



Distribution and biochronology of Camarasaurus (Dinosaria, Sauropoda) from the Jurassic Morrison Formation of the Rocky Mountain Region

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DISTRIBUTION AND BIOCHRONOLOGY OF *CAMARASAURUS* (DINOSAURIA, SAUROPODA) FROM THE JURASSIC MORRISON FORMATION OF THE ROCKY MOUNTAIN REGION

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ABSTRACT.—The stratigraphic distribution of fossil remains of *Camarasaurus* (Dinosauria, Sauropoda) allows recognition of five biozones in the upper Jurassic Morrison Formation: (1) no *Camarasaurus* Zone (early-mid Kimmeridgian), (2) *Camarasaurus grandis* Zone (mid Kimmeridgian), (3) *C. lentus* Zone (late Kimmeridgian), (4) transition Zone (early Tithonian), and (5) *C. supremus* Zone (Tithonian). Paleobiogeographically, *C. grandis* is known from south and central Wyoming, central Colorado, and New Mexico; *C. lentus* occurs in Wyoming and Utah and *C. supremus* in south-central Colorado to western Oklahoma. However, the geographic occurrences may only reflect stratigraphic distribution as locally appropriate beds may not be exposed or were eroded. *Camarasaurus* might have a much wider distribution in the Rocky Mountain area than indicated by its distribution of the fossil remains. Additionally, the data provide new insights into the taxonomy of *Camarasaurus*.

INTRODUCTION

The stratigraphic correlation of the Morrison Formation (Late Jurassic) has been studied for a long time (e.g., Owen et al., 1989; Fishman et al., 1995; Demko et al. 1996; Turner and Peterson, 1999), and the presence of consistent regional isochronous marker beds throughout Utah, Colorado, Wyoming, New Mexico, southern Montana, northwestern Oklahoma, eastern South Dakota, and northeastern Arizona is still debated. The main reasons for uncertain stratigraphic correlation are: (1) relatively complicated lithology, including various facies of fluvial and lacustrine sediments (e.g., Foster, 2003, tables 1, 2) and (2) physically isolated exposures in a number of different plateaus and drainage basins (Fig. 1).

The Morrison Formation is remarkably fossiliferous and, in particular, it is known to contain abundant dinosaur remains. Therefore, information on the relative age of the Morrison can provide a better understanding of: (1) species occurrences (e.g., biochronology, paleobiogeography), (2) taxonomy (e.g., identification of species), and (3) evolution (e.g., tempo of morphological change) of some dinosaur taxa.

Turner and Peterson (1999) first proposed the biostratigraphy of various dinosaurian taxa from the Morrison Formation. Their correlation is mostly based on mineralogy and petrology, primarily, the clay change. Above the clay change, claystones and mudstones contain abundant smectic-rich clays, altered from volcanic ash and characterized by the absence of popcorn texture in soils (Owen et al., 1989; Turner and Peterson, 1999). Significantly, the clay change is thought to separate the Upper Morrison Formation into the lower and upper members (Turner and Peterson, 1999).

Although Trujillo (2002, 2003) suggested that no significant differences in the smectitic and non-smectic mudstone based on X-ray diffraction are detectable in the Morrison Formation, her data are primarily from the Wyoming area and do not cover the entire Morrison Formation in the Rocky mountain region. In fact, the clay change is thought to be present throughout the Colorado Plateau (including Garden Park area), including the Dinosaur National Monument Area, and in central, southern, and western Wyoming (e.g., Como Bluff, Thermopolis area) (Turner and

Peterson, personal communication, 2002), but is perhaps absent in the eastern Wyoming and Black Hills (South Dakota) area (Turner and Peterson, 1999). Therefore, in this study, I excluded data from the eastern Wyoming and the Black Hills area for discussions of the distribution of *Camarasaurus*. However, using clay minerals is the only comprehensive method for stratigraphic correlation, although, geographically, the feature is limited in the Rocky Mountain region. The clay change can allow us to compare and correlate biostratigraphy of the Morrison fossil taxa as in other previous

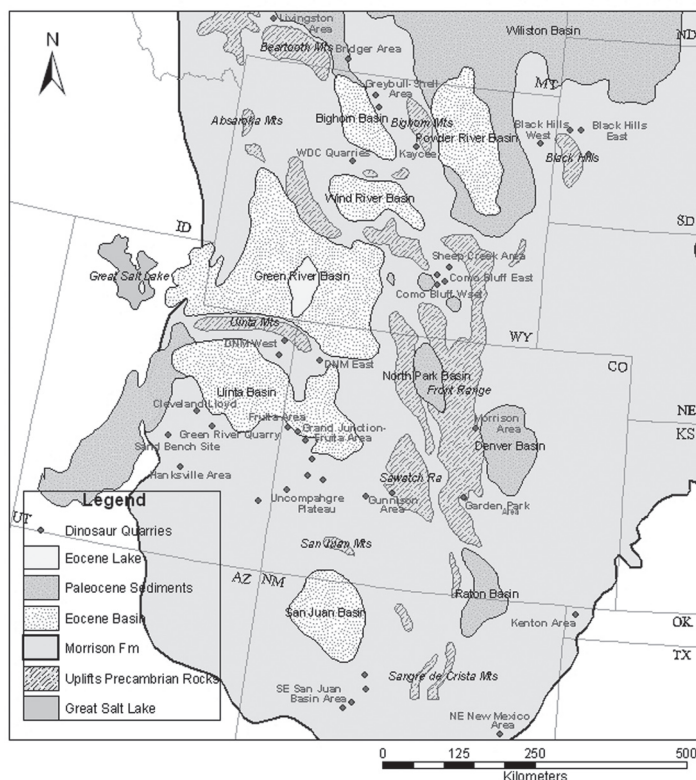


FIGURE 1. Geological features in the Rocky Mountain region and major dinosaur quarries in the Morrison Formation. The map is modified from King (1977, fig. 74). Areal definition of the Morrison Formation is based on Turner and Peterson (1999).

studies that recognized six dinosaur biozones (Foster, 2003, fig. 6) or four dinosaur biozones (Turner and Peterson, 1999).

In this paper, I review the stratigraphic distribution of *Camarasaurus* (Dinosauria, Sauropoda) in the Morrison Formation based on Turner and Peterson's (1999) idea of stratigraphic correlation of the Morrison dinosaur quarries. In *Camarasaurus*, three significant features should be noted: (1) a wide geographic distribution in the entire Rocky Mountain region, found in the nearly entire area of Morrison outcrop, (2) a stratigraphic distribution in the Morrison Formation from the upper member of the lower Morrison to the top of the formation, and (3) perhaps, it is the most common dinosaur in the formation. Therefore, a relatively large sample size from the long vertical range in the Morrison Formation allows me to establish biozones. I also examine whether the broad geographic distribution provides enough data to correlate stratigraphic positions among different areas of the Morrison Formation.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BHI**, Black Hills Institute, Hill City, South Dakota; **BYU**, Earth Science Museum, Brigham Young University, Provo, Utah; **CEU**, College of Eastern Utah Prehistoric Museum, Price; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **DMNH**, Denver Museum of Natural History (now Denver Museum of Nature and Science), Denver, Colorado; **DNM**, Dinosaur National Monument, Jensen, Utah; **FHSM**, Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas; **FMNH**, Field Museum of Natural History, Chicago, Illinois; **GMNH-PV**, Gunma Museum of Natural History Vertebrate Paleontology, Gunma, Japan; **KUVP**, University of Kansas Vertebrate Paleontology, Lawrence; **NMMNH**, New Mexico Museum of Natural History & Science, Albuquerque; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman; **SDSM**, South Dakota School of Mines and Technology, Rapid City; **SMA**, Sauriermuseum Aathal, Aathal, Switzerland; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor; **USNM**, National Museum of Natural History (formerly United States National Museum), Washington DC; **UUVP**, University of Utah Natural History, Salt Lake City; **WDC**, Wyoming Dinosaur Center, Thermopolis; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

GEOLOGICAL SETTING

The Morrison Formation is widely distributed in the Western Interior (Fig. 1). Although outcrops of the Morrison Formation are present in seven states, it also extends to western Kansas, Nebraska, North Dakota, and northern Texas in the subsurface (Foster, 2003). Most exposures are located near the edges of the uplift and basin areas such as the Black Hills, Big Horn Basin, Uinta Mountains, and Front Range (Fig. 1).

The age range of the Morrison Formation is estimated as about 140–150 Ma (Currie, 1998) or 147–155 Ma (Kowallis et al., 1998) and the end of the Jurassic is thought to be at about 141 Ma (Bralower et al., 1990; Gradstein and Ogg, 2004). Additionally, the Morrison Formation ranges from Kimmeridgian to Tithonian in age and, probably, the very late Oxfordian and Early

Cretaceous in some areas (Foster, 2003). Stratigraphically, the Morrison Formation consists of the lower and upper members. However, several Cenozoic orogenic uplifts separated the Morrison into different basins (Fig. 1), and the two members tend to have different names in each basin; e.g., the Salt Wash and Brushy Basin members on the Colorado Plateau, the upper and lower members in the Bighorn Basin; and the Westwater Canyon and upper part of Brushy Basin members near the San Juan Basin (Foster, 2003, fig. 2; Peterson and Turner-Peterson, 1987; Turner and Peterson, 1999).

SYSTEMATIC PALEONTOLOGY

REPTILIA DINOSAURIA SAUROPODA

CAMARASAURIDAE Cope, 1878

CAMARASAURUS Cope, 1877a

Apatosaurus Marsh, 1877:514 (in part).

Amphicoelias Cope, 1877b:2 (in part).

Caulodon Cope, 1877c:193.

Morosaurus Marsh, 1878a:242.

Pleurocoelus Marsh, 1888:90 (in part).

Astrodon Marsh, 1896:133 (in part).

Uintasaurus Holland, 1924:119.

Camarasaurus: McIntosh 1981:12.

Cathetosaurus Jensen, 1988:121.

Camarasaurus McIntosh 1990b:348.

Camarasaurus McIntosh et al. 1996b:74.

Range—Morrison Formation (Late Kimmeridgian–Tithonian, Late Jurassic) in Colorado, New Mexico, Oklahoma, South Dakota, Utah, and Wyoming.

Emended Diagnosis—Massive lower and upper jaws; massive vomer; short basiptyergoid process; 12 cervical and 12 dorsal vertebrae; bifurcated neural spines in all mid- and posterior-cervical vertebrae (but variable in the anterior cervical vertebrae); U-shaped rather than V-shaped (e.g., diplodocids) neural spines in some dorsal vertebrae; relatively short and massive neural spine in posterior dorsal, sacral, and proximal caudal vertebrae; relatively short tail with about 53 caudal vertebrae; distal end of scapular blade broadly expanded; forelimbs more slender than hindlimb; humero-femoral length ratio ~0.77; two carpal bones (ulnare and radia); metacarpal III to humerus length ratio ~0.33; pubis massive with short shaft; very slender ischium, especially the distal end; tibio-femoral length ratio ~0.60 (McIntosh 1990a, b; Madsen et al., 1995).

CAMARASAURUS SUPREMUS Cope, 1877a

Amphicoelias latus Cope, 1877b:4.

Caulodon diversidense Cope, 1877c:193.

Caulodon leptoganus Cope, 1877c:193.

Camarasaurus leptodirus Cope, 1879:404.

Camarasaurus supremus: Osborn and Mook 1921:262.

Holotype—AMNH 5760, composite of probably two (?) skeletons from near Cope's Nipple, Garden Park, Colorado, very top of the Morrison Formation (Carpenter, 1998; McIntosh, 1998; Turner and Peterson, 1999).

Topotype—AMNH 5761, including at least a few partial skeletons from near Cope's Nipple.

Range—Middle and upper Morrison Formation (Late Kimmeridgian–Tithonian, Late Jurassic) in south-central and, possibly, southeastern Colorado and northwestern Oklahoma.

Referred specimens—DMNH 27228, axis, cervical vertebra no. 4 (?), dorsal vertebra no. 3 (?), caudal vertebrae no. 1 and 3 (?), pubis from near Cope's Nipple (Carpenter, 1998).

Emended Diagnosis—A species of *Camarasaurus* with a large body, relatively short neural arch in dorsal vertebrae from no. 3 to 8, T-shaped neural spine in caudal vertebrae from no. 1 to 5 or 6.

CAMARASAURUS GRANDIS (Marsh, 1877)

Apatosaurus Marsh, 1877:515 (in part).

Amphicoelias Cope, 1877b:2 (in part).

Morosaurus impar Marsh, 1878a:242.

Morosaurus robustus Marsh, 1878b:414.

Pleurocoelus montanus Marsh, 1896:184.

Camarasaurus grandis: Gilmore, 1925:352.

Holotype—YPM 1901, basioccipital, several dorsal vertebrae, partial sacrum, caudal vertebrae 1 to 27, left pectoral girdle and forelimb elements, right scapulocoracoid, left sternal plate, femora, tibia, fibula, ribs from Como Bluff Quarry 1, Albany County, Wyoming.

Cotypes—All paratypes from Como Bluff Quarry 1. YPM 1900 (holotype of *Morosaurus impar*), sacrum; YPM 1903, coracoids, right scapula, left pubis, ischia, left femur; YPM 1905, a fairly complete skull, all cervical vertebrae, most or all dorsal vertebrae, partial sacrum (formerly YPM 1900), 12 anterior-mid caudal vertebrae, some chevrons, coracoids, scapulae, left humerus, right ulna, right ischium, femora, tibiae, fibulae, some pes elements.

Range—Middle and upper lower Morrison Formation (Late Kimmeridgian, Jurassic) in south-central Wyoming, Colorado, and New Mexico.

Referred specimens—DMNH 2850, three mid dorsal vertebrae from DMNH Quarry 3, Garden Park, Colorado, FMNH P25118 (paratype of *Morosaurus grandis*), right scapulocoracoid (= FMNH P6670) from Riggs Quarry #12, Mesa County, Colorado. This individual includes 20 (?) presacral vertebrae and sacrum (=FMNH P6639, 7792, 7793, 7794, 7795, 7796, 7797, 7798, 7799, 7800, 7801), but two dorsal vertebrae were exchanged to Professor Edward L. Holt at Mesa County Junior College in Grand Junction, Colorado in 1947 (William E. Simpson, written communication, 2004). GMNH-PV 101, nearly complete adult skeleton (McIntosh et al., 1996a) from just northeast of Medicine Bow, Wyoming; KUVF 1354, four dorsal vertebrae from the Freezout Hills Quarry, Wyoming; NMMNH P-21094, partial skull and jaw, isolated teeth, mid cervical vertebra, mid- and pos-

terior dorsal vertebrae, pubis, humerus from San Ysidro Quarry, central New Mexico; YPM 1902, ilium [same individual as YPM 1905(?)] from Como Bluff Quarry 1; YPM 1907, premaxillae, maxillae, left frontal and parietal, postorbitals, quadrates, pterygoids, ectopterygoid, supraoccipital, exoccipitals, opisthotics, right prootic, right laterosphenoid, basioccipital, basisphenoid, parasphenoid, dentary fragment, centra and neural arches of 22 (?) caudal vertebrae, ischia from Como Bluff Quarry 3; YPM 1908 (holotype of *Pleurocoelus montanus*), some neural arches and centra of disarticulated anterior (and mid-?) dorsal vertebrae, centra of proximal caudal vertebrae, humeri, partial right femur from Como Bluff Quarry 1.

Emended Diagnosis—A species of *Camarasaurus* with a tall neural arch in dorsal vertebrae from no. 3 to 8, T-shaped neural spine from anterior view of caudal vertebrae from no. 1 to 5 or 6.

CAMARASAURUS LENTUS (Marsh, 1889)

Morosaurus lentus Marsh, 1889:331.

Uintasaurus douglassi Holland, 1924:119.

Camarasaurus annae Ellinger, 1950:225.

Camarasaurus lentus: McIntosh 1981:12.

Camarasaurus lentus McIntosh 1990b:348.

Holotype—YPM 1910, from Quarry 13 at Como Bluff, Albany County, Wyoming. The specimen is mounted at YPM and consists of the jaws, partial braincase, 11 cervical vertebrae, 12 dorsal vertebrae, five sacral vertebrae except neural arch of sacral no. 5, 14 proximal and mid-caudal vertebrae, most (?) distal caudal vertebrae, left scapula, right coracoid, humeri, left ulna, ilia, right pubis, left ischium, left femur, tibiae, left fibula, left pes, many chevrons. Plaster coats most presacral vertebrae, and neural arches of most cervical and some dorsal vertebrae are reconstructed. The mid-section of both ilia are lengthened by plaster.

Range—Lower-middle Upper Morrison Formation (Late Kimmeridgian, Late Jurassic) in Wyoming, and eastern and central Utah.

Referred specimens—CEU 1694, semi-articulated composite (?) partial skeleton, cervical vertebrae, dorsal vertebrae, sacrum, many caudal vertebrae, scapulae, limb elements, and pelvic bones (this specimen may include more than one individual) from Cleveland Lloyd Quarry, central Utah; CM 8492, dorsal vertebrae no. 1 to 4(?); CM 11069 (holotype of *Uintasaurus douglassi*), four posterior cervical vertebrae and dorsal vertebra no. 1 (McIntosh, 1981); CM 11338, nearly complete articulated juvenile skeleton; CM 11393, skull, two mid-cervical vertebrae [no. 7 and 8 (?) belonging to UMMP V16995 (McIntosh, 1981)], some anterior-mid dorsal vertebrae, right forelimb, right femur, left fibula, right scapulocoracoid, pubis, ischium, ilium, some limb elements, some elements are still unprepared at CM, all the CM specimens above from DNM, Utah; DNM 28, an articulated skull, axis; DNM 975, nearly complete skull on cliff; USNM 13786, nearly complete articulated subadult skeleton from DNM; WDC A, jaw fragments, right quadrate, all disarticulated presacral vertebrae except dorsal vertebra no. 11(?), sacrum, some anterior caudal

vertebrae, scapulocoracoids, left humerus, left ulna, radius, ischia, pubes, femora, fibula; WDC B, braincase, jaw fragments, right quadrate, four anterior-mid-cervical vertebrae, four anterior and a few posterior dorsal vertebrae, sacrum, several anterior and mid-caudal vertebrae, left scapulocoracoid, left humerus, right ulna, right radius, pubes, ischia, and femora; indeterminate WDC specimens, both sides of upper and lower jaws, frontal, lacrimal, jugal, many cranial fragments, two sternal plates, two carpals, eight metacarpals, many cervical and thoracic ribs, and chevrons (including the first chevron). All the WDC specimens from Thermopolis, central Wyoming.

Emended Diagnosis—A species of *Camarasaurus* with relatively short, massive neural arch in anterior dorsal vertebrae (from about no. 3 to 8); gradually expanded top of neural spine in anterior caudal vertebrae (from about no. 1 to 5 or 6).

CAMARASAURUS LEWISI (Jensen, 1988)

Cathetosaurus lewisi Jensen, 1988:121.

Camarasaurus lewisi McIntosh et al. 1996b:74.

Holotype—BYU 9047, consisting of one tooth, cervical vertebrae (nearly complete cervical vertebrae from no. 1 to 8, but largely damaged cervical vertebrae from no. 9 to 12), dorsal vertebrae from no. 8 to 12, sacrum, caudal vertebrae from no. 1 to 26, 18 chevrons; right humerus, radius, ulna, distal carpal, partial right manus (metacarpals I-V, ungula phalanx I-2 and II-1), partial left ilium, left pubis, both ischia from Dominguez-Jones Quarry, Mesa County, Colorado.

Range—Middle Upper Morrison (Late Kimmeridgian-Tithonian, Jurassic) in western Colorado.

Diagnosis—A species of *Camarasaurus* with a very deep, narrow bifurcation of spines of presacral vertebrae persist back from cervical vertebra no. 3 through dorsal vertebra no. 11 with a trace showing in dorsal vertebra no. 12 (McIntosh et al., 1996b).

CAMARASAURUS sp.

Referred specimens—AMNH 690, sacrum, ilium from Bone Cabin Quarry, Como Bluff, Wyoming; AMNH 711, scapulocoracoid, femur, tibia, fibula, ulna, humerus from Reed's Quarry, Wyoming; AMNH 823, humerus, partial left manus from Bone Cabin Quarry, Wyoming; BHI 6200, fairly complete skull, all (?) cervical vertebrae (unprepared), some dorsal vertebrae, femora from Black Hills, eastern Wyoming; BYU 8967, premaxilla; BYU 13007, atlas; BYU 16953, atlas; BYU 17465, sacrum, all the BYU specimens from the Dry Mesa Quarry, western Colorado; CM 584, two cervical vertebrae, eight dorsal vertebrae, 31 caudal vertebrae, ilium, pubis, ischium, scapulocoracoid, from Sheep Creek, Albany County, Wyoming; FHSM VP-14850 (= *Camarasaurus supremus*?), a few posterior dorsal vertebrae, ischium, femur, and rib fragments from Comanche National Grasslands, Colorado; uncatalogued GMNH-PV specimens (= *C. grandis*?) from near the Bone Cabin Quarry Wyoming, 10 dorsal vertebrae, sacral vertebrae, posterior caudal vertebrae, scapula, ulna, ilium, femur, chevron, including perhaps from a few individuals;

KUVP 129714, a few dorsal vertebrae (centra and neural arches), sacrum, some mid caudal vertebrae, right scapula, left coracoid, ilia, chevrons; KUVP 129716 (= *C. supremus*?), partial skull elements, most cervical vertebrae, all dorsal vertebrae, sacrum, most caudal vertebrae, all limb bones, all pectoral and pelvic bones, many ribs, chevrons, both the KUVP specimens from Black Hills, eastern Wyoming; all OMNH specimens (= *C. supremus*?) from the Kenton area, western Oklahoma, including large isolated skeletons of OMNH 1095, mid-cervical vertebra; OMNH 1141, braincase; OMNH 1169, right maxillary; OMNH 1173, mid-cervical vertebra; OMNH 1174, intercentrum of atlas; OMNH 1321, posterior cervical vertebrae; OMNH 1324, posterior dorsal vertebra; OMNH 1239, cervical centrum; OMNH 1336, posterior dorsal vertebra; OMNH 1367, DS 1(?); OMNH 1383, mid-cervical vertebra; OMNH 1457, axial centrum; OMNH 1465, proximal caudal vertebra; OMNH juvenile elements including OMNH 1226, neural arch of cervical; OMNH 1243, posterior cervical centrum; OMNH 1245, posterior cervical centrum; OMNH 1246, cervical centrum; OMNH 1247, mid-cervical centrum; OMNH 1249, mid- or posterior cervical centrum; OMNH 1252, cervical centrum; OMNH 1253, axial centrum; OMNH 1329, posterior dorsal vertebra; OMNH 1262, neural arch of cervical vertebra; OMNH 1268, neural arch of posterior cervical vertebra; OMNH 1269, neural arch of sacral vertebra; OMNH 1273, posterior cervical vertebra (see list in Carpenter and McIntosh, 1994); RTMP 83.35.03, sacrum with both ilia; RTMP 83.35.04, left femur; RTMP 83.35.05, left fibula; RTMP 83.35.06, left tibia, all RTMP specimens from Cleveland-Lloyd Quarry; SDSM 9234, a partial ischium; SDSM 35924, ischium, both SDSM specimens are from western South Dakota near the Black Hills; SMA 0002, fairly complete disarticulated skull (cast at BHI) and nearly complete articulated postcranial skeleton from the Howe Stephens Quarry, Big Horn County, Wyoming; UUV 1045, anterior caudal; UUV 1555, axis; UUV 1859, right maxilla; UUV 1860, right maxilla; UUV 1984, quadrate; UUV 3568, braincase; UUV 3609, left dentary; UUV 3610, right dentary; UUV 3638, quadrate; UUV 4273, axis; UUV 4286, braincase; UUV 4315, mid-caudal vertebra with chevron; UUV 5309, sacrum; UUV 6341, axis; UUV 10070, braincase; UUV 11626, left dentary; UUV 10795, braincases; UUV 22940, isolated anterior caudal vertebrae; all UUV specimens (= *C. lentus*?) from Cleveland-Lloyd Quarry, central Utah; YPM 1904 (the type of *Morosaurus agilis*), originally catalogued as USNM 5384, partial cranial elements, first three cervical vertebrae from Quarry 1 in Garden Park, Colorado.

NOTES ON TAXONOMY

Camarasaurus is one of the more common dinosaurs from the Upper Jurassic in North America. Elements from this medium-large sized sauropod are commonly found throughout the Morrison Formation. However, even though hundreds of bones of *Camarasaurus* have been found, a species-level identification of individual elements is still problematic due to several factors: (1) a significant degree of ontogenetic change between juvenile and adult skeletons, (2) poor understanding of sexually dimorphic

characters, (3) a wide degree of individual morphologic variation, and (4) lack of accurate stratigraphic correlation of the widely distributed localities of *Camarasaurus* (Ikejiri, 2004b; Ikejiri et al., in press).

A reliable species-level identification of *Camarasaurus* is needed to examine the stratigraphic distributions of its species in the Morrison Formation. The taxonomy of *Camarasaurus* has been discussed previously: Ikejiri (2004b), Ikejiri et al. (in press), Madsen et al. (1995), McIntosh (1990a), and McIntosh et al. (1996a, b). Therefore, I briefly review the taxonomy of the four species here. Two morphological characteristics are thought to be significant for discussions of the taxonomy of *Camarasaurus* (Ikejiri et al., in press; McIntosh, 1990a). First, the relatively short, massive base of the neural arches in the dorsal vertebrae of *Camarasaurus lentus* (Fig. 2A) and *C. supremus* (Fig. 2B) can be easily distinguished from the elevated neural peduncle in *C. grandis* (Fig. 2, C) (McIntosh, 1990a). Additionally, this mor-

phology is applied to only no. 2 or 3 to 6 or 7 dorsal vertebrae, but the posterior dorsal vertebrae are similar and are not diagnostic enough to separate them into the three species (Ikejiri, 2004b). Furthermore, based on four growth stages for *Camarasaurus*, the diagnostic feature of *C. grandis* appears in post-juvenile stages (from stage 2 to 4), but is never found in stage 1.

Second, the degree of transverse expansion of the neural spine of the anterior caudal vertebrae can also separate *Camarasaurus lentus* from *C. supremus* and *C. grandis* (Ikejiri et al., in press) (Fig. 3). This morphology is particularly important to separate *C. lentus* and *C. supremus* because both of these species share the massive and relatively short base of the neural arches in the anterior and mid-dorsal vertebrae (Fig. 2). In *C. lentus*, the top of the neural spine is gradually expanded transversely (Fig. 3A-B); however, the two latter species exhibit a T-shaped spine, characterized by a rapid transverse expansion with a constricted mid-spinal shaft (Fig. 3C,D). Generally, the different morphology is

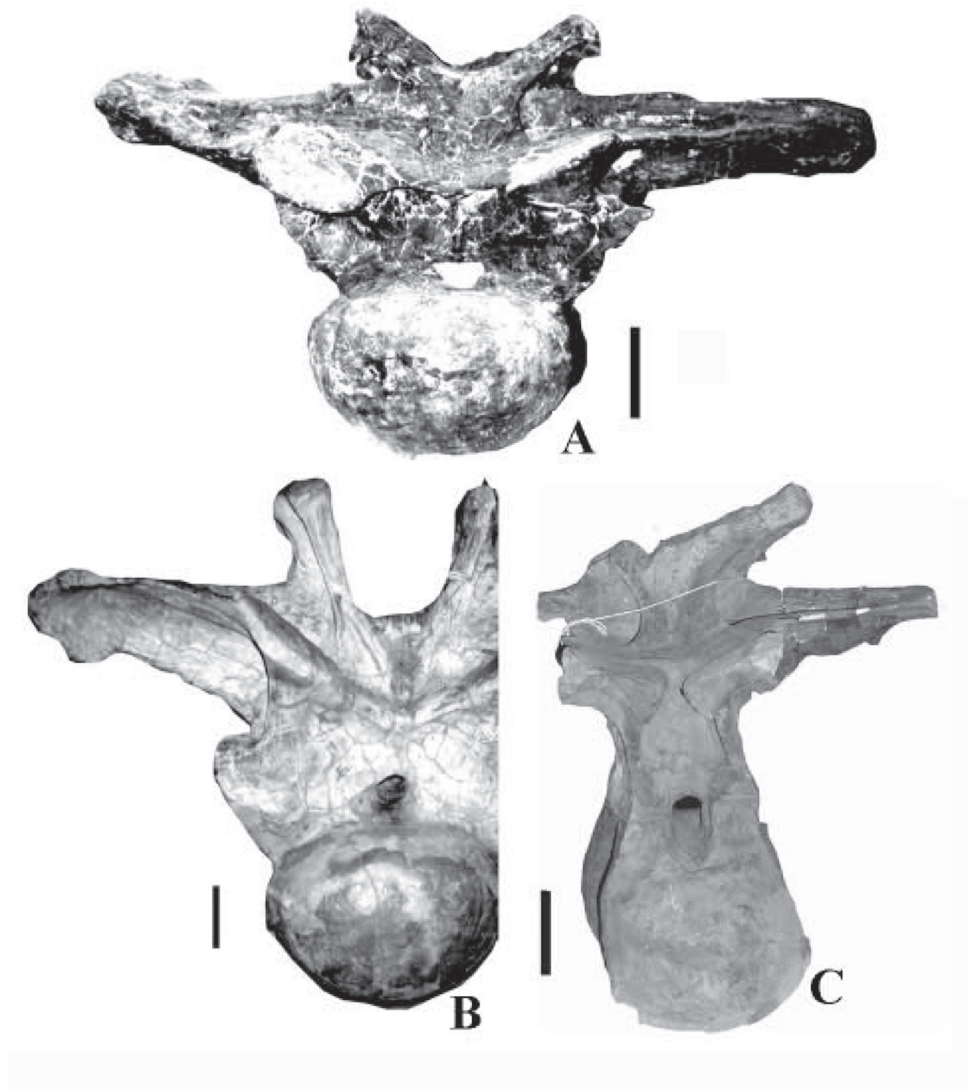


FIGURE 2. Comparison of anterior dorsal vertebrae (no. 3?) among *Camarasaurus*. A, *Camarasaurus lentus*, WDC A (BS-346); B, *C. supremus*, AMNH 5760 (D-X-132); C, *C. grandis*, YPM 1905. Anterior views. Scale bar = 10 cm.

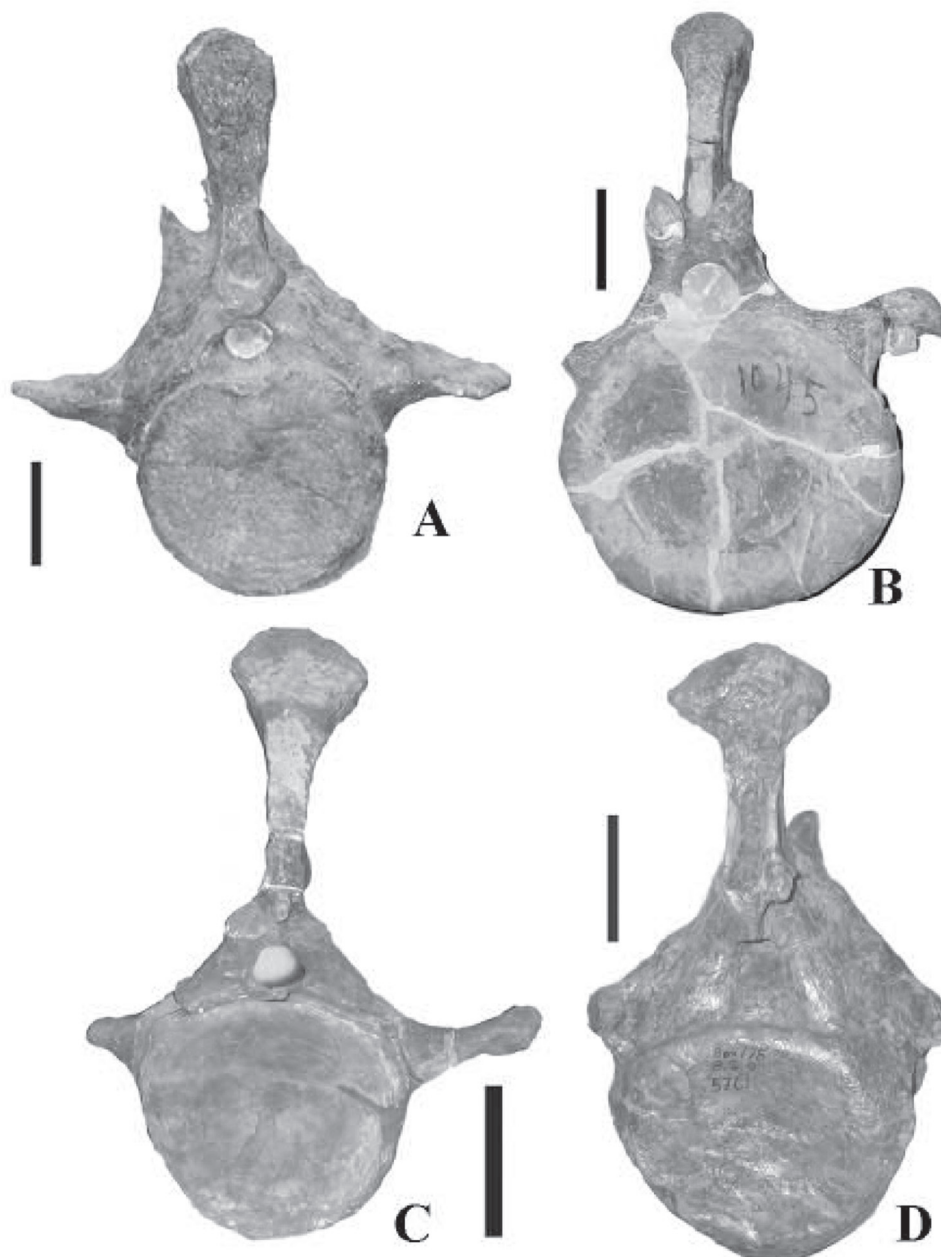


FIGURE 3. Comparison of neural spines in anterior caudal vertebrae of *Camarasaurus*. **A**, *Camarasaurus lentus*, WDC A (BS-152); **B**, *C. lentus* (?), UUVP 1045; **C**, *C. grandis*, YPM 1905; **D**, *C. supremus*, AMNH 5761. Posterior view. Scale bar = 10 cm. **C** and **D** modified from Ikejiri et al (in press).

found from the caudal vertebrae no.1 to 5 or 6, but is not apparent in the more posterior caudal vertebrae (Ikejiri, 2004b).

The very large body size of *Camarasaurus supremus* is diagnostic with the genus (McIntosh, 1990a). However, a significant question is whether or not *C. supremus* is an adult form of *C. lentus* so that they are the same species. Four growth stages are established in *Camarasaurus* based on a number of morphological features (Ikejiri, 2003, 2004a, b; Ikejiri et al., in press), and body size of individuals of relatively similar ontogenetic age can be directly compared. Based on one of the largest individuals of *C. grandis* and *C. lentus*, belonging to the oldest ontogenetic stage (stage 4; see Ikejiri et al., in press), exhibits about the same body

size, and *C. supremus* is, at least, 20 % larger than *C. grandis* and *C. lentus* (see also Morphological Variation and Its Relationship to Stratigraphic Position in DISCUSSION). Therefore, the possibility that *C. lentus* and *C. grandis* are the ontogenetically younger forms of *C. supremus* is rejected.

Only a single specimen is known of *Camarasaurus lewisi*, and this condition makes comparisons with other species or individuals difficult. The most diagnostic character of the species is the bifurcated neural spines from cervical vertebra no. 3 to the last dorsal vertebrae (McIntosh et al., 1996b). However, intraspecific variation is found in the occurrence of the bifurcated neural spines of *C. lentus*; e.g., the last occurrence is dorsal vertebra

no. 6 in CM 11338 and YPM 1910 and dorsal vertebra no. 7 in USNM 13786, and dorsal vertebra no. 8 in WDC A. Furthermore, none of the specimens of *C. grandis* and *C. lewisi* exhibit its articulated mid- and posterior dorsal. Thus, the question still remains whether the character is diagnostic in *C. lewisi* or how much intra- and interspecific variation is present. Well developed entheses (ossified ligaments) in the posterior dorsal and particularly the sacral vertebral regions, linking the spine of one vertebra with the diapophyses of the succeeding vertebra, is suggested to be another significant character of *C. lewisi* (McIntosh et al., 1996b). However, a similar entheses is also found in the sacra of the fully grown individuals of *C. lentus* (WDC A) and *C. supremus* (AMNH 5761), suggesting this feature results from ontogeny (Ikejiri et al., in press). Thus, the taxonomy of *C. lewisi* seems to be problematic, and, perhaps, it may be a synonym of *C. grandis* (see further discussion below).

RESULTS

Biostratigraphy of *Camarasaurus*

Turner and Peterson (1999) presented a comprehensive study of the biostratigraphy of Morrison dinosaurs, including the vertical distribution of the four species of *Camarasaurus*. Stratigraphically, *Camarasaurus* is found in the upper two-thirds of the Morrison Formation. *Camarasaurus grandis* is the oldest known species of the genus, with the first appearance placed about 20 m below the clay change, based on a correlation to the Carnegie Quarry at Dinosaur National Monument (Turner and Peterson, 1999, figs. 7, 10) (Fig. 4). To my knowledge, the geologically youngest record of the species is NMMNH P-21094, which is thought to occur about 20 m below the Kimmeridgian/Tithonian boundary.

The occurrence of *Camarasaurus lentus* is concentrated in the upper Kimmeridgian. All specimens seem to appear above the highest occurrence of *C. grandis*, with the exception of the holotype of *C. lentus* (YPM 1910), which is found about 10 m above the lowest appearance of *C. grandis* (Fig. 4). The highest occurrence of *C. lentus* (WDC A, B) appears slightly above the Kimmeridgian/Tithonian boundary.

A number of large individuals of *Camarasaurus supremus* from near Cope's Nipple, Garden Park, including AMNH 5760, 5761, and DMNH 27228, come from the very upper Morrison Formation (Carpenter, 1998; McIntosh, 1998) (Fig. 4). Many isolated skeletons of *Camarasaurus* from Kenton, Oklahoma (OMNH specimens listed in Systematic Paleontology) and FHSM VP-14850 from the Comanche National Grasslands, southeastern Colorado seem to be assignable to *C. supremus*. The OMNH specimens are from near the Kimmeridgian/Tithonian boundary, which is thought to occur slightly below the Beside Sauropod (BS) Quarry, Thermopolis, Wyoming (Turner and Peterson, 1999). Thus, the stratigraphic occurrence of *C. lentus* (WDC A and B) and *C. supremus* (OMNH specimens) slightly overlaps (Fig. 4). The stratigraphic position of the FHSM specimen is about 20 m below the Jurassic-Cretaceous boundary. According

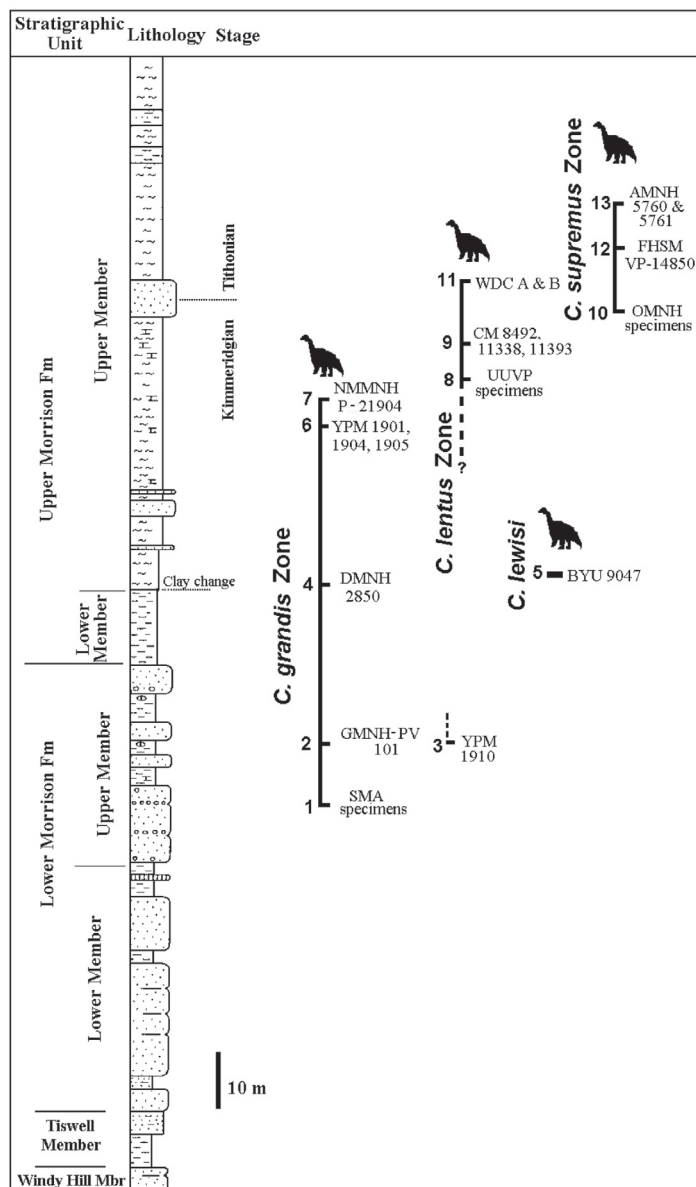


FIGURE 4. Stratigraphic distribution of *Camarasaurus* in the Morrison Formation. Stratigraphic positions are based on Turner and Peterson (1999) and Ikejiri (2002). Numbers for quarries; 1, Howe Stephens Quarry, Big Horn County; 2, WPL *Camarasaurus* Quarry, Albany County; 3, Reed's Quarry 13, East Como Bluff; 4, Lindsey's 1977 Quarry, Garden Park; 5, Dominguez-Jones Quarry, Mesa County; 6, Reed's Quarry 1 & 3, West Como Bluff; 7, San Ysidro Camarasaur Quarry, Sandoval County; 8, Cleveland Lloyd Quarry, Emery County; 9, DNM, Vernal; 10, Stovall Pits near Kenton; 11, BS Quarry, Thermopolis; 12, Cope's Nipple, Garden Park.

to Turner and Peterson (1999), this would place the specimen approximately between the BS Quarry and Cope's Nipple, near the very top of the upper Morrison.

BYU 9047 is the only known specimen of *Camarasaurus lewisi*. Stratigraphically, the specimen was found near the clay change about 10 m above the base of the Brushy Basin Member (Fig. 4) (Jensen, 1988, p. 122; Turner and Peterson, 1999).

definitions assign *Camarasaurus supremus* to the Giant-size Camarasaur Zone and *C. grandis* and *C. lentus* to the Medium-Size Zone. Therefore, the Medium-Size Camarasaur Zone could be further sub-divided into *C. grandis* Zone (lower) and *C. lentus* Zone (higher) (Fig. 5).

Distribution of *Camarasaurus*

Specimens of *Camarasaurus* are known from Colorado, Utah, Wyoming, Montana, New Mexico, Oklahoma, and South Dakota (Ikejiri, 2004b). Although some species of *Camarasaurus* overlap in their geographic ranges, there is a suggestion that the taxa may be somewhat restricted (Fig. 6). For example, *Camarasaurus supremus* is found in southern Colorado and, probably, western Oklahoma. In contrast, no *C. lentus* has been identified from this area, indicating a geographic separation between *C. supremus* and *C. lentus*. Remains of *C. lentus* have been identified from a wide area extending from northern Wyoming to eastern and central Utah. *C. grandis* has been identified from south-central Wyoming, central Colorado, and New Mexico. Although several fragmentary specimens have been recovered from eastern Wyoming, western South Dakota, and Montana (Fig. 6), none have been identified at the species level. *C. lewisi* is known only from a single specimen recovered from the Dominguez-Jones Quarry of western Colorado, so, further discussion of its range is difficult.

DISCUSSION

Morphological Variation and Its Relationship to Stratigraphic Position

Body size among species of *Camarasaurus* is variable (Ikejiri, 2002, 2004b; McIntosh, 1990a). Based on one of the largest known skeletons in each species, *Camarasaurus lewisi* (BYU 9047: ontogenetically, very old individual) is the smallest taxon, about 26 % smaller than *C. supremus* (AMNH 5761). Relative to *C. supremus*, *C. lentus* is 20 % smaller based on the length of axial centra. The body mass of *C. supremus* is estimated to reach up to 47000 kg, which is up to 50 % larger than an average *Camarasaurus* (Foster, 2003, p. 38).

Only a few minor trends of morphological change are found in the skeletons of *Camarasaurus* through the stratigraphic section of the Morrison Formation (Ikejiri, 2002, 2004b). First, the neural spines of the anterior-mid dorsal vertebrae tend to increase in the degree of massiveness. For example, *Camarasaurus grandis*, which is from an earlier period, has slender spines. Furthermore, *C. lentus* (WDC A, B), *C. lentus* (?) (UUV 5461), and *C. grandis* (YPM 1905, KUVP 1354) exhibit a large centrum relative to overall vertebral size (Fig. 7A, B). In contrast, earlier forms (*C. grandis*) tend to have small centra in the anterior dorsal vertebrae (Fig. 7C, D). For example, *C. lentus* (USNM 13786, CM 8492) and *C. grandis* (DMNH 2850) have remarkably small centra. Because the difference cannot be explained by ontogenetic, taxonomic, or sexual dimorphic variation, and they are commonly found among individuals of both *C. lentus* and *C. grandis*, this type of variation is possibly due to population variation (Ikejiri, 2004b).

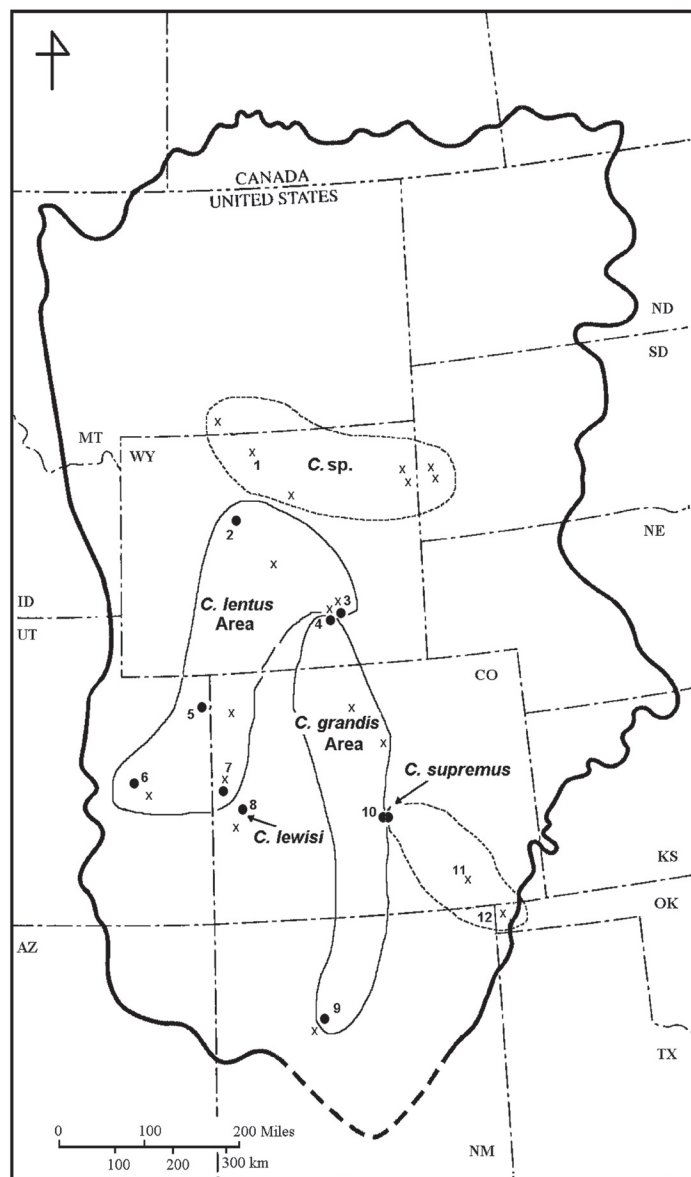


FIGURE 6. Geographic distribution of *Camarasaurus* in Morrison Formation (From Ikejiri et al., in press). Dot mark = identified species. X = *Camarasaurus* sp. Abbreviations for quarries: 1, Howe Stephens Quarry, Big Horn County; 2, BS/S Quarry in Thermopolis; 3, Reed's Quarry 13, East Como Bluff; 4, Reed's Quarry 1 & 3, West Como Bluff; 5, DNM, Uintah County; 6, CLL Quarry in Emery County; 7, Grand Valley, Mesa County; 8, Dominguez-Jones Quarry, Mesa County; 9, San Ysidro Camarasaur Quarry, Sandoval County; 10, Cope's Nipple and Lindsey's 1977 Quarry, Garden Park; 11, Comanche National Grasslands, Otero County, and 12, Stovall Pits near Kenton (Modified from Ikejiri, 2002; Turner and Peterson, 1999).

Interpretation of Distribution

It appears that the biostratigraphic zones of *Camarasaurus* are correlated with their geographic distribution. The early group (*Camarasaurus grandis*) is only found in south-central Wyo-

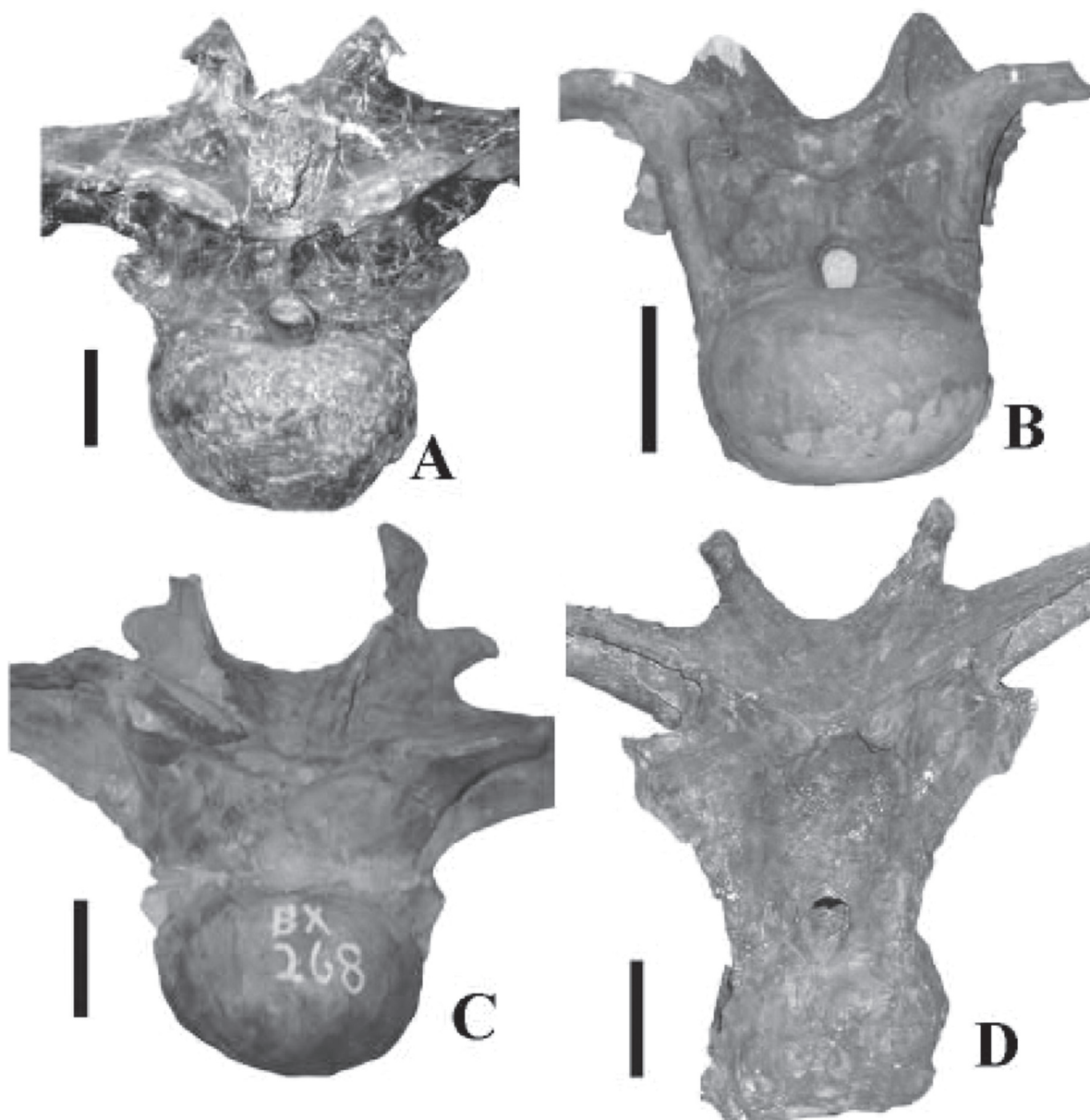


FIGURE 7. Variation in centrum size of anterior dorsal vertebrae of *Camarasaurus*. **A**, *Camarasaurus lentus* (WDC A, dorsal vertebra no. 4) and **B**, *C. grandis*, (KUVF 1354, dorsal vertebra no. 2 or 3) from central and southern Wyoming show a relatively large centrum. In contrast, **C**, *C. lentus* (CM 8492, dorsal vertebra no. 3) from the Dinosaur National Monument and **D**, *C. grandis* (DMNH 2850, dorsal vertebra no. 4?) from Garden Park, Colorado tend to have a relatively small centrum in the anterior dorsal vertebrae.

ming, central Colorado, and New Mexico. The middle biozone (*C. lentus*) is distributed in central Wyoming and eastern and central Utah. *C. supremus* from the very upper Morrison has been found only in southern Colorado-western Oklahoma.

Moreover, evidence of the distribution (Fig. 6) of *Camarasaurus* indicates that a single quarry produces only one species of *Camarasaurus*. I suspect the present geographic distribution does not represent the paleobiogeography of the species of *Camarasaurus*. It is more likely that each species was distributed over a much larger area than the data because populations of extant,

large-bodied animals have a relatively wide distribution. Because the species of *Camarasaurus* are seemingly restricted in space and time, perhaps the rocks containing other species have been eroded away or are not yet exposed, or there was something in the biology of *Camarasaurus* that restricted its distribution.

Interpretation of Taxonomy

Based on the data on the distribution and geologic occurrences of *Camarasaurus*, I suggest a few new insights into the taxon-

omy: (1) *Camarasaurus supremus* differs from *C. lentus*, (2) *C. lewisi* (BYU 9047) may be *C. grandis*, and (3) the holotype of *C. lentus* (YPM 1910) is possibly *C. grandis*. The larger body size of *C. supremus* is thought to be the only feature that distinguishes it from *C. lentus* (McIntosh, 1990a). Additionally, *C. supremus* has a transversely wider (T-shaped) top of the neural spine in the anterior caudal vertebrae than *C. lentus* (Ikejiri, 2004b; Ikejiri et al., in press). This character also allows us to separate the two species more accurately and give us a better understanding of their biostratigraphic and paleobiogeographic occurrences. Although both species seem to co-exist in the Transitional Zone (Figs. 4, 5), no *C. lentus* is known from the *C. supremus* Zone. This evidence also supports the idea that these are indeed two species.

Camarasaurus lewisi cannot seemingly be clearly separated from *C. grandis* (Ikejiri, 2004b). A relatively tall neural arch on the anterior-mid dorsal vertebrae is thought to be the most diagnostic character in *C. grandis* (McIntosh, 1990a), but they are missing in the holotype of *C. lewisi* (BYU 9047). The most diagnostic feature of *C. lewisi* is a bifurcated neural spine throughout the last dorsal vertebrae (McIntosh et al., 1996a). However, this morphology possibly results from an intraspecific variation (Ikejiri, 2004b). The anterior caudal vertebrae of BYU 9047 have T-shaped neural spines, which infers as one of the diagnostic features of *C. grandis* (Ikejiri, 2004b; Ikejiri et al., in press). Furthermore, BYU 9047 is found near the middle of the *C. grandis* Zone (Fig. 5), and *C. grandis* is common in northern-central Colorado (Fig. 6). Therefore, both morphological and biostratigraphic data indicate that BYU 9047 is *C. grandis*, but more data are needed to be certain of this.

It should be noted that the holotype of *Camarasaurus lentus* (YPM 1910) is a juvenile (stage 1 in my previous study) (see Ikejiri, 2002, 2004b; Ikejiri et al., in press), and, in *Camarasaurus*, juveniles do not contain diagnostic characteristics in any species that are found in mature individuals (Ikejiri, 2004b). This evidence raises the question of whether or not the identification of YPM 1910 is correct. Because the holotype of *C. lentus* is found in the *C. grandis* Zone (the upper lower Morrison Formation; Fig. 4), the holotype of *C. lentus* may be a juvenile *C. grandis*.

CONCLUSIONS

Paleobiogeographically, *Camarasaurus lentus* occurs in Wyoming and Utah and *Camarasaurus supremus* in south-central Colorado to western Oklahoma; *C. grandis* is known from south and central Wyoming, central Colorado, and New Mexico. However, the geographic distribution may be due to stratigraphic occurrences, as appropriate beds may not be exposed or were eroded. *Camarasaurus* might have had a much wider distribution in the Rocky Mountain area than indicated by its distribution.

Camarasaurus forms five biozones in the upper Morrison: (1) no *Camarasaurus* Zone (early-mid Kimmeridgian), (2) *Camarasaurus grandis* Zone (mid Kimmeridgian), (3) *C. lentus* Zone (late Kimmeridgian), (4) transitional Zone (early Tithonian), and (5) *C. supremus* Zone (Tithonian). Because juveniles do not contain diagnostic characteristics in any species of *Camarasaurus*, the holotype of *C. lentus* may be a juvenile *C. grandis*.

Three suggestions can be important for the taxonomy of *Camarasaurus*: (1) *Camarasaurus supremus* differs from *C. lentus*, (2) *C. lewisi* may be the same taxon as *C. grandis* or *C. lentus*, and (3) the holotype of *C. lentus* (YPM 1910) may be a *C. grandis*.

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APPENDIX I. List of selected specimens of *Camarasaurus* in each biozone (See also Figure 4).

Biozone	Species	Specimen*	Remarks
<i>C. Supremus</i> Zone	<i>C. supremus</i>	AMNH 6760, 5761	
<i>C. supremus</i> Zone	<i>C. supremus</i>	DMNH 27228	
<i>C. supremus</i> Zone	<i>C. sp.</i>	FHSM VP-14850	Possibly, <i>C. supremus</i>
<i>C. supremus</i> Zone?	<i>C. sp.</i>	KUVP 129714, 129715, 129716	Possibly, <i>C. supremus</i>
<i>C. supremus</i> Zone?	<i>C. sp.</i>	SDSM 9234, 35924	
Transitional Zone	<i>C. sp.</i>	OMNH specimens	Possibly, <i>C. supremus</i>
Transitional Zone	<i>C. lentus</i>	WDC A, B	
Transitional Zone?	<i>C. sp.</i>	BHI 6200	
<i>C. lentus</i> Zone	<i>C. lentus</i>	CM 8492, 11069, 11338, 11393	
<i>C. lentus</i> Zone	<i>C. lentus</i>	UUVP specimens	
<i>C. lentus</i> Zone	<i>C. lentus</i>	RTMP specimens	
<i>C. lentus</i> Zone	<i>C. lentus</i>	UMMP V16995	
<i>C. lentus</i> Zone	<i>C. lentus</i>	DNM 28, 965	
<i>C. lentus</i> Zone	<i>C. lentus</i>	USNM 13786	
<i>C. grandis</i> Zone	<i>C. grandis</i>	NMMNH P-21904	
<i>C. grandis</i> Zone	<i>C. sp.</i>	CM 584	
<i>C. grandis</i> Zone	<i>C. grandis</i>	FMNH P25118	
<i>C. grandis</i> Zone	<i>C. lentus</i>	YPM 1910	Possibly, <i>C. grandis</i>
<i>C. grandis</i> Zone	<i>C. grandis</i>	YPM 1901, 1902, 1904, 1905, 1908	
<i>C. grandis</i> Zone	<i>C. sp.</i>	BYU 13007, 16953, 17465	
<i>C. grandis</i> Zone	<i>C. lentus</i>	DMNH 2850	
<i>C. grandis</i> Zone	<i>C. sp.</i>	USNM 5384	
<i>C. grandis</i> Zone	<i>C. grandis</i>	KUVP 1354	
<i>C. grandis</i> Zone	<i>C. grandis</i>	GMNH-PV 101	
<i>C. grandis</i> Zone	<i>C. sp.</i>	AMNH 620, 690, 711	
<i>C. grandis</i> Zone	<i>C. sp.</i>	SMA 0002	

* See additional information for the listed specimens in Systematic Paleontology.

Note: The list ordered by stratigraphic position from younger (top) to older (bottom).