ORYCTOS, Vol. 2 : 21 - 37, Décembre 1999

NEW SAUROPOD FROM THE LOWER CRETACEOUS OF UTAH, USA

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Abstract : The sauropod record for the Lower Cretaceous is poor in North America and consists mostly of isolated bones. Recently, however, a partial semiarticulated skeleton of a brachiosaurid, *Cedarosaurus weiskopfae* n.g., n.sp, was recovered from the Yellow Cat Member of the Cedar Mountain Formation, Utah, USA. The humeral length is almost the same as the femur, while the dorsal and caudal vertebrae, and the metacarpal all display characters that identify the specimen as brachiosaurid. The forelimb and caudal vertebrae distinctly set it apart from all currently described genera in that family.

A brief review of Early to Middle Cretaceous brachiosaurs sorts through the confusing jumble of taxa that has developed over the years. In North America, most brachiosaurids found in Lower or Middle Cretaceous strata have historically been referred to the genus *Pleurocoelus.* The review illustrates the need for a reexamination of *Pleurocoelus* type material, as well as several specimens referred to that genus. Other material previously assigned to *Pleurocoelus* may yet prove to be the same as *Cedarosaurus weiskopfae*.

Key words: Lower Cretaceous, brachiosaurid, new taxon, South-central United States.

INTRODUCTION

Until recently remains of Cretaceous sauropods in North America have been limited to the advanced titanosaur *Alamosaurus* from the Maastrichtian and widely scattered specimens from the Lower Cretaceous that have been referred to *Pleurocoelus.* During the past decade numerous sauropod specimens have been collected from the Lower and Middle Cretaceous of Utah, Arizona, Texas, and Oklahoma (Britt *et al.*, 1997; Winkler & Jacobs, 1997; Cifelli *et al.*, 1997). These new finds include titanosaurids, brachiosaurids and camarasaurids, but only the brachiosaurid *Sonorosaurus* has been named and described (Ratkevich, 1998).

In 1996, the Denver Museum of Natural History opened a sauropod quarry in Eastern Utah in the Yellow Cat Member of the Cedar Mountain Formation. The single specimen (DMNH 39045) was partly articulated and preserves all major skeletal elements except the skull, cervical vertebrae and sacrum. This specimen represents a relatively small member of the Brachiosauridae. The skeleton was found with many of the dorsal and anterior caudal vertebrae in articulation. The fore and hindlimbs on the right side are almost complete, lacking the fibula and several manus and pes elements. Only the proximal end of the femur was recovered from the left side and it is likely that all other elements were eroded away. This specimen appears to be a fully adult individual, as evidenced by the fusion of the scapulae to coracoids and neural arches to centra.

Depositional Setting

The skeleton lay in a hard, maroon mudstone layer in the Yellow Cat Member of the Cedar Mountain Formation. It unconformably overlies the Brushy Basin Member of the Morrison Formation and underlies the Poison Strip Sandstone of the Cedar Mountain Formation (Kirkland *et al.*, 1997). The Yellow Cat is 20-30 m thick, although locally may thicken to 100 m. Overbank and lacustrine mudstones predominate, although local stringers of lacustrine limestone, lenses of sandstone, and calcareous nodules also occur. The Yellow Cat is most easily separated from the underlying Brushy Basin by the more drab, less variegated color, and by the absence of smectite in the weathered profile.

The skeleton lay prone ventrally, with the scapula-coracoids divergent from one another and the dorsal vertebrae lay articulated on their right side upon them (fig.1).

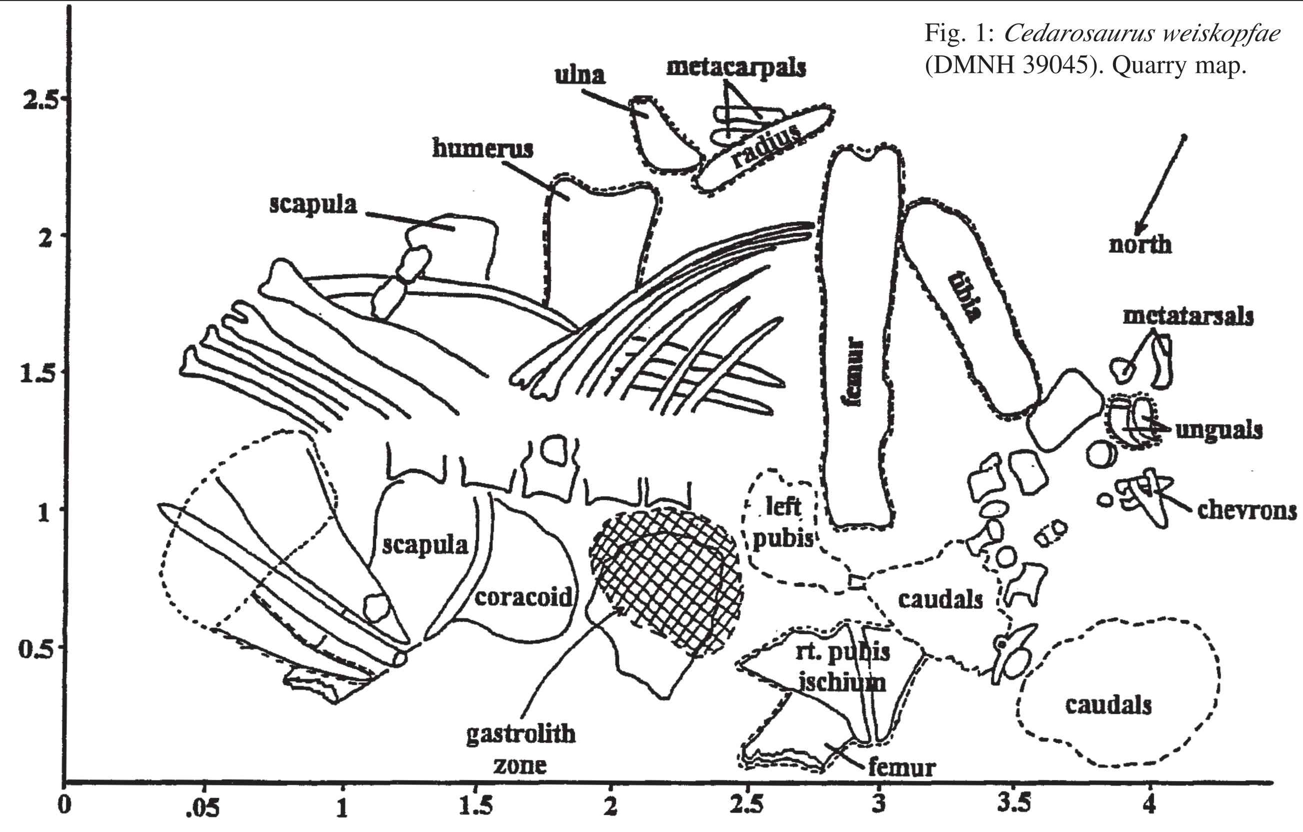


Fig. 1: *Cedarosaurus weiskopfae* (DMNH 39045). Quarry map.

A large number of gastroliths were recovered from a pile in approximately the belly region, showing that the animal remained at least partially intact after death (Sanders and Carpenter, 1998). Many of the bones show extensive erosive damage along a single somewhat irregular plane. Bone fragments on the damaged surfaces suggest that the skeleton was initially partially buried by overbank sediments. Parts of the skeleton still exposed were subject to weathering and trampling. This essentially destroyed the left side of most vertebrae, the distal ends of both scapulae, and the entire lateral side of the right femur. At some later date, the eroded surface was buried by overbank sediments.

Abbreviations : SMU, Southern Methodist University; USNM, United States National Museum United States Museum of Natural History; DMNH, Denver Museum of Natural History.

Systematics
Dinosauria Owen 1842
Saurischia Seeley 1888
Sauropoda Marsh 1878
Brachiosauridae Riggs, 1904
Genus *Cedarosaurus* gen. nov.

Type species
Cedarosaurus weiskopfae sp. nov.

Derivation of name
Named for the Cedar Mountain Formation from which the type specimen was collected.

Diagnosis
As for the type and only species

Cedarosaurus weiskopfae sp. nov.
figures 2-11

Derivation of name
For the late Carol Weiskopf for her hard work in the field and lab.

Holotype
DMNH 39045, a single specimen consisting of eight articulated dorsal vertebrae, 25 caudal vertebrae, several chevrons, proximal portions of the left and right scapulae, left and right coracoids, left and right sternal plates, right humerus, radius and ulna, metacarpal IV, right pubis, partial left pubis, proximal

portions of left and right ischia, partial left femur, right femur, right tibia, three metatarsals, one phalanx, three unguals, ribs, and numerous gastroliths.

Type Horizon and Locality:
Yellow Cat Member, Cedar Mountain Formation (Lower Cretaceous: Barremian); Grand County Utah, United States.

Diagnosis : A medium sized brachiosaurid sauropod whose anterior caudal vertebrae possess deeply concave anterior faces, in contrast to *Brachiosaurus*, *Sonorosaurus*, and *Pleurocoelus nanus*, and which lack well developed hyposphenes, in contrast to SMU 61732; posterior faces of anterior caudal vertebrae are flat to concave, lacking the posterior ball of titanosaurs; mid caudal vertebrae with sharp ridge extending axially along the sides of the neural arch; deltopectoral crest of humerus is placed closer to the midshaft than in *Brachiosaurus*, *Pleurocoelus nanus*, or SMU 61732; humerus/femoral ratio of .98 is similar to *Brachiosaurus* and higher than *Pleurocoelus nanus*; humerus is proportionally more robust than *Brachiosaurus*; radius is quite slender with two ridges beginning at mid shaft, one of which extends along the lower posterior side, the other curves along the lateral side to terminate in a prominent rugosity near the distal end, while in *Brachiosaurus* the ridge is absent; distal end of the radius is subrectangular and flat, rather than oval and lower along the lateral ventral side as in *Pleurocoelus*; ulna with prominent posterior condyle similar to *Pelorosaurus*, unlike *Brachiosaurus*, with a distinct groove separating the distal condyle from the lateral wall, in contrast to *Pleurocoelus nanus* and SMU 61732.

DESCRIPTION

Measurements are given in Tables 1 and 2**.** No skull was recovered with this specimen.

Vertebrae

The cervical vertebrae are missing, as are the first two or three dorsal vertebrae. It is possible these were lost during the erosion episode that damaged many of the bones. Eight dorsal vertebrae were found in articulation lying atop the medial surfaces of the scapulae and coracoids. Although most of the vertebrae consist of centra, three retain portions of the neural arch and right transverse process. All of the centra are strongly opisthocoelos and have medium to large pleurocoels. The anterior balls of the centra contain numerous matrix filled chambers which are separated by thin walls of bone, and resemble those in *Brachiosaurus brancai* (Janensch, 1947: fig. 71). The length of the centra decreases from the anteriormost preserved (26cm) to the posteriormost one (10cm). The vertebrae are unusually short relative to height compared with *Brachiosaurus,* yet are far too long for *Camarasaurus.* The most complete dorsal is the seventh in the series (fig.2).

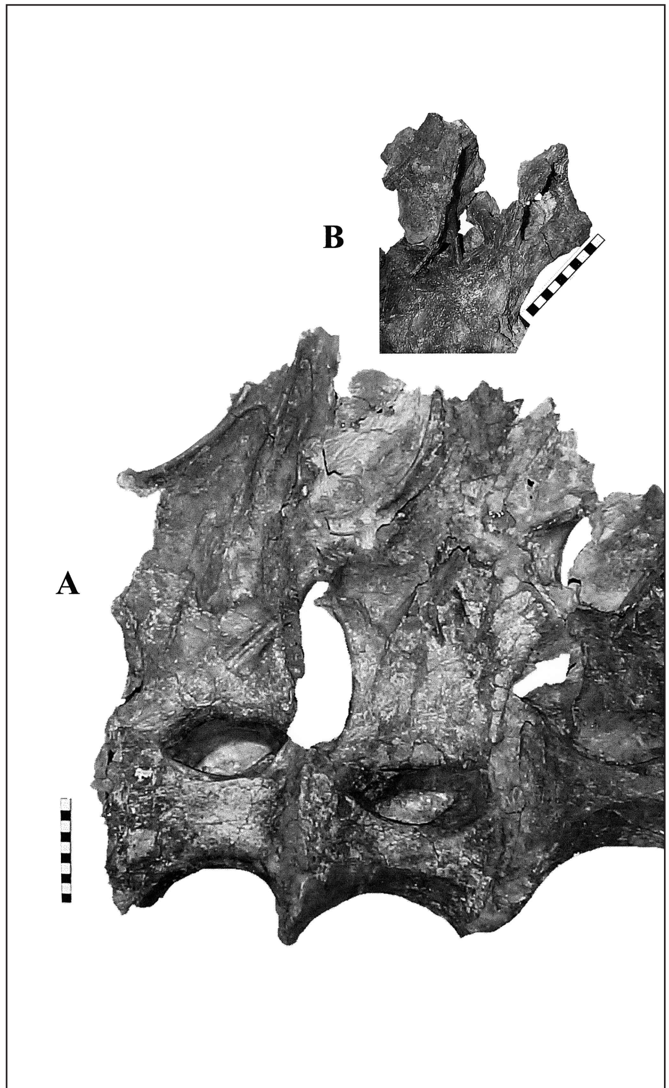


Fig. 2: *Cedarosaurus weiskopfae* (DMNH 39045). A, dorsal vertebrae in lateral view. Note strong infraprezygapophysial lamina and high neural arch. B, detail of base of diapophysial lamina with adjacent foramina.

On the right side, the transverse process is crushed upwards, yet is still attached to the centrum by the diapophysial and horizontal laminae; the laminae divide the process ventrally into anterior and posterior portions. The infraprezygapophysial lamina is stout in this vertebrae, but is less evident in the more anterior dorsals. The base of the diapophysial lamina is divided into thin anterior and posterior branches, and there is no evidence of a centroparapophysial lamina. This contrasts with titanosaurs, where the diapophysial lamina thickens near the base, and strong centroparapophysial laminae are common. Very little of the pre- and postzygapophyses are preserved. It is not known whether hyposphenes were present, due to extensive loss of the neural arch in this region. No grooves or ridges are present ventrally on any of the dorsal centra. Parapophyses are absent on the three anterior centra, indicating that these vertebrae were not the anterior-most dorsals. The estimated position of the dorsal vertebrae is Dorsal 4 through Dorsal 12.

The sacral vertebrae are missing. The caudal vertebrae consist of sixteen anterior and nine middle to posterior caudals; their measurements are given in Table 1. The centra are relatively short, although not as short proportionally as in *Pleurocoelus nanus*, and all lack the pleurocoels found in diplodocids. Several vertebrae are almost complete with coossified caudal ribs on their right sides and neural spines intact. The anterior faces of the first ten vertebrae are deeply concave, while the posterior faces are nearly flat; none display the prominent posterior ball that characterizes titanosaurs. The articular faces of the remaining six anterior caudals display a variety of shapes. Most are bi-concave, although some retain the flat posterior face found in the more proximal vertebrae.

Caudals 1-5 consist of the centra and right caudal ribs only. Unlike *Pleurocoelus nanus*, they are very broad and flat across the ventral side, with little evidence of chevron facets. Four of these anterior caudals exhibit an elongate oval depression just below the caudal rib that is up to 2 cm deep. The depression is not a true pleurocoel, which in diplodocids opens into the centrum. We do not know if this character has generic significance because similar depressions have been found on other caudals recovered from another quarry several kilometers from the *Cedarosaurus* quarry. Similar, although deeper depressions are also reported on *Camarasaurus* caudal vertebrae from the Late Jurassic Dry Mesa Quarry (Curtice, 1996).

Caudals 7-10 are the least distorted and the centra and neural arches form parallelograms in lateral profile. A similar feature is seen in the anteriormost caudal centra of *Brachiosaurus* (Janensch, 1961), as well as in the mid-anterior caudals of *Apatosaurus* (Gilmore, 1936). The lateral and ventral sides of the centra are more constricted than in *Pleurocoelus nanus*, while the anterior and posterior margins are strongly flared (fig. 3). Ventrally, two poorly developed ridges extend anteroposteriorly from the chevron facets. The anterior faces of the centra are subrectangular; that is only somewhat attributable to crushing as evidenced by the caudal ribs, which project caudolaterally with little distortion.

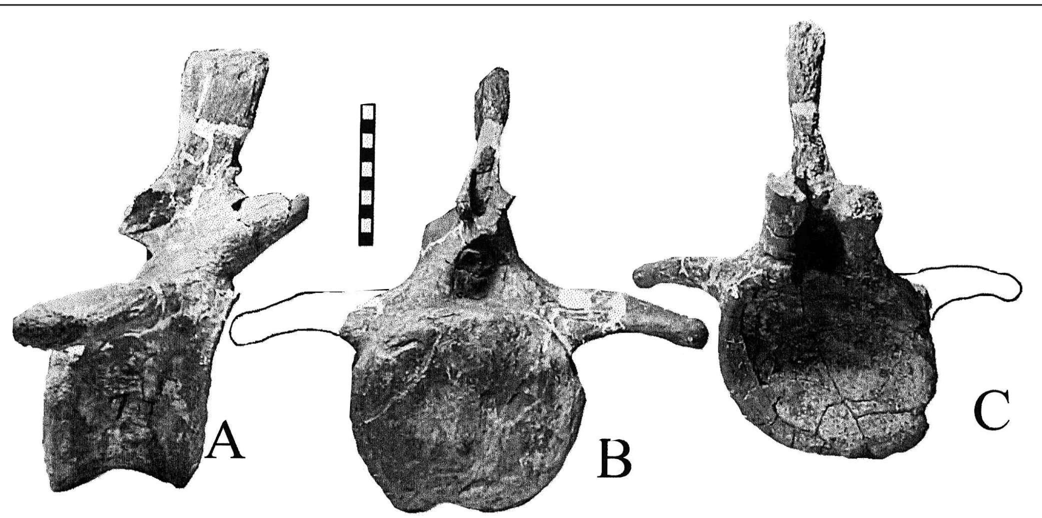


Fig. 3: *Cedarosaurus weiskopfae* (DMNH 39045). Anterior caudal vertebrae. A, lateral view. Note forward lean of neural arch. B. Posterior view. Note flat articular face and absence of hyposphene. C. Anterior view. Note concave articular face and narrow neural spine.

Six middle and posterior caudals have been recovered. Most are missing some or all of the neural spine and arch. The centra of these caudals are longer than tall and show a flared rim on the articular face. Ventrally, the centra are laterally wide and anteroposteriorly concave and have prominent facets for the chevrons. There are no lateral ridges on the centra as are typically found in *Camarasaurus*. The prezygapophyses extend well beyond the anterior face.

The neural arches occupy almost the entire length of the centra in the anterior caudals. Beginning around caudal 11, the posterior edge of the neural arch does not extend more than three-quarters the length of the centra, and only about two-thirds the centrum length on the last caudal present (caudal 25). The neural arches are anteriorly inclined through caudal 12, which is further back on the column than in SMU 61732 and *Brachiosaurus*, and are fully erect by caudal 13 (fig. 4).

Although the pre-and postzygapophyses are missing in many of the vertebrae, enough are preserved to indicate that the prezygapophyses of the anterior caudals extend somewhat dorsally and have subvertically oriented facets. By caudal 12, however, the prezygapophyses project horizontally. The prezygapophyses lack the well defined hypantra seen in SMU 61732. None of the postzygapophyses extend beyond the centra as in *Brachiosaurus* (Janensch, 1961, plate. 2). A slight hyposphene is present below the postzygapophyses of caudal 8, but it is not as developed as in the caudals of SMU 61732. While the neural spines on many of the caudals are incomplete, the first complete one is on caudal 7 and it is short, less than the height of the centrum. All of the preserved neural spines are laterally compressed with very little flaring at the distal end.

Ribs

No cervical ribs were found, although several incomplete dorsal ribs were recovered. Two of these retain portions of the rib heads and clearly show that no pneumatic foramina was present. These foramina are characteristic of brachiosaurs and titanosaurs (Wilson & Sereno, 1998) however, it is unknown if they occur in all dorsal ribs within a specimen, or are confined to the anterior ribs. All of the ribs but one show the usual triangular cross-section. The one exception is wide, flat and paddle or oar shaped. The nearly straight shaft and paddle shape identify it as the first dorsal rib.

The caudal ribs are completely fused to the corresponding centra. These get progressively longer from caudal 1 to caudal 6, then decrease in size to caudal 18. From caudal 19 on to the last preserved (caudal 25), the caudal "rib" is represented by an elongate ridge extending laterally along the base of the neural arch (fig.5).

Fig. 5: *Cedarosaurus weiskopfae* (DMNH 39045). Middle caudal vertebrae. Note elongate ridge along side of neural arch.

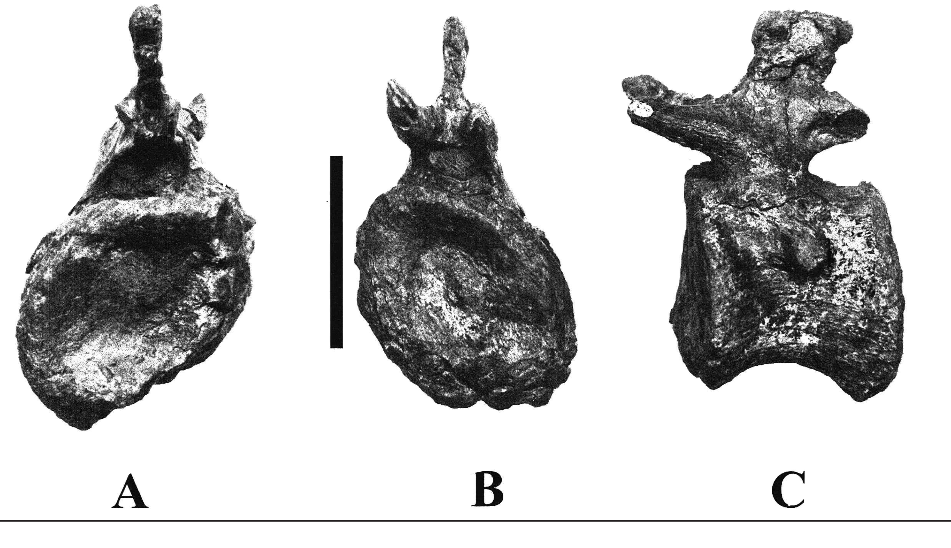


Fig. 4: *Cedarosaurus weiskopfae* (DMNH 39045). Caudal 13.
A. posterior view.
Note concave articular face.
B. Anterior view.
Note concave articular face.
C. Lateral view.
Note fully erect neural arch, with no forward lean.
scale =10cm.

At caudal 6, the horizontal plane of the caudal rib slopes posteroventrally producing a small shoulder where the rib attaches to the centrum. This shoulder is best developed on caudals 7 and 8, is less developed on caudal 9, and is practically absent on caudal 10 where the plane of the rib returns to horizontal. Caudal ribs 7 and 8 show a distinct twist along the shaft, thus, although the plane of the shoulder slopes posteriorly, the distal ends are in the horizontal plane. The peculiar features of these mid-anterior caudals (especially caudals 7 and 8) are not known by us to occur in any other sauropod this far back in the column.

Several partial chevrons were found, but only one is complete. The chevrons are from different parts of the tail and range in size from 22cm in length to 4cm. The anterior chevrons have a very deep haemal canal resembling those in *Brachiosaurus*. The proximal ends are close to one another, but do not bridge over the haemal canal.

Pectoral Girdle

Pectoral elements are not well represented among known Cretaceous brachiosaurids making comparisons difficult. Both scapulae and coracoids, and the sternal plates for *Cedarosaurus* were found in a single plane beneath the articulated dorsals and associated ribs. The distal portions of both scapulae diverge from one another. The scapulae were found adjacent to one another, with the left slightly overlapping the right in a position suggesting that the animal died on its belly (fig.6).

The distal ends of both scapula blades had eroded away soon after initial burial (see discussion above), with the loss of the distal expansion. Both scapulae are coossified with the respective coracoids, with the suture marked as a thickening of bone. The dorsal margin of the acromion is damaged on both scapulae, thus we do not know if the posterodorsal edge formed a “hook” as in *Brachiosaurus* (Janensch, 1961, plate 15). The ventral margin of the right scapula is robust, being approximately 7cm thick at the glenoid and thinning to about 4cm at the preserved portion of the scapular blade. The scapula blade gradually becomes quite thin at the dorsal edge. The glenoid on the right scapula shows extensive damage due to weathering. The right scapula shows periosteal reactive bone on the medial side near the coracoid-scapula suture that is pathological in origin.

The coracoids are taller than long, as they are in *Brachiosaurus*. The coracoid foramina are about 1.5cm in diameter and lie close to the suture with the scapula on the medial side .

Both sternal plates were recovered in close proximity to their coracoids. The lateral margins are not complete, so comparisons with the sternal plates of *Brachiosaurus* are difficult to make.

Forelimb

The forelimb closely resembles that of *Brachiosaurus* in having a long humerus, radius and metacarpal. All of the elements were found in semi-articulation, showing little displacement.

Measurements for the forelimb are found in Table 2.

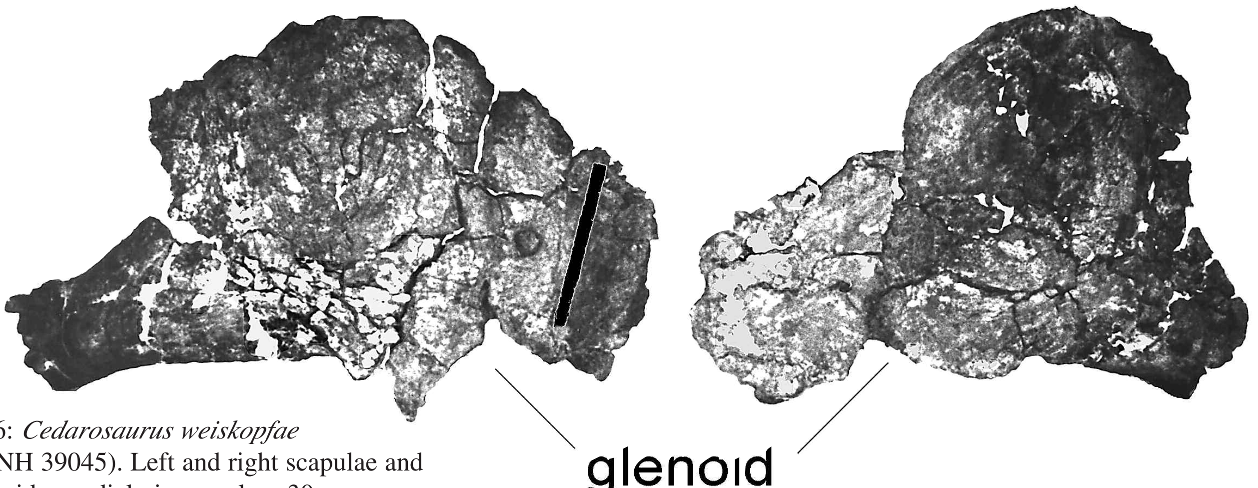


Fig. 6: *Cedarosaurus weiskopfae* (DMNH 39045). Left and right scapulae and corocoids, medial view. scale = 30cm.

The right humerus was found near its glenoid; it is well preserved and nearly complete. The length is nearly equal to that of the femur. The humerus is more robust than *Brachiosaurus* having a proportionally broader shaft (fig.7A).

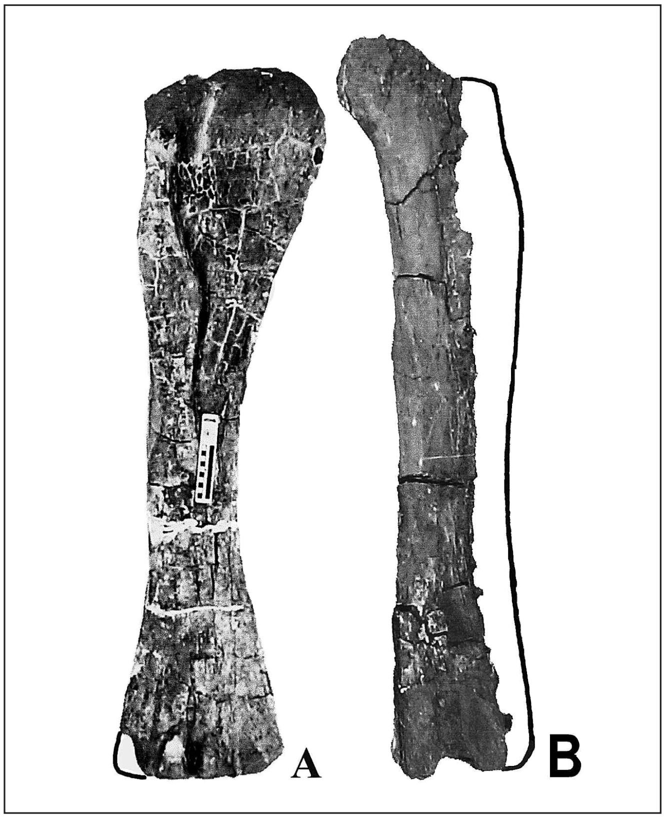
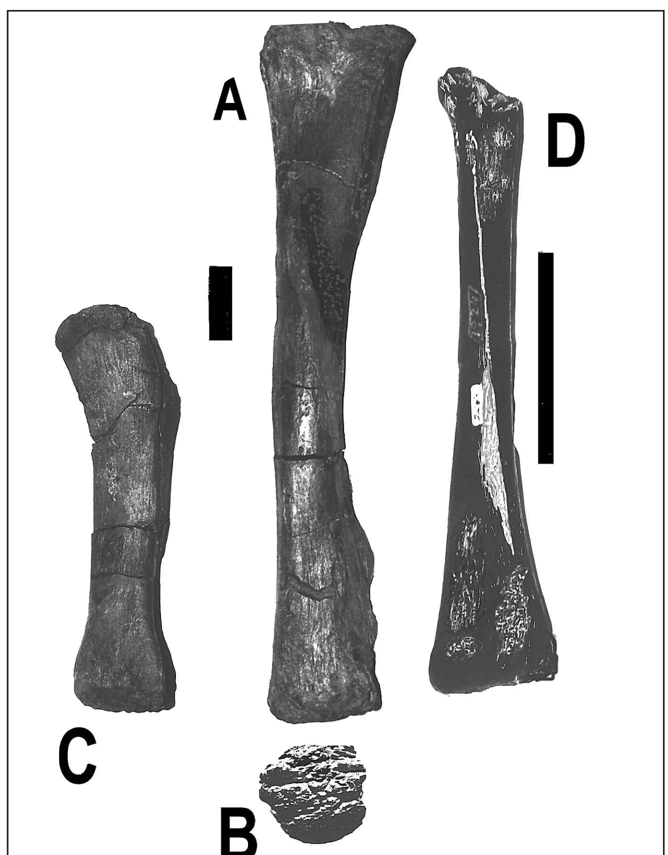


Fig. 7: *Cedarosaurus weiskopfae* (DMNH 39045). A. Right humerus, anterior view. Note position of delto/pectoral crest near midshaft, breadth of shaft and distal end. B. Right femur, posterior view. Note gracile distal condyles.

The lateral margin of the shaft is slightly bowed laterally, and the medial margin strongly concave. The proximal and distal ends are almost the same width, the distal end being about 90% the proximal; in *Brachiosaurus*, the distal end is about 85% and 96% in *Pleurocoelus nanus***.** The deltopectoral crest is more prominent in lateral profile than it is in *Brachiosaurus*. As with *Brachiosaurus*, it is almost at right angles relative to the anterior face of the shaft. It begins well below the head of the humerus and extends down to midshaft. A low ridge, 22cm in length, connects the crest with the lateral tuberosity on the proximal end. Distally, the radial and ulnar condyles are very small, and present only on the anterior face of the humeral shaft, and are separated by a small, vertical groove. This end is somewhat weathered, showing very little detail on the posterior face.

The right radius, which was recovered in nearly perfect condition, is quite slender in contrast to *Chubutisaurus* (fig. 8A). It is slightly bowed anterolaterally. There is a prominent ridge that arises near the proximal end and extends along the caudal side. A similar ridge is found in *Pleurocoelus nanus* (fig.8D). A second ridge begins at mid shaft and extends along the lateral side, terminating in a distinct bulge where the radius contacts the ulna. The ridge marks the site for the M. extensor longus digiti I. The distal end is subrectangular and blocky, rather than oval as in *Pleurocoelus nanus* and SMU 61732. It shows none of the transverse expansion often found in titanosaurs.(fig. 8B).

Fig 8: A-C: *Cedarosaurus weiskopfae* (DMNH 39045). A. Right radius in posterior view. Note weak ridge extending obliquely down the posterior side, and lateral bulge at contact with ulna. B. Right radius, distal view. Note subrectangular, blocky shape. C. Metacarpal IV, anterior view. D. *Pleurocoelus nanus* (USNM 2366). Radius, posterior view. Note wide distal end and sharp ridge extending obliquely down the posterior side. scale = 10cm



The right ulna is incomplete, lacking the distal third. The olecranon is slightly damaged, but was clearly not as tall as *Brachiosaurus* or *Sonorosaurus*. The radial notch is very well developed and the medial wall is quite broad; features shared with *Pleurocoelus nanus* and the English species *Pelorosaurus becklesii*. The posterior surface of the ulna is expanded as a ridge extending downwards from the olecranon; a similar feature appears in the ulna of *Pleurocoelus nanus*. However, in *Cedarosaurus* this expansion is separated from the lateral wall of the radial notch by a well defined groove (fig.9).

One metacarpal has been identified as mc1V and is almost complete, lacking a small portion of the proximal end (fig.8C). There is a strong flange extending along the posterior side below midshaft. The distal end is rectangular. Another incomplete metacarpal is missing the proximal third. Both exhibit the long, slender morphology typical of brachiosaur metacarpals.

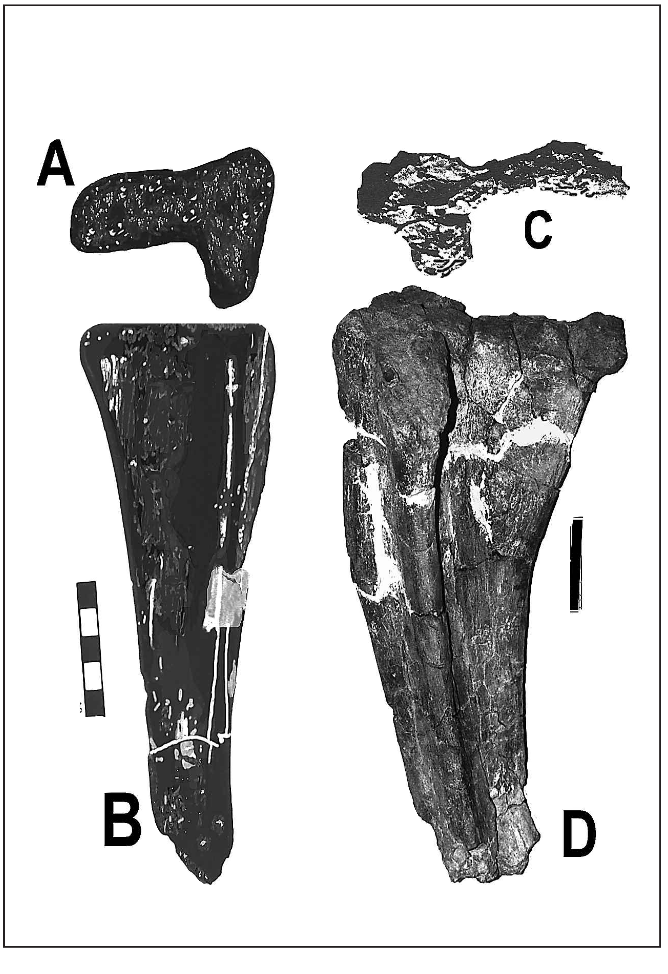


Fig 9: A&B: *Pleurocoelus nanus* (USNM 5676). Left ulna A. Proximal view. Note posterior expansion below olecranon. B. Anterior view. Note lack of groove between posterior expansion and lateral wall. C&D: *Cedarosaurus weiskopfae* (DMNH 39045) Right ulna. C. Proximal view. Note posterior/lateral expansion. D. Anterior view.
A&B scale = 5 cm, C&D scale = 10 cm.

Pelvic Girdle

The ilia are missing, but portions of both pubes, and ischia are present. The right pubis shows a considerable amount of flattening due to crushing. Much of the proximal end, which articulates with the ilium, is missing, as is the ischial articulation and some of the distal end. This has hindered comparison with other sauropod pubes. However, the central body of the pubis is intact, including the pubic foremen. The apron is wide and quite thin, and is deeply emarginated along its postero/medial edge. The body of the pubis narrows considerably towards the distal end in a manner similar to *Brachiosaurus*. A partial left pubis is represented by several large fragments which include the anterior border of the pubic foremen.

Fragments of the proximal ends of the left and right ischia were recovered in close proximity to the pubes.

Hindlimb

The nearly complete right femur is missing portions of the lateral and proximal sides of the femoral head and is badly eroded all along the lateral side of the shaft where it was exposed after the initial burial. Therefore, all signs of the greater trocanter and medial deflection are missing, as is the process lateral to the fibular condyle (fig 7B). There is moderate development of the fourth trocanter, which is located close to the medial edge. The shaft appears almost circular in cross section, although a true measure of the width of the shaft is not possible due to extensive damage on the lateral side. The distal condyles are unusually narrow, emphasizing the gracile nature of this bone, and the intercondylar groove is shallow. This differs from *Pleurocoelus nanus*, whose distal condyles are proportionally more robust. Total length is 139 cm, while least circumference is indeterminate. Additional hindlimb measurements are found in Table 2.

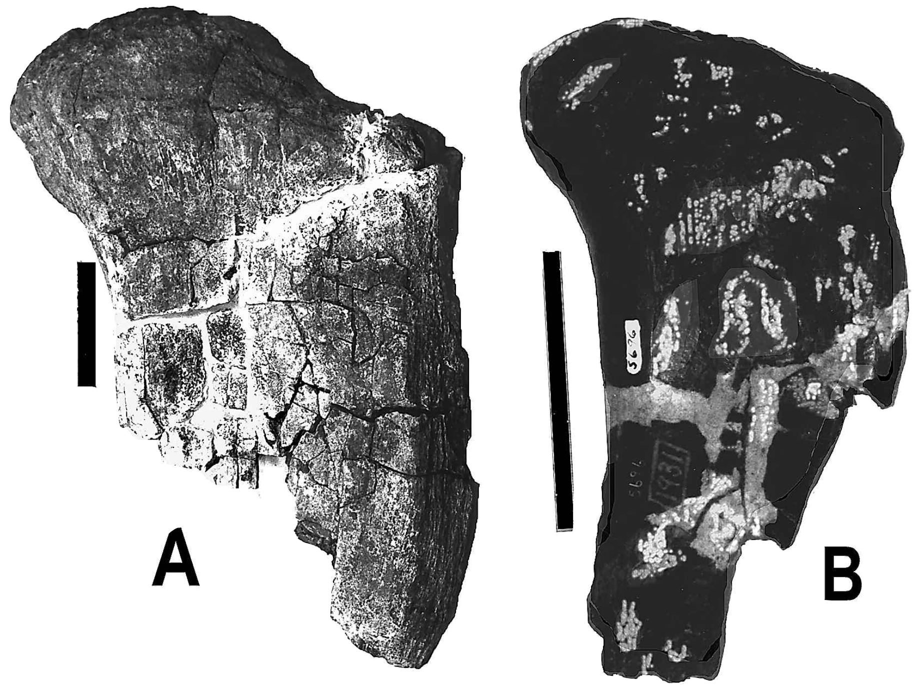


Fig. 10: A. *Cedarosaurus weiskopfae* (DMNH 39045) Left femur head. Note height of femur head above greater trocanter and slight medial deflection. B: *Pleurocoelus nanus* (USNM 5696). Note distinct lateral bulge below head. scale = 10 cm.

Only the proximal end of the left femur is preserved. The head is set distinctly higher than the sharply defined greater trocanter, as it is in *Brachiosaurus* (fig. 10 A). This differs from *Pleurocoelus*, whose femural head is more rounded (fig.10 B). In comparison with most brachiosaurs and titanosaurs, the medial deflection of the proximal end of the femur is reduced.

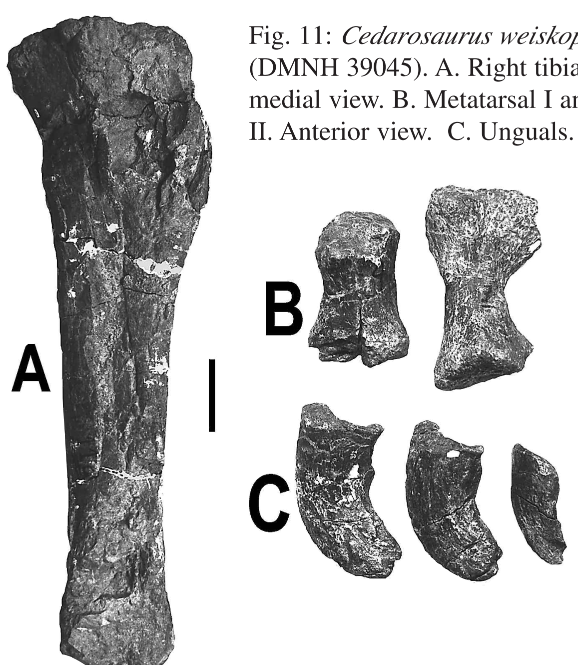


Fig. 11: *Cedarosaurus weiskopfae* (DMNH 39045). A. Right tibia, medial view. B. Metatarsal I and II. Anterior view. C. Unguals.

The right tibia is less robust than the tibia of *Brachiosaurus* (fig.11A). The proximal end is crushed antero/posteriorly and some of the cnemial crest has been lost. The distal end is heavily eroded and is missing the fibular condyle. However, it appears to lack the strong transverse expansion found in *Pleurocoelus* and some basal titanosaurs (Salgado *et al.* 1997, Gomani *et al.*, 1998)All of the pes elements were recovered in close proximity to each other, although it has not yet been determined whether they represent one hind foot, or combine elements from two. Weathering has obscured the proximal and distal ends of all the elements to some extent, making a detailed description difficult. Metatarsal I appears to be shorter than in *Brachiosaurus* and is much shorter than in *Pleurocoelus altus* (fig. 11 B). It displays some evidence of a laterodistal process, similar to the one found in *Brachiosaurus.* Metatarsal II differs from *Brachiosaurus* in having a more developed lateral flange. Metatarsal V is very slender and elongate, heavily eroded and missing one distal condyle.

One phalanx was found and resembles digit II-I of *Sonorosaurus.* Three unguals were also recovered in association with the metatarsals (fig. 11 C). They appear to represent all of the claws from a single hind foot. All are laterally compressed and display a prominent groove along the lateral surface similar to those found in *Brachiosaurus.*

DISCUSSION

Scattered remains of Lower to Middle Cretaceous sauropods are known from every continent except Antarctica (McIntosh, 1990a). In North America, these sauropods include the brachiosaurids *Pleurocoelus* and *Soronasaurus thompsoni*, as well an unnamed camarasaurid and several as yet unnamed titanosaurids (tabl. 3). These and other sauropod taxa are often assigned to particular families based on the morphology of their dorsal vertebrae because these are diagnostic in sauropods (McIntosh, 1990a). Unfortunately, the lack of any complete dorsal vertebra for *Cedarosaurus* makes its family determination difficult, requiring us to make comparisons based on other skeletal elements.

The high humeral/femoral ratio, .98, of *Cedarosaurus* is much higher than for any known camarasaur, diplodocid or titanosaur (McIntosh, 1990b). The extended length of the dorsal centra, as well as neural arch placement of the caudal vertebrae, also preclude placement in these families. Titanosaurs are characterized by procoelous caudal vertebrae having deeply concave anterior faces and a prominent ball on the posterior face. In more derived titanosaurs this feature is found even on the middle and posterior caudals, while in more primitive titanosaur species only the anterior caudals display a posterior ball (Jacobs *et al.*, 1993). This is in marked contrast to *Cedarosaurus,* which shows deeply concave anterior faces, yet the posterior faces are flat to slightly concave, even in the most proximal caudals. The radius and metacarpals more closely resemble brachiosaurids than titanosaurids in being quite slender and elongate. We conclude, based primarily on the humerus-femur ratio, length of radius and metacarpals, and lack of a posterior ball on anterior caudal vertebrae, that *Cedarosaurus* belongs in the family Brachiosauridae.

Comparisons of *Cedarosaurus* with other Lower and Middle Cretaceous Sauropods

England

Several poorly preserved dorsal vertebrae were recovered from Lower and Middle Cretaceous quarries in England during the mid 1800's. Some were isolated elements, others found in association. All have been assigned to a variety of taxonomic groups over the years, resulting in a complex history, which Blows has recently attempted to sort out (Blows, 1995). He has separated these specimens into *Ornithopsis hulkei*, represented by a single dorsal centrum, and the genus - *Eucamerotus* - which contains six dorsal vertebrae, but no limb or girdle elements. Unfortunately, *Cedarosaurus* has poorly preserved dorsals. Nevertheless, the dorsal centra do resemble those of *Eucamerotus* in that they are quite long relative to their height and contain large pleurocoels. However, these features are common to all brachiosaurid dorsals. More recent finds in Europe have been referred to this genus, but have not yet been adequately described (Blows, 1998).

Pelorosaurus consists of a humerus, several caudal vertebrae, sacrum, pelvis and isolated dorsal vertebrae from several different quarries. McIntosh (1990a) considers *Pelorosaurus* to be a valid genus, although few characteristics were found to separate it from *Brachiosaurus*. The right ulna of *Pelorosaurus becklesii* resembles that of *Cedarosaurus* in having a well developed radial notch and broad medial plate. These features are also found in *Pleurocoelus nanus*. Upchurch (1995) considers *Pelorosaurus becklesii* a basal titanosaur based on the anteromedial proximal process of the ulna. This area shows a pronounced concavity in *Saltasaurus*, *Janenschia* and *Pelorosaurus becklesii*. It is not present, however, in *Cedarosaurus* or *Pleurocoelus nanus*. Blows (1995) considers *Pelorosaurus* to be *nomen vanum*, and the type specimen, the proximal end of a humerus, to be undiagnostic.

South America

In Argentina, *Chubutisaurus insignis* was described by Del Corro (1975) and placed into a new family Chubutisauridae. McIntosh (1990a) reassigned the genus provisionally to the Brachiosauridae. More recently, Salgado (1993) noted that the more robust humerus and metacarpals indicated that it might be a titanosaur. The radius is very robust, and is broader than that of *Cedarosaurus*. The humero-femural ratio is .86 for *Chubutisaurus*, in contrast to .96 in *Cedarosaurus*. The anterior caudals in *Chubutisaurus* are amphiplatyan rather than anteriorly concave.

North America

Sonorosaurus, from the Middle Cretaceous of Arizona (Ratkevich, 1998) is represented by postcrania. The dorsal centra have typical brachiosaurid characteristics, including a long centrum, a wide posterior concavity and large pleurocoels. The anterior caudals are slightly procoelous, whereas the corresponding vertebrae in *Cedarosaurus* possess deeply concave anterior caudal faces. The radius of *Sonorosaurus* lacks the distinct ridge down the lateral side which is prominent in *Cedarosaurus*, while the sharply triangular proximal end of the ulna differs from the posteriorly expanded aspect of *Cedarosaurus*. Therefore, it appears that *Cedarosaurus* differs significantly from *Sonorosaurus*.

Pleurocoelus nanus (Marsh 1888) is known from many disarticulated, juvenile elements recovered from the basal Albian of Maryland (a second species, *P. altus*, based on a tibia and fibula, is indistinguishable from that in other sauropods, Salgado *et al.*, 1995, and is a nomen dubium). The holotype of the genus consists of a juvenile dorsal centrum with an enormous pleurocoel. Similar appearing centra from the Upper Jurassic Morrison Formation have been referred to the genus (Hatcher, 1903), but the specimens are those of a juvenile *Camarasaurus grandis* (Carpenter & McIntosh, 1994). As noted by Carpenter and McIntosh (1994), the enormous pleurocoels typify juvenile sauropod presacral centra. Considering that the shape of sauropod vertebrae changes considerably as they proceed through several growth stages (Curtice, 1998), we conclude that, although *Pleurocoelus nanus* is probably a valid taxon, it cannot be defined from the holotype dorsal. Therefore, a new type needs to be designated. Until that time, we accept that the material described by Lull (1911) and other more recently collected material in National Museum of Natural History are those of *Pleurocoelus nanus* and make our comparisons with *Cedarosaurus* on that material. McIntosh (1990a) provisionally assigned *Pleurocoelus* to the family Brachiosauridae. However, recent studies have questioned the phylogenetic position of *Pleurocoelus*, suggesting the type material is a sister taxon to titanosaurids (Salgado *et al.*, 1995). Although these studies raise valid issues, we prefer to retain *Pleurocoelus* within the Brachiosauridae for the purpose of this study, pending a future reevaluation of that genus.

Dorsal vertebrae of mature individuals are among the most diagnostic skeletal elements in sauropods (McIntosh, 1990a). However, comparisons with the dorsals of *Cedarosaurus* are hampered by the absence of neural arches and spines for *Pleurocoelus*. The anterior caudal centra of *Pleurocoelus* are antero-posteriorly very short, with circular amphiplatyan faces, which is in marked contrast to the wider- than- tall, deeply concave anterior faces of *Cedarosaurus* (figs.12 &3).

Recently it has been demonstrated that comparison of sauropod limb elements of differing ontogenetic stages is more reliable than comparison of vertebra (Wilhite and Curtice, 1998). Unfortunately none of the material of *Pleurocoelus* was found articulated or in close association, making comparisons difficult between the humerus/femur length of this genus and *Cedarosaurus.* Lull suggests that *Pleurocoelus* humerus USNM 2263, and femur USNM 2263 might

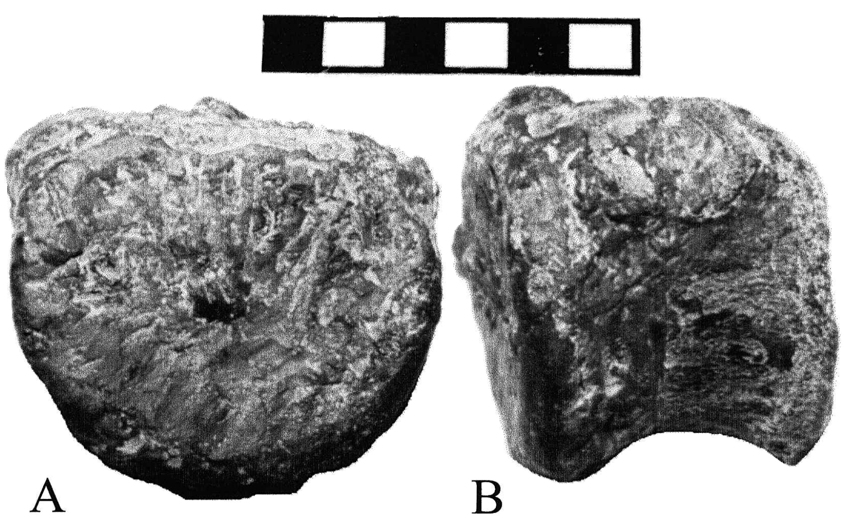


Fig. 12: *Pleurocoelus nanus* (USNM 8488). Anterior caudal centrum. A. Anterior view. Note flat articular face. B. Lateral view.

belong to a single individual. If correct, this would give a humerus-femur ratio of .92, which is close to .98 for *Cedarosaurus.* The deltopectoral crest of the *Pleurocoelus* humerus is placed close to the proximal end, rather than further down the shaft, as in *Cedarosaurus*. The distal end of the radius in *Pleurocoelus* is a transversely expanded oval, whereas it is subrectangular in *Cedarosaurus* (fig.8).

The ulna of both *Pleurocoelus* and *Cedarosaurus* have a similarly wide medial wall and distinct posterior expansion. However, in *Pleurocoelus*, there is no groove separating this expansion from the lateral wall as is found in *Cedarosaurus* (fig.9). In the femur, *Pleurocoelus* has a prominent lateral deflection that is so characteristic of brachiosaurids, but which is less developed in *Cedarosaurus* (fig.10). We conclude the differences displayed by these limb elements require placement of these specimens in separate genera.

Langston (1974) referred several specimens from the Lower Cretaceous of Texas to *Pleurocoelus* based on similarities of the distal caudals: slender, spool-shaped, amphiplatyan centrum, with the neural arch occupying the cranial half of the centrum. However, such distal caudals are common to all brachiosaurids and many titanosaurids. There are greater differences in the anterior caudals of *Pleurocoelus* and the Texas "*Pleurocoelus",* demonstrating that they are distinct genera. In *Pleurocoelus*, the centra are amphiplatyan (fig.11), while the anterior faces of the Texas "*Pleurocoelus"* (SMU 61732) are strongly concave and thus resemble those of *Cedarosaurus.* Langston (1974) reports the presence of well developed hyposphenes in the anterior to mid-caudals of SMU 61732 (fig.13). Upchurch (1998) has noted the presence of hyposphenes or hyposphenal ridges on the caudals of several sauropod taxa, but none are as prominent nor extend as far back in the column as in the Texas "*Pleurocoelus.*" The anterior caudal neural spine of *Pleurocoelus nanus* (USNM 5650) shows little indication of a hyposphene (fig.14).

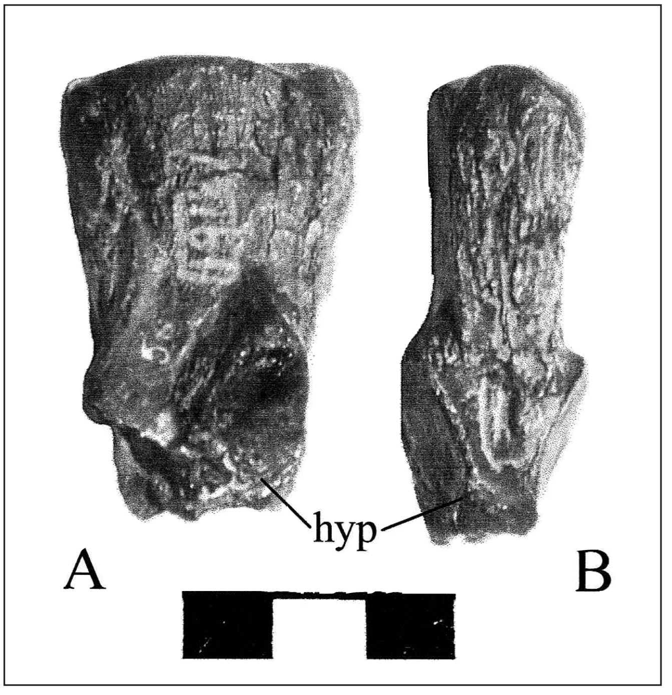


Fig 14: *Pleurocoelus nanus* (USNM 5650). Neural spine of anterior caudal vertebra. A. Lateral view. B. Posterior view. Note slight hyposphene.

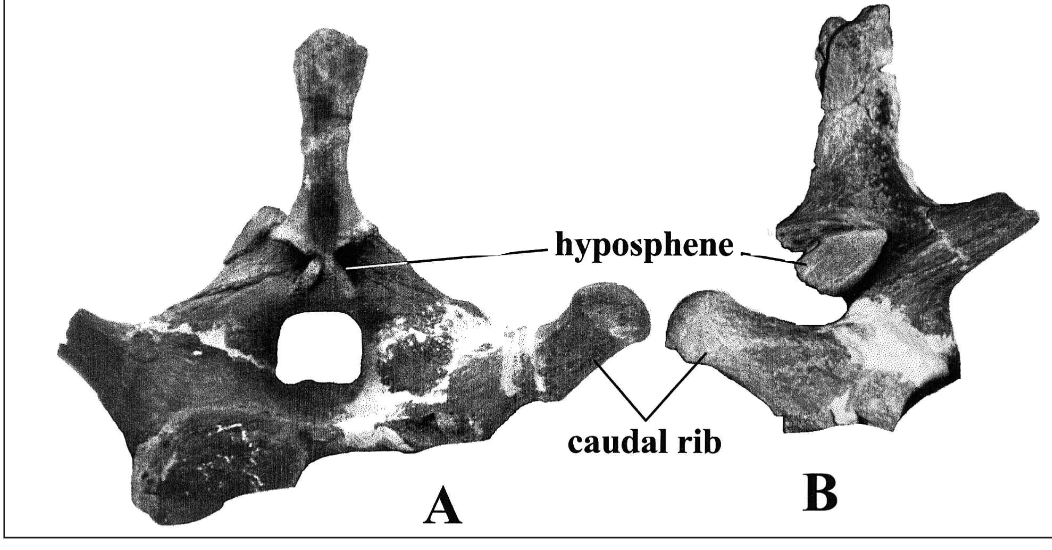


Fig. 13: *"Pleurocoelus"* (SMU 61732).
A. Proximal caudal vertebra, posterior view. Note prominent hyposphene, height of caudal ribs.
B. Anterior caudal neural arch and spine.. Note prominent hyposphene and posterior/dorsal angle of caudal rib.

In *Cedarosaurus*, only caudal 8 shows a small hyposphene. On all other caudals the postzygapophyses extend down to the neural canal, leaving little room for such structures (fig.3). In addition, there are no interlocking hypantra on the prezygapophyses, as are found on SMU 61732. In describing the Texas specimen, Langston considered the hyposphenes to be a major diagnostic feature, a point on which McIntosh (1990) agrees. Their absence in *Cedarosaurus* most likely indicates a generic difference between these specimens.

We believe that the presence of concave anterior faces and of hyposphenes on the anterior caudal vertebrae of SMU 61732 preclude its referral to the genus *Pleurocoelus.* Recently other authors have also questioned this referral, suggesting that this material bears a closer relationship to titanosaurids than to brachiosaurids (Salgado *et al.*, 1995; Gomani *et al.*, 1998). This hypothesis may be confirmed when a number of additional sauropod specimens that have recently been excavated in Texas (Winkler *et al.*, 1997) are prepared. Although it is clear that SMU 61732 cannot be referred to *Pleurocoelus*, its relationship to *Cedarosaurus* remains in doubt until the remainder of the SMU material is prepared.

CONCLUSION

Until recently studies of North American Early and Middle Cretaceous sauropods were severely restricted due to the low number of specimens which had been recovered. The last ten years have seen a remarkable upsurge in the quantity and diversity of taxa which have been found. Many have been referred to *Pleurocoelus*, although none have been properly described and compared with that genus. Thus, our comparison of *Cedarosaurus* with the holotype and referred material of *Pleurocoelus* is the first such study. It illustrates the difficulties that arise in comparing fully adult individuals with very young type specimens.

DMNH 39045 is one of the most complete Early Cretaceous brachiosaurids known. This designation is based on humero/femural ratios and characteristics of the forelimb and caudal vertebrae. *Pleurocoelus* most closely resembles *Cedarosaurus* in general morphology. However, significant differences in the caudal vertebrae and limb elements prevent the placement of the Denver specimen within this genus. We therefore designate DMNH 39045 a new genus and species: *Cedarosaurus weiskopfae.*

ACKNOWLEDGMENTS

Comparative studies of other sauropod specimens would not have been possible without the cooperation of Robert Purdy, United States Museum of Natural History; Louis Jacobs, Dale Winkler, and Elizabeth Gomani at Southern Methodist University; and Timothy Rowe and Chris Bell at University of Texas and Texas Memorial Museum.

The holotype of *Cedarosaurus weiskopfae* was collected under Bureau of Land Management Excavation Permit No. UT-EX-97-004. It was discovered by Denver Museum of Natural History volunteer Billy Kinneer, and was excavated over the course of two years by Kenneth Carpenter, Virginia Tidwell, Bill Brooks, Carol Weiskopf, Frank Sanders, Philip and Pepperanne Pauli, Kathy Crouse, Tom Garner, Lorrie McWhinney, Juliana Van Pelt, Tim Seeber, Tony Dicroce, Sue Meyer, Brenda Johnson, Angela Maithias, Jeannie McKinney, Judy Peterson, Steve Mohr and Bob McCarroll.

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Table 1. Measurements of caudal vertebrae (mm) for *Cedarosaurus weiskopfae* DMNH 39045

W- Width; H- Height

Caudal #	**Length**	**Anterior Centrum W - H**	**Posterior Centrum W - H**	**Height Prezyg.**	**Height Postzyg.**	**Diapoph. Spread ***
caudal 2	92	177 - 106	195 - 123	—	—	231
caudal 3	95	202 - 134	196 - —	—	—	—
caudal 4	113	191 - 83	230 - 102	—	—	—
caudal 5	95	193 - 116	161 - 110	—	—	282
caudal 6	97	180 - 93	176 - 95	123	—	361
caudal 7	105	160 - 142	150- 133	210	182	323
caudal 8	112	152 - 141	145 - 142	221	210	282
caudal 9	107	153 - 122	— - 113	162	181	201
caudal 10	—	151 - 110	— - 112	161	—	95
caudal 11	113	162 - 95	151 - 90	—	142	—
caudal 12	102	146 - 97	142 - 97	133	—	—
caudal 13	100	119 - 101	— - 98	134	129	—
caudal 14	98	133 - 103	130 - 105	—	—	—
caudal 15	101	107 - 102	108 - 91	115	—	—
caudal 16	100	— - —	— - —	—	—	—
caudal 17	105	92 - 91	— - —	—	—	—
caudal 18	112	89 - 87	95 - 83	—	—	—
caudal 19	100	100 - 75	94 - 81	110	111	—
caudal 20	117	95 - 66	93 - 67	85	—	—
caudal 21	115	83 - 75	— - —	—	—	—
caudal 22	112	88 - 51	81 - 64	—	—	—
caudal 23	110	89 - 60	80 - 49	—	—	—
caudal 24	111	61 - 64	59 - 71	—	—	—
caudal 25	105	71 - 65	63 - 59	—	—	—

* based on length of right caudal ribs

Table 2. Measurements of limbs (mm) for *Cedarosaurus weiskopfae* DMNH 39045

Right humerus	
Length	1380
Breadth, proximal	390
Breadth, shaft	185
Breadth, distal	335
Minimum circumference	445
Right radius	
Length	812
Breadth, proximal	180
Breadth, shaft	118
Breadth, distal	132
Minimum circumference	245
Right ulna	
Breadth, proximal	330
Breadth, shaft	132
Metacarpal	
Length	428
Breadth, distal	97
Left femur	
Breadth, proximal	378
Right femur	
Length	1395
Breadth, distal	210
Right tibia	
Length	884*
Breadth, shaft	173
Breadth, distal	162
Least circumference	326
Metatarsal I	
Length	152
Metatarsal II	
Length	201

*Right tibia distal end heavily weathered.

Table 3 Lower and "Middle" Cretaceous Sauropods of North America.

Taxon	Stratigraphy (Age)	Reference
Pleurocoelus nanus	Arundel Fm. (basal Albian), Maryland	Marsh 1888; Lull 1911
Cedarosaurus weiskopfae	Yellow Cat Member, Cedar Mountain Fm. (Barremian), Utah	this paper
camarasaurid	Yellow Cat Member, Cedar Mountain Fm. (Barremian), Utah	Britt and Stadtman, 1996
titanosaurid	Yellow Cat Member, Cedar Mountain Fm. (Barremian), Utah	Britt and Stadtman, 1996
titanosaurid	Ruby Ranch Member, Cedar Mountain Fm. (Aptian), Utah	Carpenter, notes
titanosaurid (?)	Paluxy Fm. (Albian), Texas	Langston, 1974
titanosaurid	Cloverly Fm. (Aptian-Albian)	Ostrom, 1970
Soronasaurus thompsoni	Turney Ranch Fm. (Cenomanian), Arizona	Ratkevich 1998

Note reçue le 12-05-1999
acceptée après révision le 20-07-1999