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SLENDER AND ROBUST SKELETAL MORPHOTYPES OF *CAMARASAURUS*
(DINOSAURIA, SAUROPODA) FROM THE MORRISON FORMATION
(UPPER JURASSIC) OF THE ROCKY MOUNTAIN REGION AND THEIR
IMPLICATIONS FOR SEXUAL DIMORPHISM

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ABSTRACT

The sauropod dinosaur *Camarasaurus* from the Morrison Formation (Upper Jurassic) of the Rocky Mountain region exhibits slender and robust skeletal morphotypes. The three most common species, *Camarasaurus lentus*, *C. grandis* and *C. supremus*, exhibit similar kinds of intraspecific variation in some bones. This intraspecific variation can be characterized as either continuous or discontinuous. Continuous variation (e.g., robustness of limb bones) indicates either robust or slender morphotype, although those characteristics need to be quantified. Discontinuous variation (e.g., the presence or absence of specific vertebral laminae) refers to distinct dimorphic features, which subsequently require identification to either the slender or robust type for these characters. Once all characteristics examined in different bones are compared, then the robust and slender morphs of the skeleton are identified. The two types of the skeletons are commonly found in these three species, and the dimorphic characteristics tend to be more evident in mature individuals than in juveniles. Therefore, the robust and slender skeletal morphs most likely represent sexual dimorphism. However, the identification of male and female is still difficult due to a lack of direct evidence such as sexual organs, courtship displays or mating behaviors.

INTRODUCTION

Males and females exhibit morphologically distinct phenotypes in many species, and such knowledge about sexual dimorphism features is important for studies of various topics in evolution. However, studies of sexual dimorphism are challenging especially in extinct taxonomic groups such as non-avian dinosaurs because of a lack of direct evidence, such as sexual organs, and courtship and mating behaviors. Padian et al. (2005) noted that sexual dimorphism of dinosaurs was generally based on weak evidence that makes these kinds of studies difficult due to very limited sample size, poor preservation (e.g., distortion due to diagenetic processes) or possibly the absence of dimorphic characteristics in the skeleton. Such limited information in fossil skeletons can lead to problems for understanding of sexual dimorphic variation, which is particularly true

in many dinosaurian species (Molnar, 2005). Because of limited sample size, such difficulty in the examination of sexual dimorphism is also true in the largest known terrestrial animals, sauropods (Chapman et al., 1997; Carpenter 1999). Moreover, most sauropods seem not to have identical sexual displays (e.g., frills, horns) that can be preserved in fossils.

In this paper, various kinds of dimorphic variation in the Jurassic sauropod *Camarasaurus* are discussed. Three species of *Camarasaurus* have a number of articulated or fairly complete skeletons that provide one of the largest samples for sauropods (Foster, 2001). These specimens allow examining different types of intraspecific (e.g., ontogenetic, geographic) and interspecific variation in the genus (Ikejiri, 2004). Based on size, shape and absence or presence of specific characteristics, the skeletons of *Camarasaurus* tend to

be separated into two morphotypes: either slender or robust morph. The two skeletal morphotypes possibly represent sexual dimorphism in each species of *Camarasaurus*. To test this hypothesis, the patterns of various dimorphic characters that appear in the skeletons are analyzed separately in each individual and in four different ontogenetic stages. An analysis at the individual level shows that how either robust or slender types of characteristics are consistently found in the skeleton. Combining the data of the ontogenetic stages may allow a further investigation of the timing of possible sexual dimorphism. Understanding the series of the dimorphic characteristics also helps to reduce oversplit taxonomy of *Camarasaurus* at the species level.

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; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DNM, Dinosaur National Monument, Jensen, Utah; GMNH-PV, Gunma Museum of Natural History Vertebrate Paleontology, Gunma, Japan; KUVVP, University of Kansas Vertebrate Paleontology, Lawrence; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman; RTMP, Royal Tyrrell Museum Paleontology, Drumheller, Alberta; USNM, National Museum of Natural History, formerly United States National Museum, Washington DC; UUVVP, University of Utah Vertebrate Paleontology, Salt Lake City; WDC, Wyoming Dinosaur Center, Thermopolis; YPM, Yale Peabody Museum, New Haven, Connecticut.

MATERIALS

Camarasaurus is known only from the Jurassic Morrison Formation (Kimmeridgian to Tithonian in age) of the Rocky Mountain Region. Four species, *C. grandis*, *C. lentus*, *C. lewisi* and *C. supremus*, are generally accepted based on a number of fairly complete skeletons (Upchurch et al., 2004). General information (e.g., identification of species, preserved elements, fossil localities, and stratigraphic occurrences) of these representative specimens that are examined in this study is listed in Ikejiri (2005).

Although multiple skeletons were recovered in *C. grandis*, *C. lentus* and *C. supremus*, *C. lewisi* consists of only a single specimen (the holotype BYU 9047: McIntosh et al. 1996b). Although the BYU specimen provides information for general comparisons with *C. grandis*, *C. lentus* and *C. supremus*, the three common species were preliminary examined for this study.

VARIATION IN SKELETON OF *CAMARASAURUS* Cranial Skeleton

The cranial and jaw elements are generally less useful for an identification of the species level than the postcranial elements because of lack of diagnostic features (Madsen et al., 1995; McIntosh et al., 1996a). However, Madsen et al. (1995) suggested two morphotypes of cranial bones in the genus, such as the lacrimals (robust or slender), the pterygoid processes (directed laterally or ventrolaterally) and the paraoccipital processes (directed laterally or ventrolaterally). McIntosh et al. (1996a) found a relatively gracile lacrimal in the mature individual of *C. grandis* (GMNH-PV 101). The lacrimal has a narrow mid-shaft, which is

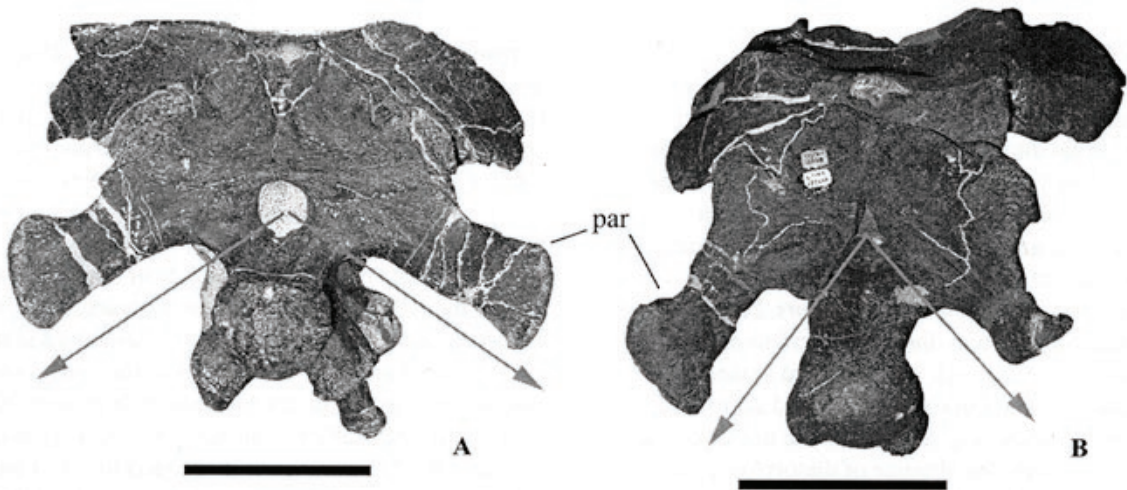


FIGURE 1. Two morphotypes in braincase of *Camarasaurus lentus*. Posterior view. A, UUVVP 10795; B, UUVVP 3568. The angle of the paraoccipital processes (par), which is indicated by gray arrows, is wider in A (robust type) than B (slender type). Scar bar = 10 cm.

narrower than half the width of the proximal shaft (near the lacrimal foramen) in either lateral or medial view. This slender type of the lacrimal is also found in *C. lentus* (CM 11393, DNM 28, UUV 10070) (Appendix 1, characteristic 2). In contrast, a wide mid-shaft relative to the proximal width is found in *C. lentus* (CM 11338, USNM 13786, UUV 3371) and *Camarasaurus* sp. (BHI 6200).

Massive, heavily built braincases are the most commonly preserved elements of the cranium of *Camarasaurus*. Those elements should be worthwhile to look into various types of morphological variation. Madsen et al. (1995) noticed that the occipital condyle of *C. lentus* (DNM 28) is more heavily-built than *C. grandis* (GMNH-PV 101) even though the two skulls are about the same size. This comparison is based on the two different species. However, a number of isolated braincases of *C. lentus* from the Cleveland Lloyd Quarry in central Utah can be separated into either a slender and robust type, too. Based on qualitative comparisons, UUV 3568 and 10070 have a relatively small diameter of the occipital condyle with a short and dorsally constricted base of the condyle in lateral view. Those morphological features differ from UUV 4286 and 10795 that has a heavily-built overall structure. Although the two types of the braincases are found in other specimens of *C. lentus* and other species (Appendix 1, character 1), the sample size may be too small to quantify the intraspecific variation of the braincases.

Two morphotypes can be distinguished on the basis of the angle of the paraoccipital processes (from the midsagittal axis through the foramen magnum in posterior view) (Fig. 1). This angle exceeds 110° that is

found in a number of specimens of *C. lentus* (e.g., CM 11338, 11393, UUV 10795, WDC B), although other specimens show less than 110° of the angle (e.g., DNM 28, USNM 13786, UUV 3568, WDC A) (Appendix 1, characteristic 3). Any braincases that obviously lost the original angle of the paraoccipital processes (e.g., due to distortion during the fossilization or preparation) are easily distinguished, and these elements are not included here. In addition, the relatively narrow angles of the paraoccipital processes tend to correlate with the slender morph of the braincase.

The quadrates can be separated into either slender or robust type based on a degree of an expansion of the distal end (the articular surface of the articular). The slender type of the quadrate is found in *C. lentus* (DNM 28, UUV 1984) and *C. grandis* (YPM 1905, GMNH-PV 101) that exhibit a constricted shaft in the distal end that also has a hooked anterior extension in either medial or lateral view. In contrast, the entire distal end tends to be robust transversely, but the anterior hook is not well-developed in *C. lentus* (CM 11393, USNM 13786), *Camarasaurus* sp. (UUV 1984, 3638) and *C. grandis* (YPM 1905). Their quadrates are considered the robust type (Appendix 1, character 4).

Axial Skeleton

Cervical Vertebrae — Axes tend to be separated into two phenotypes based on morphology of the centrum (Fig. 2) (Appendix 1, characteristic 5 and 6). Both slender and robust types of the axis are identified in two mature individuals of *C. lentus* from a single quarry near Thermopolis, Wyoming. The slender morph of the axis (WDC A) is characterized by a transversely narrow mid-centrum (Ikejiri et al., 2005, Fig. 6.3C).

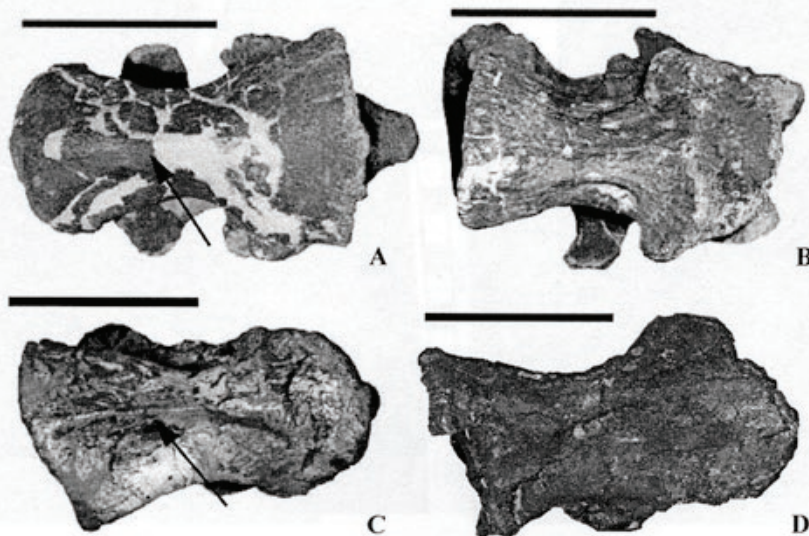


FIGURE 2. Two morphotypes in axes of *Camarasaurus*. Ventral view. A, *C. grandis* (GMNH PV-101); B, *C. grandis* (YPM 1905); C, *C. supremus* (AMNH 5761); D, *C. supremus* (DMNH 27228). A and C are slender type. B and D are robust type. An arrow indicates a ventral keel in A and C. Scale bars = 10 cm.

The mid-section of the ventral surface is strongly constricted medially and forms a developed ridge which runs anteroposteriorly (Fig. 2A, C). In contrast, the whole structure of another axis (WDC B) is more robust than that of WDC A. This robust type is characterized by a transversely wide and flat ventral centrum, but a lack of the medial constriction or the keel-like ridge (Fig. 2B, D). Most axes of fully-grown individuals show either type of the axis. However, the slender type of the axial centrum seems rarely to occur in juveniles, including *C. lentus* (CM 11338, YPM 1910) and *Camarasaurus* sp. (OMNH 1253) (Appendix 1).

A single neural spine (or bifurcated spines with a very shallow crest) is generally found in the anterior cervical vertebrae (no. 3 to approximately no. 6) in *Camarasaurus*. The anterior cervicals show two morphotypes: either the presence or absence of the spinoprezygapophyseal lamina (Ikejiri et al., 2005). In some individuals (Appendix 1, character 7), a well-developed spinoprezygapophyseal lamina strongly connects the top of the neural spine (or metapophysis) and the lateral edge of the prezygapophysis (Fig. 3A). In contrast, the connection is absent, and a short lamina is placed only on the anterolateral margin of a neural spine, but stops near the base of the neural spine (Fig. 3B). It should be noted that the two laminar morphologies are consistent in an articulated anterior cervicals of, at least, *C. lentus* and *C. grandis* (Appendix 1, characteristic 7). Thus, either the presence or absence of the spinoprezygapophyseal lamina is possibly useful to separate individuals into the two types.

Dorsal Vertebrae — The anterior and mid-dorsal vertebrae have two types of the centropostzygapophyseal and posterior centrodiapophyseal laminae (Ikejiri et al., 2005). The large *C. lentus* (WDC A) has the slender type of the dorsal vertebrae based on dorsoventrally elongated tall centropostzygapophyseal laminae that connect to the edge of the dorsal surface of the posterior centrum (Appendix 1, characteristic 8) (Fig. 4B). The specimen also shows relatively narrow and constricted posterior centrodiapophyseal laminae that make the entire structure of the vertebra look slender (Fig. 5) (Appendix 1, characteristic 9). In contrast, the robust type of the dorsal vertebrae exhibit much shorter (terminating above the neural canal) thick centropostzygapophyseal laminae (Fig. 4B) and laterally expanded posterior centrodiapophyseal lamina (Fig. 5), as found in another large *C. lentus* (WDC B). The two types of the laminae are generally found in the dorsal no. 2 to no. 5 in WDC A and B. Although the occurrence of the two laminar morphologies in the dorsal series possibly varies, a number of articulated skeletons and isolated anterior dorsals of *C. grandis*, *C. lentus* and *C. supremus* can be separated into either type. Thus, the two laminar morphologies are useful for separating the anterior dorsals into the two morphotypes in the genus.

Caudal Vertebrae — McIntosh et al. (1996a, p. 29) suggested that two types of the neural spine (either transversely narrow or wide type) are found in the anterior caudal vertebrae of *Camarasaurus*: (Appendix 1, characteristic 10). These types of the spine can be



FIGURE 3. Variation in spinoprezygapophyseal lamina in anterior cervical vertebrae of *Camarasaurus lentus*. Dorsal view. **A**, WDC A (cervical no. 3); **B**, WDC B (cervical no. 4). Dorsal view. In WDC A, SPRL directly connects from the top of the neural spine (NS) to the prezygapophysis (PRZ). This lamina is absent in B; a short lamina from the top of the neural spine (NS) stops near the base of the spine (white arrow). This variation is commonly found in at least cervical no. 3 to 5 in the two specimens.

distinguishable up to caudal no. 5 to 8, but the degree of the spinal expansion decreases rapidly in the more posterior caudal vertebrae that make a separation of the two morph types difficult.

Some individuals of *C. grandis* and *C. supremus* have a T-shaped spine that is characterized by a strong transverse expansion of the spine with a constricted shaft. Such a sharp expansion is absent in all individuals of *C. lentus*. Thus, this morphology is possibly useful to separate *C. lentus* from *C. grandis* and *C. supremus* (Ikejiri, 2005, Fig. 3). However, it should be noted that the three species commonly exhibit both the narrow and wide types of the spine that indicate the existence of dimorphism.

A pair of fused centra in the mid-caudal vertebrae was thought to be a result of a sexual dimorphism rather than a pathologic character found in *Apatosaurus*, *Camarasaurus* and *Diplodocus* (Rothschild, 1994; Chapman et al., 1997). The authors suggested that fusion seems to support an extra weight in the tail of females as they kept their tails elevated. However, in *Camarasaurus*, fused mid-caudals that are associated with a skeleton are too scattered to investigate this hypothesis further. Moreover, ossification of various vertebral elements (e.g., centrum, neural arch, caudal rib) generally progresses during ontogeny. This general trend implies that these ossified caudals might result

from aging. More data are needed to draw a conclusion in *Camarasaurus*.

Appendicular Skeleton

Limb Bones — For comparing a degree of robustness of limb bones, various measurements were taken (e.g., greatest length, transverse and anteroposterior breadths of the proximal end, distal end, and mid-shaft, least circumference). Because both proximal and distal ends are often damaged in those specimens of *Camarasaurus*, those parameters from the mid-shaft, which provides the largest data set, are the most useful. Ratios of the least circumference-to-the greatest length (LC/L) and the transverse mid-shaft breadth at the least point-to-greatest length (MB/L) are used for comparisons of the robustness of the limb bones. Using the two different measurements is important because some limb bones are badly deformed being flattened transversely or sagittally. When a limb element is extremely flattened, the ratio of MB/L can be much higher than expected.

The variability of robustness in five limb bones is shown in table 1. A result of the fibulae is excluded in the table because the sample size is too small. All data were taken from 14 skeletons that include juveniles to adults, but isolated limb elements are not used for two reasons. First, two morphotypes of the skeletons are of particular interest, instead of isolated elements. Second,

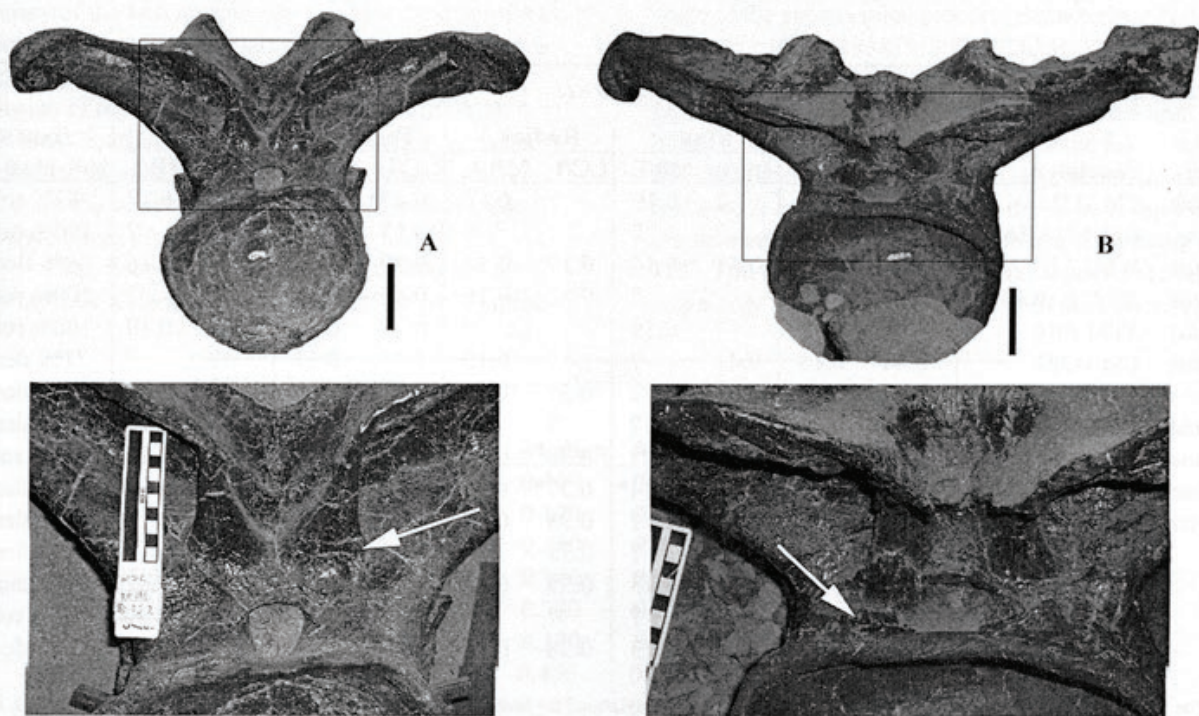


FIGURE 4. No.2 dorsal vertebrae of *Camarasaurus lentus*. Posterior views. A, WDC B (BS-191) with short centropostzygapophyseal laminae (robust morphotype), which stops above the neural canal (white arrow). B, WDC A (BS-191) showing long centropostzygapophyseal laminae (slender morphotype) reaching the dorsal margin of the centrum (white arrow).

isolated limb bones are generally difficult to identify at the species or even the generic level.

A summary of statistics of the limb ratios is shown in table 2. Sample size (N), variables (LC and MB) and variability (S.D.) are primarily important. A relatively low sample size of the tibiae may be critical in the data set. Apparently, the LC/L ratio of the humeri and femora has much greater variability than the lower limb bones, indicating that the two upper limb bones are possibly more useful than the lower limb bones. Although the LC/L ratio is higher in the humeri, radii and femora than the ulnae and tibiae, the two lower limb bones exhibit higher ratios of MB/L. Thus, the MB/L ratio may be more useful for the ulnae and tibiae than the LC/L ratios. Median is used for the identification of the robust and slender types of the limb bones because it gives the two different ranges in the samples (table 1; Appendix 1, characteristics 11-15).

Pelvic Girdles — The large *C. lentus* (WDC A) has a strongly curved pubic blade forming a broad apron (Ikejiri, 2004). The pubis exhibits a strongly curved ischial peduncle with a step-like shape; the mid-section of the pubis directs medially rather than ventrally. Such a strong curvature is also found in a mature *C. grandis* (GMNH-PV 101) (Fig. 6) and *C. supremus* (AMNH 5761 Pb.1 and Pb.2). In contrast, the ischial peduncle has a much straighter shape in some other individuals; e.g., *C. supremus* (AMNH 5761 Pb.3

and Pb.4, DMNH 27228), *C. lentus* (USNM 13786), *C. grandis* (NMMNH 21094) (Appendix 1, characteristic 17).

A fairly large pelvis of *Camarasaurus* sp. (BYU 17465) has strongly flared preacetabular processes of the ilium (Tidwell et al., 2005). The same type of the iliac blade is also found in *C. grandis* (GMNH-PV 101; Fig. 6), *C. lentus* (WDC A), *C. supremus* (AMNH 5761; Osborn and Mook, 1921, Fig. 90) and *Camarasaurus* sp. (AMNH 690; Fig. 7B). In contrast, the curvature of the preacetabular processes of the ilium is much gentler in *Camarasaurus* sp. (RTMP 83.35.03) (Fig. 7A) and *C. supremus* (AMNH 5761; Osborn and Mook, 1921, Fig. 89). Thus, this morphology possibly separates the ilium of *Camarasaurus* into two morphotypes (Appendix 1, characteristic 16), although the anterior margin of the ilium is damaged in many specimen. Additionally, immature individuals such as *C. lentus* (CM 11338, USNM 13786, YPM 1910) and *C. grandis* (YPM 1901, 1905) tend to have gently curved preacetabular processes. These young specimens indicate that this morphology may change during ontogeny.

DISCUSSION

Two Types of Characteristics

A total of 17 characteristics (Appendix 1) are considered binary for identifying the two skeletal morphs of *Camarasaurus*. Using the binary statuses is advantageous for examining a general pattern of either

TABLE 1. Degree of robustness in limb bones of *Camarasaurus*.

Species	Specimen	Humerus		Ulna		Radius		Femur		Tibia		Type in individual (%)
		LC/L	MB/L	LC/L	MB/L	LC/L	MB/L	LC/L	MB/L	LC/L	MB/L	
<i>C. lentus</i>	CM 11338	?	0.20	?	0.19	?	0.12	0.47*	0.20	?	0.17	83% robust
<i>C. lentus</i>	USNM 13786	0.47	0.18	?	?	?	?	0.53	0.20	?	?	100% robust
<i>C. lentus</i>	WDC A (BS-107)	0.49	0.17	0.41	0.14	0.39	0.14	0.39	0.15	0.49	0.16	60% slender
<i>C. lentus</i>	WDC B (BS-13)	?	?	?	?	0.42	0.16	0.45	0.18	?	?	100% robust
<i>C. lentus</i>	YPM 1910	0.50	0.17	?	0.19	?	?	0.47	0.18	?	0.19	100% robust
<i>C. lentus</i>	CM 11393	0.44	0.15	0.41	?	?	0.15	0.45	0.17	?	?	71% slender
<i>C. grandis</i>	FMNH P25182	0.44	0.16	0.39	0.12	0.37	0.13	0.45	?	?	?	86% slender
<i>C. grandis</i>	GMNH-PV 101**	0.42	0.15	?	?	?	?	0.42	0.15	0.46	0.13	100% slender
<i>C. grandis</i>	YPM 1905	0.50	0.17	?	?	0.38	0.15	0.45	0.17	0.45	0.17	63% robust
<i>C. grandis</i>	YPM 1901	0.44	0.16	0.38*	0.14*	0.37*	0.11*	?	?	?	?	83% slender
<i>C. lewisi</i>	BYU 9047*	0.44	0.15	?	?	0.38	0.13	?	?	?	?	100% slender
<i>C. sp.</i>	AMNH 711*	0.42	0.14	0.35	?	0.33	?	?	?	?	?	75% slender
<i>C. sp.</i>	AMNH 823*	0.45	0.17	0.38	0.13	0.35	0.15	?	?	?	?	68% slender
<i>C. sp.</i>	BHI 6200	?	?	?	?	?	?	?	0.19	?	?	100% robust
<i>C. sp.</i>	KUVP 129716	0.49	0.18	0.38	0.13	0.38	0.13	?	0.17	0.47	0.18	67% slender

Note: The robust or slender type represents either male or female. Abbreviations for limb ratios: L, greatest length; LC, least circumference; MB, least mid-shaft breadth. Morphotype of each individual (right column) is identify based on a total number of robust (greater than median) or slender (equal to or less than median) ratios.

*Measurement from McIntosh et al (1996b). **Measurements from McIntosh et al (1996a). Morphotype is identified by a number of slender or robust ratios (based on median)-to-a total number.

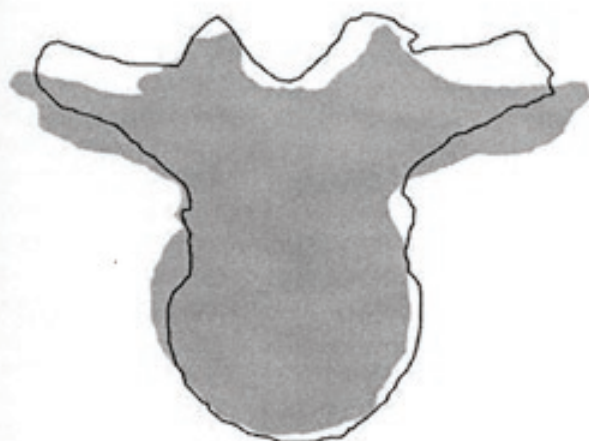


FIGURE 5. Two morphotypes of anterior dorsal vertebrae of *Camarasaurus*. Gray color represents slender type (WDC A:BS-271). Black line shows more laterally expanded type (WDC B:BS-191). The slender morphotype (gray) shows more medially constricted posterior centrodiapophyseal lamina than the robust morphotype (black line). Two types of the posterior centrodiapophyseal lamina are also shown in Figure 4.

robust or slender skeletal type. This procedure possibly allows a further investigation of sexual dimorphism.

The 17 characteristics are classified into either continuous or discontinuous variation (Table 3). The continuous variation consists of sequential morphological changes. Because this type of variation lacks a clear boundary of the two morphs, data need to be quantified. However, using the continuous variation is advantageous for identifying slender or robust morphotypes; e.g., the degree of robustness of the limb bones (Table 1). A direct identification of the two morphs is also found in three characteristics from the cranium, three characteristics from the vertebrae and two characteristics from the pelvic bones (Table 3).

Five discontinuous characteristics do not directly indicate a slender or robust morphotype (e.g., the

presence or absence of the ventral keel in the axis or the spinoprezygopophyseal laminae in the anterior cervical vertebrae; Table 3). However, the five discontinuous characteristics show clearer dimorphic features than the continuous characteristics. Thus, a combination of both the continuous and discontinuous characteristics is appropriate for a better identification of the two morphs of the skeletons.

Variation Consistency among Skeletons

Ideally, each skeleton only consists of either slender or robust type of bones, but both types may be found in different bones of a single skeleton (e.g., robust humerus and slender cervical vertebrae). This odd combination possibly occurs due to misidentification of the two morphotypes of bones or the natural occurrence. Although causes of such odd combination in a skeleton are uncertain, an analysis of a consistency of two morphotypes of bones highlight what patterns occur in the skeletons of *Camarasaurus*.

In 28 articulated or associated skeletons of *C. grandis*, *C. lentus*, *C. lewisi* and *C. supremus*, all characteristics are scored either A or B (Appendix 1). The status of the score A directly indicates the robust type for the all continuous characteristics (Table 3). However, the four discontinuous characteristics (characteristic 3, 5, 7 and 8 in Appendix 1) do not directly allow identifying either the slender or robust morphotype. Thus, these characteristics need to be justified individually. In the angle of the paraoccipital process (characteristic 3), four braincases (CM 11338, 11393, WDC B, YPM 1905) have a relatively wide angle that belongs to the robust type of the occipital condyle (character 1) and limb bones (characteristic 11-15; except for the juvenile CM 11338). The angle that is equal to or greater than 110° is scored A for the robust morph; the score B represents the slender type based on the angle that is narrower than 110° . The ventral keel of the axis (character 5) tends commonly to occur in these axes with the transversely

TABLE 2. Statistic analysis of five limb bones of *Camarasaurus*

Variables	N	Median	Mean	S.D.	Min.	Max.
Humerus (LC/L)	12	0.449	0.459	0.030	0.42	0.49
Humerus (MB/L)	14	0.170	0.166	0.016	0.14	0.18
Ulna (LC/L)	7	0.380	0.381	0.024	0.35	0.41
Ulna (MB/L)	8	0.140	0.150	0.027	0.12	0.19
Radius (LC/L)	10	0.380	0.374	0.026	0.33	0.43
Radius (MB/L)	11	0.140	0.139	0.017	0.11	0.16
Femur (LC/L)	9	0.450	0.453	0.038	0.42	0.47
Femur (MB/L)	11	0.175	0.176	0.018	0.15	0.20
Tibia (LC/L)	4	0.465	0.468	0.017	0.45	0.49
Tibia (MB/L)	6	0.170	0.167	0.021	0.13	0.19

Abbreviations for measurements are shown in Table 1.

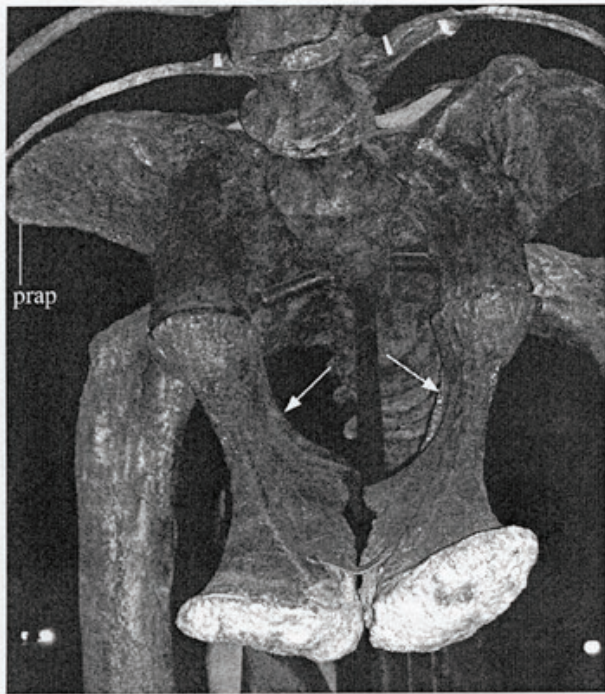


FIGURE 6. Pelvis of *Camarasaurus grandis* (GMNH-PV 101). Anteroventral view. Note the transversely expanded preacetabular process (prap) of the ilium is strongly curved transversely. Strongly curved pubis (white arrows) show a relatively large space of the pelvic cavity.

narrow mid-centrum (character 6). Thus, the two characteristics most likely represent a slender type (score B). 16 skeletons allow examining the presence or absence of the spinoprezygapophyseal lamina (character 7). In all specimens the absence of the lamina belongs to the robust type (score A). Because the laterally extended posterior centrodiapophyseal lamina (characteristic 8) and the short centropostzygapophyseal laminae (characteristic 9) are commonly found in the anterior and mid-dorsal vertebrae, both characteristics are considered the robust type (score A). Based on a combination of the discontinuous and the continuous characteristics, I suggest that the robust type is assigned to score A, and the slender type is B in Appendix I.

All characteristics are treated as evenly significant in this analysis; then, a total number of score A (robust) and B (slender) were counted for an identification of skeletal morphotypes (the right column "Type" in Appendix 1). In each skeleton, variation consistency, which is a gap between a total number of scored characteristics and either robust or slender characteristics, was calculated (Appendix 1). For example, in *C. grandis* (YPM 1905), 13 characteristics were scored, including 11 robust (scored A) and one slender (scored B) characteristics; then, this ratio (variation consistency) is calculated: $11/13 \times 100(\%) = 84.6\%$. Variation consistency shows how each morphotype of bones or characteris-

TABLE 3. An analysis of types of morphological variations in skeletons of *Camarasaurus*.

Body portion	Type of variation	Characteristic numbers*
Cranial elements	Continuous	1, 2, 4
	Discontinuous	3
Vertebrae	Continuous	6, 9, 10
	Discontinuous	5, 7, 8
Limb bones	Continuous	11, 12, 13, 14
	Discontinuous	N/A
Pelvic girdle bones	Continuous	15, 16
	Discontinuous	N/A

*Characteristic numbers are listed in Appendix I.

tics consistently occurs in a skeleton. When variation consistency is 100% (the highest), no conflict is found in any bones. When a skeleton has same numbers of robust and slender characteristics, variation consistency indicates 50% (the lowest).

A relatively low value of variation consistency is found in three individuals of *C. grandis* and *C. lentus*: YPM 1901 (66.7%), CM 11338 (64.7%) and YPM 1910 (66.7%) (Appendix 1). It should be noted that the three specimens are immature individuals (ontogenetic stage 1; Ikejiri et al., 2005). In contrast, variation consistency tends to be higher in fully-grown individuals in all species of *Camarasaurus*. Such a gap between the young and old individuals indicates that a pattern of the appearance of the two skeletal morphs might change during ontogeny (see Ontogeny below).

INTERPRETATION

Significances for Taxonomic Assignment at the Species Level

McIntosh et al. (1996a, p. 30) suggested that *C. lentus* seemed to have more robust limb bones than *C. grandis*. The circumference to length ratio of the femora (LC/L in Table 1) indicates that *C. lentus* is slightly more robust (48%) than *C. grandis* (44%). However, in a few cases, the robust morph of *C. grandis* has more robust limb bones than the slender morph of *C. lentus*; e.g., *C. grandis* (YPM 1905: robust skeletal morph) has a greater ratio in the humerus and femur than *C. lentus* (USNM 13786, WDC A: slender skeletal morph) (Table 1). This evidence indicates that both the slender and robust types of limb bones occur in *C. lentus* and *C. grandis*. Thus, I suggest that the dimorphic feature found in the limb bones of the two species possibly results from intraspecific variation instead of interspecific variation in *Camarasaurus*. More data from articulated skeletons are needed for a further discussion of a relationship between the intraspecific and interspecific variations of the limb bones.

C. lentus has been suggested to be a junior synonym of *C. supremus* based on two main characters: their relatively short base of the neural arch in the dorsal vertebrae that are clearly distinguished from tall elevated neural peduncles of *C. grandis* (Madsen et al., 1995). McIntosh (1990) suggested that the only morphological difference between *C. lentus* and *C. supremus* is body size. The latter species tend to be 20 to 30% larger than the former species based on comparisons of body mass (Foster, 2003) or the femoral and axial length (Ikejiri, 2005). If the two taxa belong to the same species, an explanation for a difference in body size is (sexually) dimorphic variation. However, it should be noted that both slender and robust types of skeletons are identified in both *C. lentus* and *C. supremus* (Appendix I). Furthermore, additional morphological difference between the two species is found in the neural spine of the anterior caudals (Ikejiri, 2004, 2005). Thus, the series of evidence rejects the hypothesis that the two taxa are the same species.

Ontogeny

The two skeletal morphs occur more evidently in the later ontogenetic stage than the earlier on the basis of comparisons of the variation consistency (Fig. 8). According to four ontogenetic stages of *Camarasaurus* (i.e., juvenile, subadult, adult and very old adult; Ikejiri et al., 2005) based on a degree of fusion in various postcranial skeletal elements, the juveniles (body length reaching about 46% from the largest known individual; Table 4) have significantly lower variation consistency (ranging from 62.5 to 68.8%) than the old or very old individuals (Fig. 8). This finding indicates that the dimorphism of the two morphs of the skeleton start appearing more clearly in the late subadult stage when body length reaches 57 to 72% from the largest known individual of *C. lentus* (Table 4).

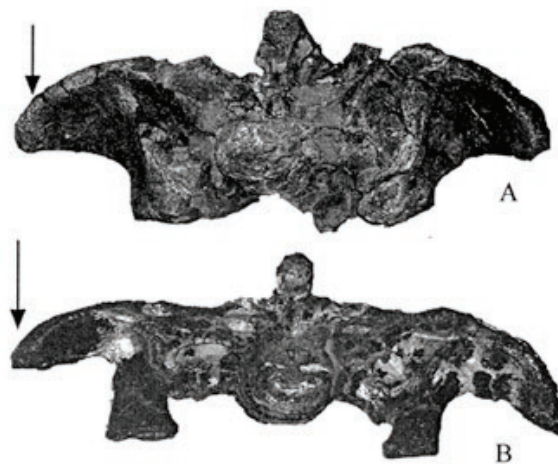


FIGURE 7. Variation in ilia of *Camarasaurus*. A, *Camarasaurus* sp. (RTMP 83.35.03); B, *Camarasaurus* sp. (AMNH 690); C, *C. lentus* (USNM 13786). A, B, anterior view. C, dorsal view. The arrow points the preacetabular process.

Another important feature which is related to ontogeny is the robustness of the limb bones. Most limb elements that belong to mature individuals [e.g., *Camarasaurus* sp. (KUV 129716), *C. grandis* (GMNH-PV 101), *C. lentus* (CM 11393)] are assigned to the slender type. In contrast, the juvenile and subadult *C. lentus* (e.g., CM 11338, YPM 1910) and *C. grandis* (e.g., YPM 1905) tend to have relatively robust limb bones (Table 1). Possibly, a degree of the robustness might increase in a much earlier stage (e.g., the hatchling stage) in *Camarasaurus*. However, skeletons of such young individuals are rare, and more data are needed for a further investigation of this phenomenon.

Sexual Dimorphism

The slender or robust skeletal morph is more evident in the adults than the juveniles, and these

TABLE 4. Comparison of body length in male and female *Camarasaurus*.

Taxon	Specimen	Body length*	%	Ontogenetic stage**	Morph
<i>C. lentus</i>	CM 11338	5.08 m	35.3	Stage 1	Robust?
<i>C. lentus</i>	YPM 1910	6.61 m	45.9	Stage 1	Robust?
<i>C. lentus</i>	USNM 13786	8.22 m	57.1	Stage 2	Robust
<i>C. grandis</i>	YPM 1901	10.8 m	75.1	Stage 2	Slender
<i>C. grandis</i>	YPM 1905	10.3 m	71.8	Stage 2	Robust
<i>C. sp.</i>	KUV 129716	13.2 m	91.8	Stage 2 or 3	Slender
<i>C. sp.</i>	BHI 6200	12.6 m	87.5	Stage 3	Slender
<i>C. lentus</i>	WDC B	14.4 m	100	Stage 3	Robust
<i>C. grandis</i>	GMNH-PV 101	13.6 m	94.5	Stage 3-4	Slender
<i>C. lentus</i>	WDC A	12.6 m	87.3	Stage 4	Slender
<i>C. lentus</i>	CM 11393	14.4 m	100	Stage 4	Slender

* Body length is estimated by the greatest length of the femur (or the axial length) based on the most complete skeleton CM 11338. Based on the largest known individual of *C. lentus* (CM 11339 and WDC B), body size is compared in those specimens (%).

** The identification of ontogenetic stages is from Ikejiri et al. (2005).

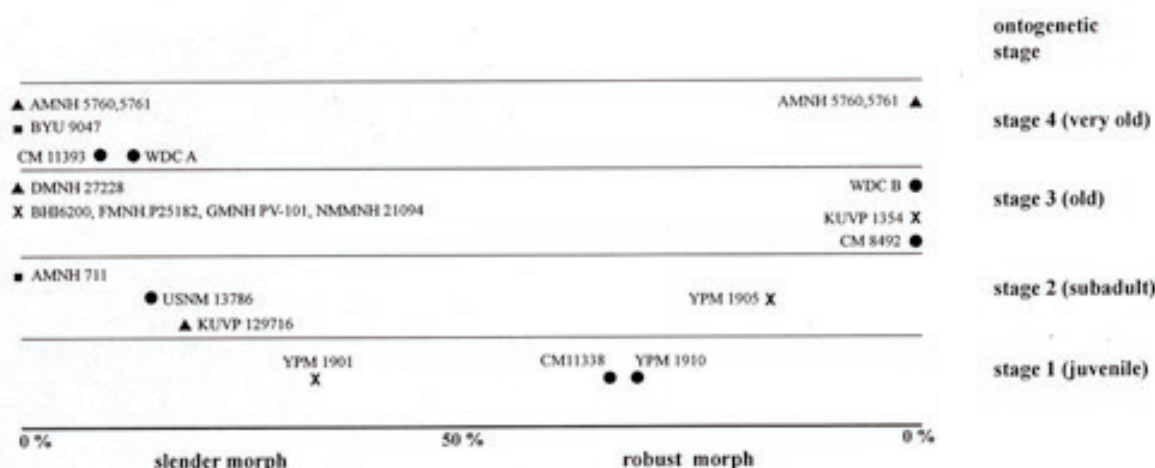


FIGURE 8. Distribution of robust and slender types of skeleton of *Camarasaurus*. The horizontal axis represents variation consistency (i.e., ratio of a number of slender or robust characteristics to a total number of characteristics in a skeleton). When this ratio is close to 100%, a skeleton consists of either slender or robust bones. Identification of species is listed in Appendix I. The vertical axis represents four ontogenetic stages established by Ikejiri et al. (2005). Symbols for species: X, *C. grandis*; circle, *C. lentus*; triangle, *C. supremus*; square, *C. lewisi* (BYU 9047) or indeterminate species (other specimens).

dimorphic characters commonly found in *C. lentus*, *C. grandis* and *C. supremus*. These two types of the skeletons most likely result from sexual dimorphism. Although sexual dimorphic variation is identified in some bones, an identification of sex should be considered a separate question. Generally, the identification of male and female dinosaurs is very difficult (Padian et al., 2005) because direct evidence (e.g., a maternal skeleton with eggs; Sato et al., 2005) is rarely found.

Although body size is a useful character for the identification of male and female in many extant reptilian species, this character seems not to give a direct answer to *Camarasaurus*. In mature individuals of *C. lentus*, the robust morph (e.g., WDC B) tends to have larger body size than the slender morph (e.g., WDC A), but the difference is relatively small (less than 10%; Table 4). If female *Camarasaurus* are larger than male *Camarasaurus*, their heavily built body of females might be advantageous for housing eggs, as Carpenter (1990) suggested in *Tyrannosaurus rex*. However, fully-grown individuals of *Camarasaurus* reach over 10 m in body length. A difference in body size of the slender and robust morphs is about 10% in fully-grown individuals of *Camarasaurus*, which seems not to be significant for carrying eggs during pregnancy.

Another difficulty in using body size is due to reverse sexual dimorphism. Although males are larger than females in many species of large-bodied mammals (e.g., elephants, humans, elephant seals, toothed whales), lizards and crocodiles (Clutton-Brock and Harvey, 1977; Clutton-Brock et al., 1980; Fitch, 1981;

Games, 1990; Jarman, 1974, 1983; Zug et al., 2001), opposite cases are also largely known. For example, in some extant avian taxa such as Gruiformes, Charadriiformes and Falconiformes, females are significantly larger than males (Jehl and Murray, 1986). Such reverse sexual dimorphism might occur in some dinosaurs, too (Molnar, 2005).

Besides body size, another potential source of information for the identification of sex is morphology of the pelvic bones. A wider or more enlarged pelvic cavity is generally found in females than males in various species of tetrapods; e.g., mammoths, extant African and Indian elephants (Lister, 1996), humans (Aiello and Dean, 1990), squirrel monkey (Gingerich, 1972), antillean lizards (Butler and Losos, 2002). An idea of this morphological feature is used for extant archosaurs; e.g., pterosaurs (Bennett, 1992), protoceratopsids (Tereshchenko, 2001). In *Camarasaurus*, a more curved ischial peduncle in the pubes is found in the smaller and slender-bodied individuals. Those curved pubes possibly provide an extra space in the pelvic region to stock eggs. Unfortunately, the ilia and pubes are often damaged due to taphonomic and diagenetic processes. Also, an enough number of the pelvic bones that are associated with those skeletons of *Camarasaurus* are absent. Therefore, identification of male and female *Camarasaurus* is still uncertain although sexual dimorphism is more-likely present in the skeletons.

CONCLUSIONS

Dimorphic characteristics found in the axis, anterior cervicals, anterior and mid-dorsals, anterior

Appendix 1. Occurrence of slender and robust characteristics in various bones of *Camarasaurus*.

Character number	5	0	5	Variation consistency ³	Type
Species	Specimen ²				
<i>C. grandis</i>	FMNH P25182	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B B B B B B B B B B B B B B B B B	100 %	Slender
<i>C. grandis</i>	GMNH PV-101	B B B B B B B B ? ? ? ? ? ? ? ? ? ? ? ?	B B ? ? B B B ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. grandis</i>	KUVP 1354	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	A A ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. grandis</i>	NMMNH -21904	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. grandis</i>	YPM 1901	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B A B A B ? ? ? ? ? ? ? ? ? ? ? ?	66.7 %	Slender
<i>C. grandis</i>	YPM 1905	A ? A B A A A A A A B A ? A A A ? ?	A A A A A A A A A A A A A A A A A A	84.6 %	Robust
<i>C. lentus</i>	CM 8492	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	A A A A A A A A ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. lentus</i>	CM 11338	A A A A A A A A A A A A B A B B B B	A A A A A A A A A A A A A A A A A A	64.7 %	Robust
<i>C. lentus</i>	CM 11339	? B B B ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B ? A B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	83.3 %	Slender
<i>C. lentus</i>	DNM 28	B B B ? B ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B B B B B B B B B A B A B B B B B	100 %	Slender
<i>C. lentus(?)</i>	UUVP 4286	A ? A ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	A ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. lentus(?)</i>	UUVP 10070	B ? B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B ? B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. lentus(?)</i>	UUVP 10795	B ? B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B ? B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. lentus</i>	USNM 13786	B B B B B B B B B B B B A ? ? A ? B ?	B B B B B B B B B B A ? ? A ? B ? ? ?	84.6 %	Slender
<i>C. lentus</i>	WDC A	B ? B ? B B B B B B B B A B A B B B	B ? B ? B B B B B B A B A B B B B B	86.7 %	Slender
<i>C. lentus</i>	WDC B	A ? A A A A A A A A A A A A ? ? A	A ? A A A A A A A A A A A A ? ? A	100 %	Robust
<i>C. lentus</i>	YPM 1910	A ? ? ? ? B A ? ? ? ? ? ? ? ? ? ? ? ?	B B A ? A A A ? A A A ? A A A ? ? ?	66.7 %	Robust
<i>C. lewisi</i>	BYU 9047	? ? ? ? ? B B B ? ? ? ? ? ? ? ? ? ? ? ?	B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. supremus</i>	AMNH 5760 ¹	? ? ? ? ? ? A A A A A A ? ? ? ? ? ? ? ?	A A A A A A A A ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. supremus</i>	AMNH 5760(a)	? ? ? ? ? ? B B B B B B ? ? ? ? ? ? ? ?	B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. supremus</i>	AMNH 5761 ¹	? ? ? ? ? ? A A A A A A ? ? ? ? ? ? ? ?	A A A A A A A A ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. supremus</i>	AMNH 5761(b)	? ? ? ? ? ? B B B B B B ? ? ? ? ? ? ? ?	B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. supremus</i>	DMNH27228	? ? ? ? ? ? A A A ? ? ? ? ? ? ? ? ? ? ? ?	A A A ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. sp.</i>	BHI 6200	B B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. sp.</i>	CM 584	? ? ? ? ? ? ? A A ? ? ? ? ? ? ? ? ? ? ? ?	A A ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Robust
<i>C. sp.</i>	KUVP 129716	? ? ? ? ? ? ? B B B B A B B B A B ?	B B B B A B B B B A B ? ? ? ? ? ? ? ?	80 %	Slender
<i>C. sp.</i>	AMNH 711	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender
<i>C. sp.</i>	AMNH 823	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	B B B ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?	100 %	Slender

¹ AMNH 5760 and 5761 consist of composite skeletons of possibly several individuals (McIntosh, 1998; Ikejiri, 2005), but cervical and dorsal series have some association as shown in plates of Osborn and Mook (1921).

² Additional information on these specimens is in Ikejiri (2005).

³ Variation consistency (%) is calculated by a number of dimorphic characteristic (either A or B) divided by a total number of characteristics in each specimen; e.g., in YPM 1910, 6 (a number of A) divided by 9 (a total score) X 100 (%) = 66.7%.

List of characteristics

Cranial bones:

1. Size of occipital condyle: relatively large (A); or small (B).
2. Robustness of lacrimal: in lateral or medial view, least width of a mid-shaft wider (A); or narrower (B) than half of the proximal width (usually near the lacrimal foramen).
3. Direction of paraoccipital process (Fig. 1): in posterior view of braincase, angle between left and right paraoccipital process is equal to or greater than 110° (A); or narrower (B).
4. Distal shaft of quadrate: robust (A); or slender with anterior extension (B).

Vertebrae:

5. Ventral surface of axial centrum (Fig. 2): flat (A); or keeled (B).
6. Mid-centrum of axis and anterior cervical vertebrae (Fig. 2): transversely wide (A); or strictly constricted (B) centrum in ventral view.
7. Spinoprezygapophyseal lamina in anterior and mid-cervical vertebrae (Fig. 3): absent (A); or present (B).
8. Centropostzygapophyseal laminae in anterior or mid-dorsal vertebrae (Fig. 5): short, stops above neural canal (A); or long extended to ventral margin of a centrum (B).
9. Posterior centrodiapophyseal lamina in anterior and mid-dorsal vertebrae (Figs 4, 5): expanded laterally (A); or constricted laterally (B).
10. Neural spine of anterior caudal vertebrae: greatly expanded transversely (A); or moderately expanded (B).

Limb bones:

11. Robustness of humerus (ratio of least circumference-to-greatest length): greater than 0.447 (A); or equal or less than 0.447 (B).
12. Robustness of ulna (ratio of least mid shaft width-to-greatest length): greater than 0.140 (A); or equal or less than 0.140 (B).
13. Robustness of radius (ratio of least circumference-to-greatest length): greater than 0.375 (A); or equal or less than 0.375 (B).
14. Robustness of femur (ratio of least circumference-to-greatest length): greater than 0.450 (A); or equal or less than 0.450 (B).
15. Robustness of tibia (ratio of least mid shaft width-to-greatest length): greater than 0.170 (A); or equal or less than 0.170 (B).

Pelvic girdles:

16. Precetabular process of ilium (Fig. 7): gently curved (A); or greatly expanded laterally (B).
17. Curvature of mid-shaft of pubis (Fig. 6): relatively straight (A); or strongly curved mid-shaft (B).

caudals, and limb bones indicate that *Camarasaurus* has two morphotypes of the skeletons. Because robust and slender morphotypes of the skeletons are commonly found in *C. grandis*, *C. lentus* and *C. supremus*, those dimorphic features more likely result from intraspecific variation instead of interspecific variation in the genus. This intraspecific variation seems to be sexual dimorphic because robust or slender morphs of bones are more pronounced in the adults than in the juveniles. The robust-morphotype is 5 to 10% larger than the slender-type in overall body size of fully-grown individuals, although the identification of sex is uncertain.

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