to-posterior caudal vertebra of *Brontomerus* lacks the distinctive sharp ridge extending along the edge of the neural arch described by Tidwell et al. (1999: 25, fig. 5); but other differences such as its greater elongation and greatly reduced neural spine are not inconsistent with the caudals of *Cedarosaurus*, taking into account that the *Brontomerus* caudal is from a more distal position in the caudal sequence than any of those figured by Tidwell et al. (1999). In conclusion, the preponderance of the scant morphological evidence supports the generic separation of *Brontomerus* from *Cedarosaurus*. Furthermore, the Yellow Cat Member is no younger than Barremian in age, and may be Berriasian–Valanginian (Sames and Madsen 2007), giving *Cedarosaurus* a minimum age of 121 Mya and a maximum age of ~140 Mya, while the Aptian–Albian position of the Hotel Mesa Quarry at the top of the Ruby Ranch Member suggests a much younger age. While this gap does not in itself prove generic separation, it corroborates this conclusion.

Venenosaurus.—*Venenosaurus* was originally described from a single small adult specimen, DMNH 40932, although elements from one or more juveniles were also present in the quarry (Tidwell et al. 2001: 140). Some of the juvenile material was subsequently described by Tidwell and Wilhite (2005), but none of this material overlaps with that of *Brontomerus*, so comparisons with *Venenosaurus* must be made on the basis of the type specimen alone. The overlapping material consists of caudal vertebrae, dorsal ribs, and a left scapula. The "distal" caudal of *Venenosaurus* figured by Tidwell et al. (2001: fig. 11.4C) is similar to the mid-to-posterior caudal of *Brontomerus* in the proportions of the centrum and in the elongation of the posteriorly directed postzygapophyseal ramus. However, the *Venenosaurus* distal caudal has very much shorter prezygapophyses, and a much less tall neural arch which is set forward almost to the margin of the centrum rather than set back 10% of the centrum's length. It also lacks the characteristic ventral process that hangs from the postzygapophyseal ramus in *Brontomerus* and bears the postzygapophyseal facets. The scapula of *Venenosaurus* figured by Tidwell et al. (2001: fig. 11.5A) does not resemble that of *Brontomerus*, having a more curved ventral border, a much less steep ascent of the dorsal border towards the anterior expansion, a less expanded posterior blade, and no sign of the "steps" apparent on both borders of the blade of *Brontomerus*. The illustrated dorsal rib head of *Venenosaurus* (Tidwell et al. 2001: fig. 11.9) differs from that of *Brontomerus*, having a very short tuberculum, a capitulum no broader than the ramus that supports it, and a very different pneumatic excavation which invades the bone in a dorsal direction, penetrating the capitulum, rather than ventrally, penetrating the shaft. These differences of the ribs, however, may be less significant than they appear: the tuberculum of the *Venenosaurus* rib is "somewhat eroded" (Tidwell et al. 2001: 153) which may explain its shortness; the degree of expansion of the capitular head may vary serially, with the *Venenosaurus* rib being from a more posterior position than the *Brontomerus* rib; and pneumatic features tend to vary both serially and between individuals, and even on occasion between the two sides of a single element (e.g., in *Xenoposeidon*: see Taylor and Naish 2007:

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1552–1553). Nevertheless, the balance of evidence strongly indicates that *Brontomerus* is distinct from *Venenosaurus*.

Paluxysaurus.—The internal structure of the presacral vertebrae of *Paluxysaurus* seems to be camellate, like that of *Brontomerus*, based on the referred isolated dorsal centrum FWMSH 93B-10-48 (Rose 2007: 17, 44–45). Some of the "distal" caudal vertebrae of *Paluxysaurus* (Rose 2007: fig. 17) somewhat resemble the *Brontomerus* mid-to-posterior caudal, but none has the very elongate prezygapophyses or ventral process of the postzygapophyseal ramus that characterize the latter, and the *Paluxysaurus* caudals have distinct, dorsally projecting neural spines. The figured ribs of *Paluxysaurus* (Rose 2007: fig. 15) differ from that of *Brontomerus* in every respect save the pneumatic invasion of the rib-head in the direction of the shaft, but these ribs are too badly damaged for useful comparison and in any case are probably from a more posterior position. The prepared scapulae of *Paluxysaurus* (Rose 2007: fig. 20) differ from that of *Brontomerus* in their more concave ventral border, narrower blade, less expanded posterior extremity, and lack of "steps" on the anterior and posterior borders. The sternal plates of *Paluxysaurus* are much less proportionally elongate than those of *Brontomerus*. The ilium of *Paluxysaurus* is not figured, but according to the description it differs in almost every respect from that of *Brontomerus*. In conclusion, significant differences in the mid-caudal vertebrae, scapulae and sternal plates and probably in the ribs demonstrate that these two genera are separate.

Phylogenetic analysis

On the assumption that the referred material belongs to *Brontomerus*, we attempted to establish the phylogenetic position of the new taxon by means of a phylogenetic analysis. We used the matrix of Harris (2006) as a basis, adding the single new taxon to yield a matrix of 31 taxa (29 ingroups and two outgroups) and 331 characters. The only other change made was the rescoring of character 261 for *Rapetosaurus* ("in lateral view, the anteroventralmost point on the iliac preacetabular process") changing it from state 1 ("is posterior to the anteriormost part of the process (process is semicircular with posteroventral excursion of cartilage cap") to state 0 ("is also the anteriormost point (preacetabular process is pointed"). *Brontomerus* could be scored for 20 of the 331 characters, 6% of the total (Table 5).

Following Harris (2006), PAUP* 4.0b10 (Swofford 2002) was used to perform a heuristic search using random step-

Table 5. Character scores for the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah in the matrix used for the phylogenetic analysis of this paper. Apart from the addition of *Brontomerus* and the rescoring of character 261 for *Rapetosaurus*, the matrix is identical to that of Harris (2006). *Brontomerus* is scored only for the listed characters. Conventional anatomical nomenclature is here used in place of the avian nomenclature of Harris (2006).

Character		Score	
184	Ratio of centrum length:height in middle caudal vertebrae	1	2.0
185	Sharp ridge on lateral surface of middle caudal centra at arch-body junction	0	absent
186	Morphology of articular surfaces in middle caudal centra	0	subcircular
187	Ventral longitudinal excavation on anterior and middle caudal centra	0	absent
188	Morphology of anterior articular face of middle and posterior caudal centra	0	amphicoelous/amphiplatyan
189	Position of neural arches over centra on middle caudal vertebrae	1	located mostly or entirely over anterior half of centrum
191	Morphology of posterior caudal centra	0	cylindrical
197	Proximal pneumatic foramina on dorsal ribs	1	present
198	Morphology of proximal ends of anterior dorsal ribs	1	strongly convex anteriorly and deeply concave posteriorly
199	Cross-sectional shape of anterior dorsal ribs	0	subcircular
208	Size of scapular acromion	1	broad (dorsoventral width more than 150% minimum width of scapular body)
210	Morphology of portion of acromion posterior to deltoid crest	0	flat or convex and decreases in mediolateral thickness toward posterior margin
212	Morphology of scapular body	2	posterior end racquet-shaped (dorsoventrally expanded)
221	Morphology of sternal plate	2	elliptical with concave lateral margin
259	Morphology of dorsal margin of ilium body (in lateral view)	1	semicircular (markedly convex)
260	Position of dorsalmost point on ilium	1	anterior to base of pubic process
261	In lateral view, the most anteroventral point on the iliac preacetabular process	0	is also the most anterior point (preacetabular lobe is pointed)
262	Orientation of preacetabular lobe of ilium with respect to axis of body	1	anterolateral in vertical plane
263	Size of ischiadic peduncle of ilium	1	low and rounded (long axis of ilium oriented anterodorsally-posteroventrally)
264	Projected line connecting articular surfaces of ischiadic and pubic peduncles of ilium	0	passes ventral to ventral margin of postacetabular lobe of ilium

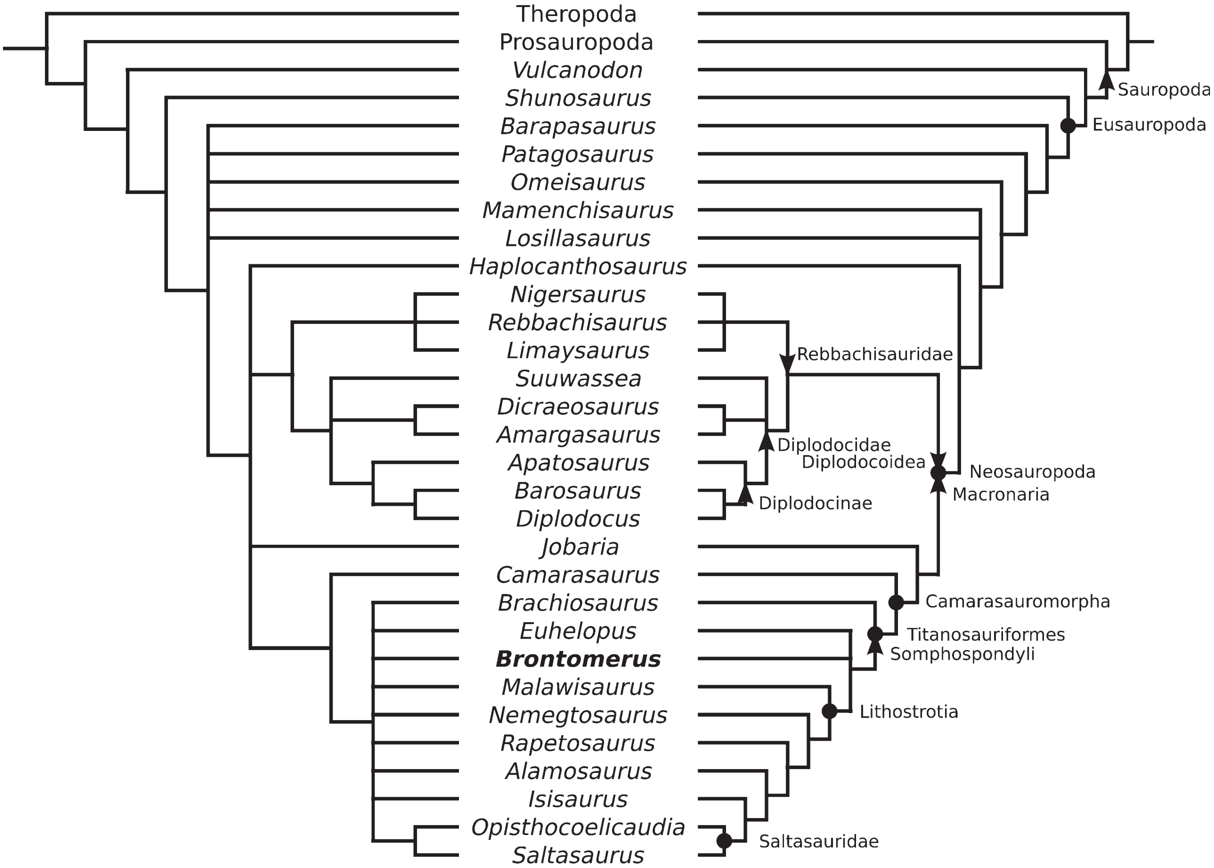

Fig. 11. Phylogenetic relationships of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah, produced using PAUP* 4.0b10 on the matrix of Harris (2006) augmented by *Brontomerus*, having 31 taxa and 331 characters. Left side, strict consensus of 180 most parsimonious trees (length = 788; CI = 0.5228; RI = 0.6848; RC = 0.3581); right side, 50% majority rule consensus.

wise addition with 50 replicates and with maximum trees = 500,000. The analysis yielded 180 equally parsimonious trees with length = 788, consistency index (CI) = 0.5228, retention index (RI) = 0.6848, and rescaled consistency index (RC) = 0.3581.

The strict consensus tree (Fig. 11A) is poorly resolved, with Titanosauriformes collapsing into a broad polytomy within which only Saltasauridae is differentiated. This represents a dramatic loss of resolution compared to the results without *Brontomerus* (Harris 2006: fig. 5A). A posteriori deletion of *Brontomerus*, however, yields a well resolved Macronaria similar to that of Harris's (2006) analysis, with *Camarasaurus*; *Brachiosaurus* Riggs, 1903; *Euhelopus* Romer, 1956; and *Malawisaurus* Jacobs, Winkler, Downs, and Gomani, 1993 as successive singleton outgroups to a group of more derived titanosaurians. This demonstrates that the addition of *Brontomerus* to the matrix does not cause instability in the relationships between these more fully represented taxa, and that it is only the position of *Brontomerus* itself that is unstable. Among the equally most parsimonious positions of *Brontomerus* are as a non-titanosauriform camarasauromorph, a basal titanosauriform, a basal somphospondyl, the sister taxon to *Euhelopus*, a basal titanosaurian, a basal lithostrotian and a derived non-saltasaurid lithostrotian. One further step is sufficient to place *Brontomerus* as a brachiosaurid, a basal (non-camarasauromorph) macronarian, a basal (non-diplodocid) diplodocoid or even a non-neosauropod. Three further steps are required for *Brontomerus* to be recovered as a saltasaurid, specifically an opisthocoelicaudiine.

In the 50% majority rule tree (Fig. 11B) all the standard sauropod clades are recovered. This tree shows the most likely position of *Brontomerus* as a basal somphospondyl, in a trichotomy with *Euhelopus* and Titanosauria.

In order to investigate a possible source of instability, we also re-ran the analysis with the *Rapetosaurus* ilium character restored to the state given by Harris (2006), and found that the value of this character made no difference to the results: all trees are one step longer with the new value, but the topology of all consensus trees (strict, semistrict, and majority rule) is unaffected by the changed scoring.

When *Brontomerus* is scored for the holotype ilium only, and the referred elements are ignored, the strict consensus constrains *Brontomerus* only to be a eusauropod more derived than *Shunosaurus* Dong, Zhou, and Zhang, 1983.

Discussion

Functional anatomy.—The functional significance of the unusual ilium of *Brontomerus* is difficult to interpret due to

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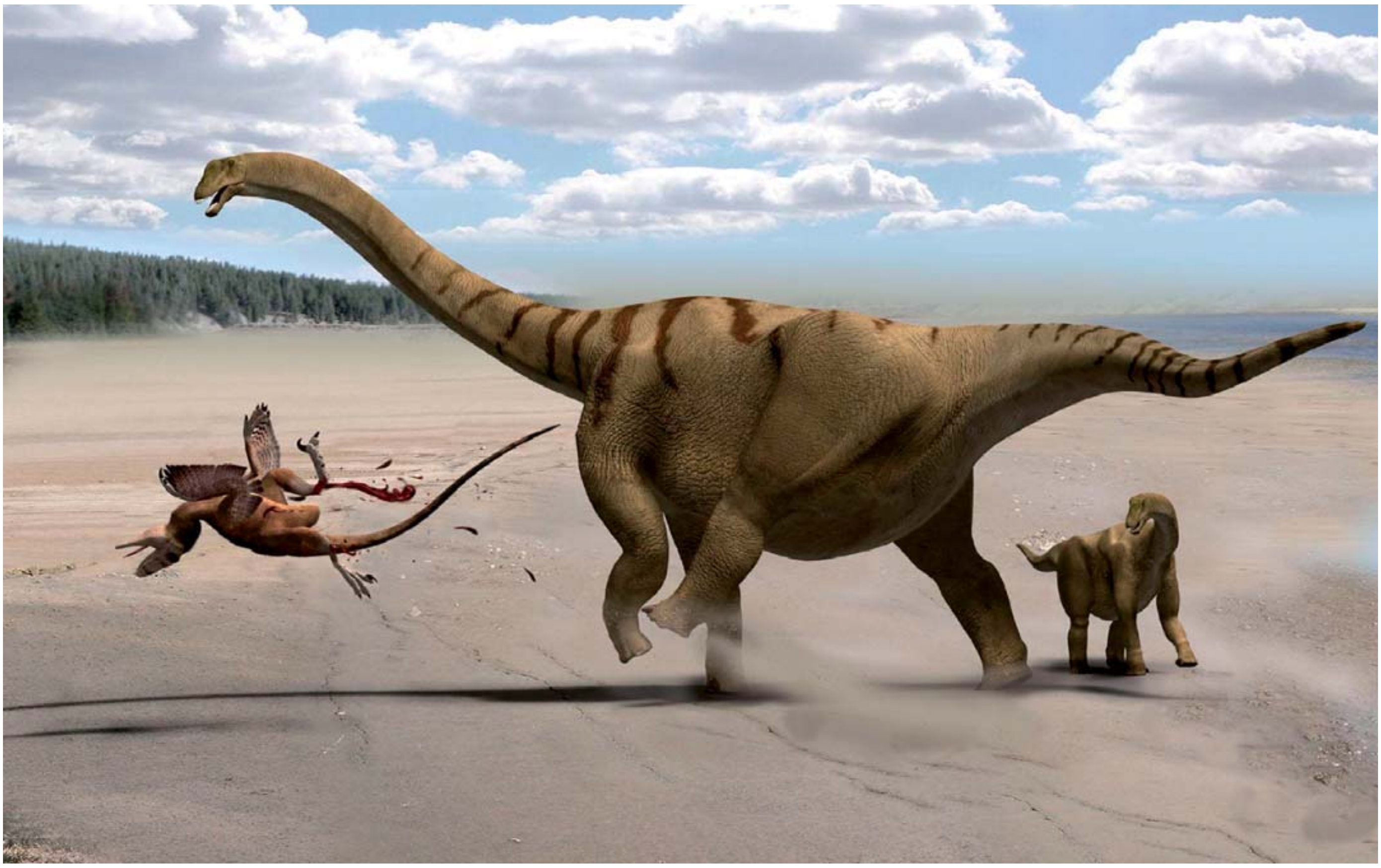

Fig. 12. Speculative life restoration of the camarasauromorph sauropod *Brontomerus mcintoshi* gen. et sp. nov. from the Lower Cretaceous Cedar Mountain Formation of Utah. Adult individual (sized according to the referred scapula) protects juvenile (sized according to the holotype ilium) from a *Utahraptor*: the enlarged femoral protractors may have enabled a powerful kick. Executed by Francisco Gascó under direction from MPT and MJW, reproduced with permission.

the absence of functionally related skeletal elements such as the pubis and ischium, posterior dorsal and anterior caudal vertebrae, and femur. In life, these elements work together as a functional complex, each affecting the function of the others. Some speculation is warranted, however.

The large preacetabular blade of the ilium provides an anchor for large protraction muscles, which would have allowed the leg to be moved forwards powerfully; this is surprising as femoral retraction is required for forward locomotion, requiring large muscles to pull the femur backwards, and the ilium of *Brontomerus* offers almost no attachment area for posteriorly located muscles. The caudofemoralis muscle is the main power generator in locomotion for extant reptiles, and osteological correlates such as the fourth trochanter of the femur indicate that this was also true of non-avian dinosaurs. This muscle connects the femur to the tail, so in the absence of proximal caudal vertebrae and chevrons of *Brontomerus* it is not possible to determine whether the femoral retractors were enlarged in proportion with the protractors. If so, then this increase in musculature would indicate that *Brontomerus* may have been unusually athletic for a sauropod. Another possibility is that powerful femoral protraction was useful for delivering a strong kick (Fig. 12).

As well as protractors, the preacetabular blade of the ilium also anchors abductors (i.e., muscles which draw the leg laterally away from the median plane). These muscles are important for creating abduction torque when standing, and may have facilitated occasional bipedal stance or even limited bipedal walking.

A third possibility is that the proportionally large leg muscles were required to drive unusually long legs. The large anterior expansion of the scapula provides weak additional support for this hypothesis. If this interpretation were correct, *Brontomerus* might have resembled a giraffe in gross morphology.

Did sauropods really decline in the Early Cretaceous of North America?—Apart from *Cetiosaurus oxoniensis* Phillips, 1871, the first reasonably complete remains of sauropods were discovered in the Morrison Formation of the American West in the 1870s and 1880s, and these remains provided the first accurate understanding of the size and bauplan of the clade (Cope 1877, 1878; Marsh 1877). Sauropod remains had previously been assumed to represent gigantic crocodiles (Owen 1859) or pterosaur-bird intermediates (Seeley 1870). Nineteenth century workers also quickly recognized that sauropods were common in the Morrison Formation and essentially absent in the Early Cretaceous “Dakota” Formations,

Table 6. Early Cretaceous North American sauropod diversity. MNI = Minimum Number of Individuals.

Unit		Stage	Taxa	MNI	References
Arundel Formation		Aptian–Albian	*Astrodon* (= *Pleurocoelus*)	2+	Johnston (1859), Leidy (1865), Marsh (1888), Lull (1911), Kingham (1962), Tidwell and Carpenter (2005)
Antlers Formation		Aptian–Albian	*Sauroposeidon proteles*	1	Wedel et al. (2000a, b)
			isolated coracoid	1	Larkin (1910)
			teeth	?	Cifelli et al. (1997a)
Trinity Group		Aptian–Albian	"*Pleurocoelus*"	2+	Langston (1974), Gallup (1989)
Twin Mountains Formation		Aptian	*Paluxysaurus*	4	Winkler et al. (1997a), Gomani et al. (1999), Rose (2007)
			unnamed braincase	1	Carpenter and Tidwell (2003)
Turney Ranch Formation		Albian–Cenomanian	*Sonorasaurus thompsoni*	1	Ratkevich (1998), Curtice (2000)
Cloverly Formation	Unit V	Aptian–Albian	cf. *Brachiosaurus*	3	Wedel (2000)
	Unit VI		?titanosaurian humerus	1	Ostrom (1970)
	Unit VII		unnamed basal titanosauriform	1	Ostrom (1970), D'Emic and Britt (2008)
			cf. *Sauroposeidon*	1	Ostrom (1970), Wedel et al. (2000a, b)
Cedar Mountain Formation	Yellow Cat	Barremian	Dalton Wells titanosaurian	14	Britt and Stadtman (1996, 1997), Britt et al. (1997, 1998, 2004)
			Dalton Wells camarasaur	2	Britt et al. (1997, 2004)
			Dalton Wells brachiosaur	3	Britt et al. (2004)
			Cedarosaurus weiskopfae	1	Tidwell et al. (1999)
			titanosaurian cervicals	1	Tidwell and Carpenter (2007)
	Poison Strip	Aptian	*Venenosaurus dicrocei*	2	Tidwell et al. (2001); Tidwell and Wilhite (2005)
	Ruby Ranch	Aptian–Albian	Long Walk brachiosaur	2	DeCourten (1991)
			CEU brachiosaur	6	Burge et al. (2000), Burge and Bird (2001), Coulson et al. (2004), Bird (2005)
			Brontomerus mcintoshi	2	this study
	Mussentuchit	Albian–Cenomanian	*Abydosaurus mcintoshi*	4	Chure et al. (2010)
			dwarf teeth	?	Maxwell and Cifelli (2000)

which at the time included the Cloverly and Cedar Mountain Formations in addition to the Dakota Formation itself (Witzke and Ludvigson 1994). In fact, the absence of sauropods from Early Cretaceous rocks was so well-established that Marsh (1888) erroneously identified the age of the Potomac Formation (now the Potomac Group) as Late Jurassic based on the presence of the sauropod *Pleurocoelus* (now synonymized with *Astrodon*; Carpenter and Tidwell 2005).

In the following century, the infrequent recovery of sauropod material from Early Cretaceous deposits across North America (e.g., Larkin 1910; Ostrom 1970; Langston 1974) reinforced the perception that the Late Jurassic was the apex of sauropod success, and the Early Cretaceous its nadir. This apparent dichotomy became entrenched in both scientific (Bakker 1978; Behrensmeyer et al. 1992) and popular (Bakker 1986) accounts of the evolutionary history and paleoecology of dinosaurs, including previous publications by the junior authors (Wedel et al. 2000a, b; Wedel and Cifelli 2005). However, a wave of discovery of new material of Early Cretaceous sauropods (Britt and Stadtman 1996, 1997; Britt et al. 1997, 1998, 2004; Winkler et al. 1997a; Gomani et al. 1999; Burge et al. 2000; Maxwell and Cifelli 2000; Burge and Bird 2001; Coulson et al. 2004; Bird 2005; Tidwell and Carpenter 2007) and the description of many new taxa in the past decade (reviewed below and in Table 6) prompts us to reconsider the question of whether sauropods really did decline in the Early Cretaceous of North America.

The diversity of Early Cretaceous North American sauropods.—To date, eight sauropod genera have been described from the Early Cretaceous of North America: *Astrodon*, including *Pleurocoelus* (Leidy 1865; Marsh 1888), *Sonorasaurus* (Ratkevich 1998), *Cedarosaurus* (Tidwell et al. 1999), *Sauroposeidon* (Wedel et al. 2000a), *Venenosaurus* (Tidwell et al. 2001), *Paluxysaurus* (Rose 2007), *Abydosaurus* (Chure et al. 2010), and now *Brontomerus* (this paper).

The pool of named taxa will always be only a subset of the taxa that have been or are being studied, and the taxa under study are in turn only a subset of the pool of potentially new taxa that have been discovered in the field, excavated, and prepared. Almost all of the Early Cretaceous North American sauropods that have been recently described or are currently under study were discovered and excavated in the 1990s or 2000s. Sauropod fossils are often logistically challenging to excavate, prepare, manipulate, photograph, and even measure, simply because they are so large and heavy. In our experience the process of preparation and description of a new sauropod can be very protracted compared to the preparation and description of other, smaller vertebrates. The recently named taxa represent the first "graduates" of the ardu-

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ous descriptive process, and many more new taxa will probably be described in the coming decade. These include:

- From the Yellow Cat Member of the Cedar Mountain Formation, a camarasaurid, a brachiosaurid, and a titanosaurian from the Dalton Wells Quarry, all represented by multiple individuals (Britt and Stadtman 1996, 1997; Britt et al. 1997, 1998, 2004).
- From the Ruby Ranch Member of the Cedar Mountain Formation, the Long Walk Quarry brachiosaurid (DeCourten 1991), which is currently under study by Virginia Tidwell and Kenneth Carpenter and may represent a new taxon; and the CEU brachiosaurid, which is represented by remains of at least 6 individuals, including a cervical vertebra 128 cm long, and which is apparently similar to or perhaps even synonymous with *Sauroposeidon* (Burge et al. 2000; Burge and Bird 2001; Coulson et al. 2004; Bird 2005).
- From Unit VII of the Cloverly Formation, numerous vertebrae and appendicular elements of a possibly new basal titanosauriform (interpreted as a titanosaurian by Ostrom 1970), which is currently under study by Michael D'Emic at the University of Michigan, and possibly a second as-yet unidentified sauropod taxon (D'Emic and Britt 2008).

Additional sauropod remains that are extremely incomplete or not diagnostic, and therefore unfit for naming, are known from several formations. Some of these may eventually be referred to existing or forthcoming named taxa, or might attain holotype status following the discovery of more complete material or additional study. This material includes:

- From the Antlers Formation, the isolated coracoid described by Larkin (1910), and isolated teeth (Cifelli et al. 1997a). Available evidence neither supports nor contradicts the possibility that this material pertains to *Sauroposeidon* (for which the coracoid is unknown), although the coracoid does not resemble those of other brachiosaurids, including *Brachiosaurus altithorax* (Riggs 1904) and *Giraffatitan brancai* (Janensch 1950).
- From the Yellow Cat Member of the Cedar Mountain Formation, a series of partial cervical vertebrae of a titanosaurian (Tidwell and Carpenter 2007).
- From the Mussentuchit Member of the Cedar Mountain Formation, numerous teeth similar to those of *Astrodon* that may represent a dwarf titanosauriform (Maxwell and Cifelli 2000).
- From Unit V of the Cloverly Formation, a brachiosaurid very similar to *Brachiosaurus* (Wedel 2000).
- From Unit VI of the Cloverly Formation, a humerus similar to those of titanosaurians (Ostrom 1970).
- From Unit VII of the Cloverly Formation, a very elongate cervical vertebra of a juvenile sauropod that shares several apomorphies with *Sauroposeidon* (Ostrom 1970; Wedel et al. 2000a, b; Wedel and Cifelli 2005).
- From the Trinity Group, the titanosauriform braincase described by Tidwell and Carpenter (2003), and postcranial material from multiple localities that cannot be referred to *Paluxysaurus* with certainty (Langston 1974; Gallup 1989; Rose 2007).

If all of the apparently diagnostic sets of material (first list, above) were named as new genera, the generic diversity of Early Cretaceous North American sauropods could rise from the current total of 8 to as many as 15. On the other hand, some of this undescribed material may eventually be referred to existing genera, and even some of the eight existing genera might eventually be synonymized. For example, the *Sauroposeidon* type material might represent the neck of *Cedarosaurus* or of *Venenosaurus*; in the former case *Sauroposeidon* would become a junior synonym of *Cedarosaurus* and in the latter *Venenosaurus* would become a junior synonym of *Sauroposeidon*. Note however, that no existing evidence supports these hypothetical synonymizations and they seem unlikely given the temporal and geographic distance separating the taxa concerned.

The statistical analysis of Mannion et al. (2010: 17–18) reported that, when apparent diversity is corrected for availability of relevantly-aged rocks, the Early Cretaceous represents a time of low diversity for sauropods. However, their analysis was based only on validly named genera, and as shown here there is evidence for many additional genera that are yet to be formally recognized.

The diversity of Early Cretaceous North American sauropods has traditionally been contrasted with that of the sauropod taxa of the Late Jurassic Morrison Formation, which is reviewed below.

The diversity of Morrison sauropods.—Six well-known genera have been recognized from the Morrison Formation for over a century: *Apatosaurus*, *Barosaurus*, *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, and *Haplocanthosaurus*. Several other taxa that have long been recognized are poorly represented but nevertheless probably valid: *Dystrophaeus*, *Amphicoelias*, and "*Apatosaurus*" *minimus*, which is not referable to *Apatosaurus* and is probably not even a diplodocoid (McIntosh 1990: 398; Upchurch et al. 2004a: 298). In addition, several new taxa have been described in recent decades or are currently under study: *Supersaurus*, *Eobrontosaurus*, *Suuwassea*, and an apparently new diplodocoid announced by Vietti and Hartman (2004). Upchurch et al. (2004b: 307) suggested that *Eobrontosaurus* is referrable to *Camarasaurus* but this assertion was not based on the identification of any shared apomorphies. The holotype is distinct from both *Camarasaurus* and *Apatosaurus* and probably represents a valid taxon (Ray Wilhite, personal communication, May 2008). Finally, at least five Morrison Formation genera have been synonymized in recent years: *Cathetosaurus* is now classified as a distinct species of *Camarasaurus* (*C. lewisi*; McIntosh et al. 1996), *Ultrasauros* and *Dystylosaurus* are both junior synonyms of *Supersaurus* (Curtice et al. 1996; Curtice and Stadtman 2001), *Elosaurus* is a juvenile *Apatosaurus* (Upchurch et al. 2004b), and *Seismosaurus* has been synonymized with *Diplodocus*: as a distinct species, *D. hallorum*, by Lucas et al. (2006), and as the existing species *D. longus* by Lovelace et al. (2008). This leaves a current total of 12 named genera, plus one potentially new genus under study.

Early Cretaceous and Morrison sauropods compared.—If we simply count existing genera, then Early Cretaceous North American sauropods are only two thirds as diverse as their Morrison forebears (8 genera compared to 12). If we include all of the potentially new taxa that are currently under study, the diversity of sauropods in the Early Cretaceous of North America may eventually exceed that of the Morrison (16 genera to 13). However, so simple a comparison of the sauropod faunas of the North American Late Jurassic and Early Cretaceous is misleading, for the following reasons.

First, the North American Early Cretaceous rock units, separately or together, are simply dwarfed by the Morrison Formation. Foster (2003) listed more than 270 vertebrate localities in the Morrison Formation, in Arizona, Colorado, Idaho, Kansas, Montana, New Mexico, Oklahoma, South Dakota, Utah, and Wyoming. Based on the sheer volume and outcrop area of the Morrison Formation, we might expect its vertebrate fauna to appear more diverse than those of the Early Cretaceous units.

Second, the Morrison Formation is exposed along the Rocky Mountains and in part of the Great Basin, whereas the North American Lower Cretaceous units are scattered across the continent, from the Arundel Formation on the eastern seaboard to the Turney Ranch Formation in the desert southwest, and from the Cloverly Formation in southern Montana to the Trinity Group in central Texas. Although there is some evidence for biogeographic differentiation within the Morrison Formation (Harris and Dodson 2004), the Lower Cretaceous units span much more of the continent and much more time. Temporal differences among the Lower Cretaceous dinosaur faunas are well established (Kirkland et al. 1997), and there may have been biogeographic differentiation as well (Jacobs and Winkler 1998; Nydam and Cifelli 2002). Most relevant in this context are the Aptian–Albian assemblages of the Trinity Group, Texas (Winkler et al. 1990) and Oklahoma (Brinkman et al. 1998); and the Arundel Clay facies of the Potomac Group, Maryland (Kranz 1998). On this basis, we might therefore expect the combined fauna of the Lower Cretaceous units to be more diverse than that of the Morrison Formation.

Third, the Morrison Formation and the various Lower Cretaceous terrestrial units do not represent equivalent amounts of time. The Morrison Formation represents about seven million years of deposition, from 155–148 Mya (Kowallis et al. 1998). The most temporally extensive North American Lower Cretaceous unit is the Cedar Mountain Formation, the dinosaur-bearing parts of which span at least 28 million years from the Barremian (126 ± 2.5 Mya; Kirkland and Madsen 2007) to the earliest Cenomanian (98.37 ± 0.07 Mya; Cifelli et al. 1997b). If the Yellow Cat Member of the Cedar Mountain Formation is indeed Berriasian–Valanginian (Sames and Madsen 2007), the Cedar Mountain Formation may span 40 million years or more (albeit with large depositional hiatuses). All of the other Lower Cretaceous units fall into the span of time represented by the Cedar Mountain Formation, which is four to six times as long as that represented by the Morrison Formation. On this basis, we might also expect the faunas of the Lower Cretaceous units, or even that of the Cedar Mountain Formation by itself, to be more diverse than that of the Morrison Formation.

Fourth, the Morrison Formation has been intensively sampled for more than 130 years, and numerous expeditions have gone to the Morrison Formation in the express hope of finding complete skeletons of sauropods. The less spectacular material of the Lower Cretaceous units has drawn much less attention from both paleontologists and the public. The Cloverly Formation has only been intensively sampled since the 1960s, and the Antlers and Cedar Mountain Formations since the 1990s (although earlier collections had been made from all of these formations). The explosive growth of our knowledge of Early Cretaceous sauropods in North America is a direct result of more intensive sampling of all of the North American Lower Cretaceous units in the past two to three decades. This new pulse of collecting is mitigating the collector bias that favored the Morrison Formation, but a serious imbalance still persists and may never be completely alleviated. This is partly because fieldwork in the Morrison Formation has not stopped and probably will not in the foreseeable future, and new sauropods continue to be discovered (e.g., Vietti and Hartman 2004) and described (e.g., *Suuwassea*, Harris and Dodson 2004) from the Morrison Formation.

In summary, four factors bias our perception of sauropod diversity in the Late Jurassic and Early Cretaceous of North America: the Morrison Formation is larger than all of the Lower Cretaceous units combined and has been more intensively sampled and for much longer, but the Lower Cretaceous units span more space and time. It is not clear how these various biases should be weighted. Nevertheless, three major conclusions can be drawn.

First, the North American sauropod fauna shifted from being diplodocoid-dominated during the Late Jurassic, with a low diversity of macronarians, to being exclusively composed of macronarians during the Early Cretaceous. In particular, the Morrison Formation is dominated by diplodocids, which seem to have hit their global peak of diversity during the Kimmeridgian and Tithonian (including *Tornieria* and *Australodocus* in Africa; Remes 2006, 2007) and then swiftly disappeared. No definitive Cretaceous diplodocid is known from anywhere in the world, although other diplodocoid clades (Rebbachisauridae and Dicraeosauridae) persisted on southern continents (Salgado and Bonaparte 1991; Sereno et al. 1999, 2007; Rauhut et al. 2005). Upchurch and Mannion (2009) referred an isolated partial anterior caudal vertebra from the Early Cretaceous of China to Diplodocidae, but this referral has been questioned (Whitlock et al. 2011). Thus the clade Diplodocidae, generally considered successful, seems to have been limited in both time and space (Taylor 2006).

Second, per fauna and per quarry diversity of sauropods is much lower in the Lower Cretaceous than in the Morrison Formation. The Cedar Mountain Formation may eventually have as many as 10 named genera of sauropods, but these are spread across at least three members, each with their own distinct dinosaurian faunas, and no single fauna is yet known to contain more than three sauropod genera. Large quarries in the

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Morrison Formation often have more than one sauropod genus present, and the Marsh-Felch and Dry Mesa quarries each contain five sauropod genera—until recently, more than were known from the entire Lower Cretaceous of North America.

Third, whereas sauropods are the most abundant large vertebrates in the Morrison Formation, they are among the rarest elements in their respective faunas in the North American Lower Cretaceous. The "big six" Morrison Formation genera—*Apatosaurus*, *Barosaurus*, *Brachiosaurus*, *Camarasaurus*, *Diplodocus*, and *Haplocanthosaurus*—are all represented by more than 10 individuals, and *Camarasaurus*, *Diplodocus*, and *Apatosaurus* are represented by close to 100 or more (Foster 2003: table 5). In contrast, the Early Cretaceous sauropods known from the most specimens are the Dalton Wells titanosaurian (14), the CEU brachiosaur (6), *Paluxysaurus* (4), and *Abydosaurus* (4), of which the first two are currently undescribed. Most of the named taxa are known from only one or two individuals.

Summary.—Sauropods are both diverse and abundant in the Morrison Formation, multiple sauropod genera are often found together in a quarry, and these sauropods are mostly diplodocids and *Camarasaurus*. Representatives of other sauropod clades are sparse. In particular, macronarians are not diverse, although *Camarasaurus* is abundant, and titanosauriforms are represented only by *Brachiosaurus*. (*Haplocanthosaurus* may also be a macronarian, having been recovered within this clade by the phylogenetic analyses of Wilson and Sereno [1998] and Upchurch et al. [2004a], but as a non-diplodocimorph diplodocoid by Wilson [2002]. However, it is among the rarest of Morrison Formation sauropods.)

In contrast, during the Early Cretaceous of North America sauropods were relatively rare (at least compared to their Morrison Formation abundance). Although the total diversity of sauropods across all North American Early Cretaceous formations is high, the diversity within each fauna is low, and co-occurrence of multiple taxa at a single locality is the exception rather than the rule. All known Early Cretaceous North American sauropods are macronarians, and most are brachiosaurids or other basal titanosauriforms, although a few titanosaurians and one probable camarasaurid are also present. The implications of these differences for Mesozoic paleoecology, especially energy flow and nutrient cycling in terrestrial ecosystems, are only beginning to be explored (e.g., Farlow et al. 2010).

Earliest Cretaceous sauropods and the fate of Diplodocidae.—Understanding of the history and evolution of sauropods in the mid-Mesozoic has been impaired by the unavailability of rocks from the earliest Cretaceous in many parts of the world. Possibly for this reason, the fossil record of diplodocids is extremely limited, with all known definitive diplodocid genera worldwide having arisen in the Kimmeridgian–Tithonian (Taylor 2006: 137)—although non-diplodocid diplodocoids, notably rebbachisaurids, are known to have persisted well into the Cretaceous. However, it is also possible that, rather than becoming extinct at the end of the Jurassic, diplodocids persisted into the earliest Cretaceous and were only gradually replaced by the macronarian sauropod fauna that characterizes the Cedar Mountain Formation and other North American Lower Cretaceous units.

This idea can be investigated by searching for late-surviving diplodocids in the lowest parts of the Cedar Mountain Formation and in earliest Cretaceous strata outside North America. Until the recognition of the possible diplodocid *Dinheirosaurus* Bonaparte and Mateus, 1999 from the Late Jurassic of Portugal, no diplodocid genus had been named from outside North America, although the type species of *Lourinhasaurus* Dantas, Sanz, Silva, Ortega, Santos, and Cachão, 1998, "*Apatosaurus*" *alenquerensis* Lapparent and Zbyszewski, 1957, was considered by its describers to represent a diplodocid and the referred species "*Barosaurus*" *africanus* Fraas, 1908 was known from Tendaguru in Tanzania. The African "*Barosaurus*" material is now recognised as comprising two distinct new diplodocid genera, *Tornieria* Sternfeld, 1911 (Remes 2006) and *Australodocus* Remes, 2007, both in fact belonging to Diplodocinae, so the existence of Late Jurassic diplodocids is now well established outside North America, with representatives in both Europe and Africa. Both the Portuguese Lourinhă Formation and the African Tendaguru Formation end at the Jurassic/Cretaceous boundary, but other latest-Jurassic formations in Portugal are conformably overlain by Lower Cretaceous strata correlative with the Wealden Supergroup of England. It is in these strata that Early Cretaceous diplodocids may most usefully be sought, and there are signs that diplodocids may indeed have been present in the Wealden: Taylor and Naish (2007: 1560) reported the presence of a large sauropod metacarpal from the Hastings Group of the Wealden which has been identified as diplodocid, and Naish and Martill (2001: 232–234) discussed other putative, though not definitive, Wealden diplodocid material. Thus it seems likely that diplodocids did indeed survive into the Cretaceous, at least in Europe and possibly also in North America, and that their apparent end-Jurassic extinction is actually an artifact produced by the lack of representative strata from the earliest Cretaceous.

Conclusions

Brontomerus mcintoshi is a new genus and species of macronarian sauropod from the Ruby Ranch Member of the Cedar Mountain Formation of Utah. The new taxon is represented by at least two individuals of different sizes, probably a juvenile and an adult. It is clearly separate from all previously known Cedar Mountain Formation sauropods, and is distinguished from all other sauropods by several unique characters of the ilium and the scapula. The new taxon is probably a fairly basal camarasauromorph, although resolution is poor due to the incompleteness of the material. The distinctive characters of the ilium (e.g., huge preacetabular blade, no postacetabular blade, very tall overall, transversely thin) probably have functional significance, but this is difficult to assess in the absence of other pelvic elements, femora and proximal caudals.

The improving record of Early Cretaceous sauropods in North America is extended by the new genus, so that generic-level diversity of sauropods in this epoch now approaches that of the Late Jurassic. The most striking differences between Late Jurassic and Early Cretaceous sauropods in North America is that the former are abundant and dominated by diplodocids, whereas the latter are comparatively scarce and dominated by macronarians. It is currently impossible to determine whether this shift happened suddenly, or gradually over many millions of years in the earliest Cretaceous. It is natural to assume that if the shift was sudden, it happened at the end of the Jurassic, but that is not necessarily the case. The timing and tempo of this faunal shift remain uncertain; future inferences will have to be based on improved understanding of global changes in conditions in the earliest Cretaceous, and careful analysis of faunal changes on neighbouring continents, especially Europe.

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