



A NEW SPECIES OF *CAMPTOSAURUS* (ORNITHOPODA: DINOSAURIA) FROM THE MORRISON FORMATION (UPPER JURASSIC) OF DINOSAUR NATIONAL MONUMENT, UTAH, AND A BIOMECHANICAL ANALYSIS OF ITS FORELIMB

KENNETH CARPENTER

Department of Earth Sciences, Denver Museum of Nature & Science, 2001 Colorado Blvd., Denver, CO 80205
ken.carpenter@dmns.org

YVONNE WILSON

Department of Earth Sciences, Denver Museum of Nature & Science, 2001 Colorado Blvd., Denver, CO 80205
yvonesaurus@msn.com

ABSTRACT

A new species, *Camptosaurus aphanocetes*, is named for a partial skeleton of ornithopod dinosaur from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument, Utah. The specimen was originally described as *Camptosaurus medius* Marsh, 1894, and later referred to *Camptosaurus dispar* (Marsh, 1879). Comparison of the specimen with a large sample of *C. dispar* from Quarry 13 shows differences in the proportions and shape of various axial and appendicular elements. Based on the dorsoventrally depressed form of the ilium, *Camptosaurus depressus* Gilmore, 1909 (Lower Cretaceous of South Dakota) is assigned to the Barremian genus *Planicoxa* DiCroce and Carpenter, 2001, as *Planicoxa depressa*, new combination. The well-preserved, undistorted forelimb material of *C. aphanocetes* allows for a biomechanical analysis. The range of motion is rather limited throughout the forelimb. The analysis supports the quadrupedal locomotion previously hypothesized for *Camptosaurus* Marsh, 1885, from limb ratios, fusion of the wrist, and presence of short digits.

KEY WORDS: *Camptosaurus aphanocetes*, *Camptosaurus dispar*, biomechanics, quadrupedal, *Planicoxa depressa*

INTRODUCTION

Ornithopod dinosaurs from the Morrison Formation are rare components of the Late Jurassic ecosystem in North America, comprising about 14% of all dinosaur specimens collected from the Morrison (data from Foster 2003: table 5). The largest of these, *Camptosaurus* Marsh, 1885, comprises about 7% of all dinosaur specimens collected and 47% of all ornithopods. *Camptosaurus* was originally named *Camptonotus* by O.C. Marsh in 1879 for material received from Wyoming. The name was changed to *Camptosaurus* by Marsh in 1885 because *Camptonotus* had been used for a leaf-rolling cricket by Uhler (1864).

The material upon which Marsh established *Camptosaurus* was collected from William Reed's Quarry 13, located north of Pine Tree Ridge (also known as east Como Bluff), Wyoming (Gilmore 1909). The site was discovered by William Reed on September 4, 1879:

“Como Sept 4th 1879
Prof O C Marsh
Dear Sir

... We have to day [sic] found an entirely new bone yard[. I]t is something new[.] I hope and think it is in a formation below laosaurus [sic] and above sauranodon[. I]t is the same as the place where Mr [illegible] has made his discovery which he says he found and I object to that statement for I found bones in that horison [sic] and on the same ground where he is at work[. H]e was with me at the time and I pic[k]ed up the end of a hol[l]ow bone and showed it him and said there was bones there now[. H]e claims the discovery but about my new one [i.e., site] the bones are all hol[l]ow and are very plenty [sic] and in good preservation and are located about 12 miles east of quarry no 4 on [R]ock [C]reek[. T]here is about two acres of ground that is full of bones[. T]hey are not large

saurian[. T]he vertebra are about four inches in diameter[. T]hat is the largest of them[. W]ill send on a box in about 4 days[.]
yours truley [sic]
WH Reed.” (Letter to O.C. Marsh).

This letter was followed by another:

“Como Sept 5th 1879
Prof O C Marsh
Dear Sir

I and Mr Ashley have bin [sic] exploreing [sic] the new discovery that I wrote you about yesterday and have found it very rich in all kinds of bones[. W]e got out six jaw bones with teeth in them[. T]he teeth look like laosaurus [sic] but are much larger[.] I send one of them by mail[. W]e also found two bunches of toe bones and I think they will nearly make the whole foot[.] I have called this quare [sic] now 13 east as we comenced [sic] on the east end of the exposure to work no more at present[.]”

Quarry 13 was worked sporadically until 1887 when it was deemed played out. From the hundreds of bones excavated from the site, Marsh named three species of *Camptosaurus*: *Camptosaurus dispar* (Marsh, 1879), *Camptosaurus medius* Marsh, 1894, and *Camptosaurus nanus* Marsh, 1894. He differentiated them primarily on size, with *C. dispar* as the largest and *C. nanus* as the smallest (Marsh 1894). In addition, he noted that *C. nanus* had a “long sigmoid scapula” that “is in strong contrast with the short, straight scapula of *C. dispar*...” (Marsh 1894:85). Most of the specimens from Reed Quarry 13 were transferred to the U.S. National Museum (now the National Museum of Natural History) in 1900, where preparation of

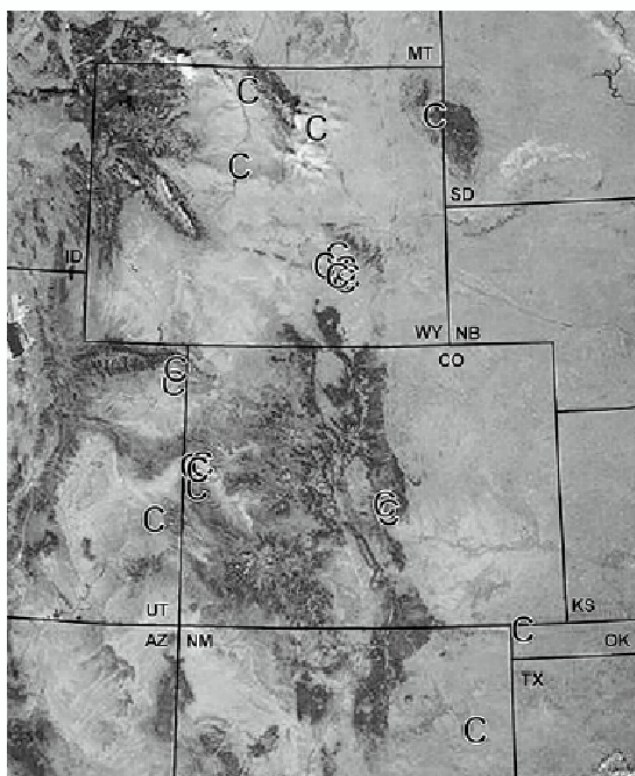


Fig. 1.—Map showing the geographic distribution of *Camptosaurus* in the western United States. The distribution corresponds with the middle and southern portions of the Morrison Formation.

the specimens was completed (Gilmore 1909). From this material, Gilmore (1909) named a fourth species, *Camptosaurus browni*, for a partial skeleton. Approximately 17 individuals of different size-classes are represented by the Quarry 13 specimens (Foster 2003), which was one reason Galton and Powell (1980) argued for recognition of a single species, *C. dispar*.

Since the initial discovery of *Camptosaurus* at Quarry 13, specimens have been found from a wide geographical area (Fig. 1). Unfortunately, many of these occurrences are of fragmentary specimens and their identity is questionable. For example, the holotype of *Symphyrophus musculosus* (Cope, 1878), currently referred to *C. dispar* (e.g., Norman 2004), may include more than one taxon, including crocodilian vertebrae as Osborn and Mook (1921) originally suggested, possibly even to *Goniopholis lucasii* (Cope, 1878) known from the same locality. Several sites have produced partial skeletons. These include Bone Cabin Quarry, Wyoming, worked by the American Museum of Natural History between 1898 and 1905. During the last year of excavation, a partial, juvenile skeleton of *Camptosaurus* was excavated and was referred to *C. nanus* by Gilmore (1909). The area just west of the Quarry (Bone Cabin Quarry West) was reopened in 1990 by Western Paleontological Laboratories and worked until 2000. Three *Camptosaurus* skeletons were excavated, including one

with a disarticulated skull (Miles and Hamblin 1999).

Camptosaurus was also excavated by Carnegie Museum of Natural History at Carnegie Quarry in what is now Dinosaur National Monument. A minimum of eight individuals is known based on hindlimb material. One partial, semiarticulated skeleton is also known, which was described by Gilmore (1925) to supplement an earlier, more detailed osteology of *Camptosaurus* based primarily on specimens from Quarry 13 (Gilmore 1909). This specimen is described further below as a new species of *Camptosaurus*. *Camptosaurus* is also known from disarticulated and scattered material, which represents five individuals, from the Cleveland-Lloyd Quarry, Utah (Gates 2005). Some of this material was used to make a composite mount, casts of which are widely distributed. *Camptosaurus* has also been identified in England (Galton and Powell 1980; Norman and Barrett 2002).

Camptosaurus in the United States has an extensive stratigraphic range (Turner and Peterson 1999: fig. 10) and by implication, a long geochronological age from the earliest Oxfordian to middle Tithonian, a span of more than 10 Ma (time scale is that of Pálffy et al. 2000). One of the oldest occurrences may be Reed's Quarry 13, which occurs about 35 m below the 156.3 ± 2 Ma age for strata at the level of Reed's Quarry 9 (Trujillo et al. 2006). Such

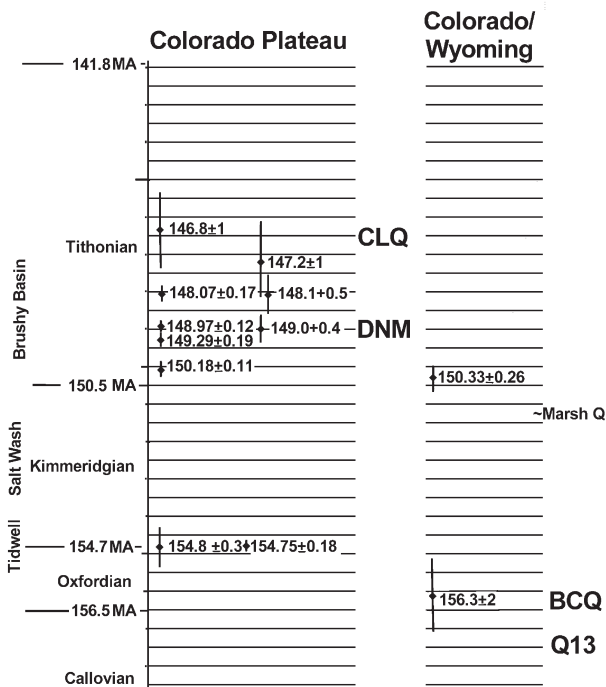


Fig. 2.—Geochronological distribution of *Camptosaurus* in the Morrison Formation. Based on regional correlations from dated horizons, *C. dispar* from Quarry 13 is latest Oxfordian-earliest Kimmeridgian, whereas *C. aphanoeetes* from Dinosaur National Monument is early Tithonian. Radiometric dates from Kowallis et al. (1998), Bilbey (1998) and Trujillo et al. (2006). Time scale used is that of Pálffy et al. (2000). Abbreviations: BCQ - Bone Cabin Quarry, Wyoming; CLQ - Cleveland Lloyd Quarry, Utah; DNM - Dinosaur National Monument, Utah; Q13 - Quarry 13, Como Bluff, Wyoming.

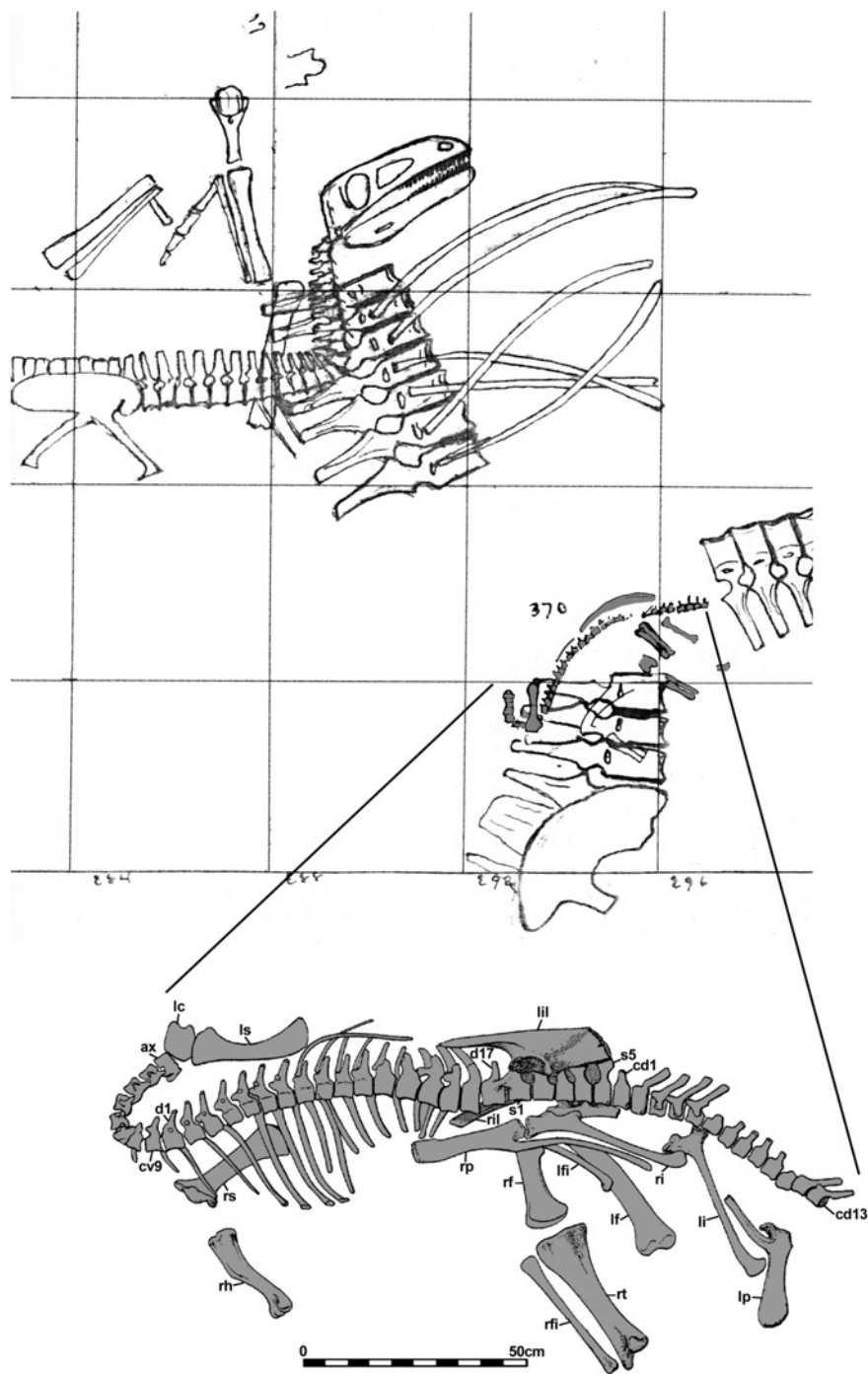


Fig. 3.—Quarry map showing the location of *Camptosaurus aphanoecetes* (CM 11337) at the east end of Carnegie Quarry, near the University of Utah *Allosaurus* Marsh, 1877 (UMNH VP-7435). Inset from Gilmore (1925). Abbreviations: ax, axis; cd1, caudal 1; cd13, caudal 13; cv9, cervical 9; d1, dorsal 1; d17, dorsal 17; lc, left coracoid; lf, left femur; lfi, left fibula; li, left ischium; lil, left ilium; lp, left pubis; ls, left scapula; rf, right femur; rfi, right fibula; rh, right humerus; ri, right ischium; ril, right ilium; rp, right pubis; rs, right scapula; rt, right tibia; s1, sacral 1; s5, sacral 5. Scale in cm.

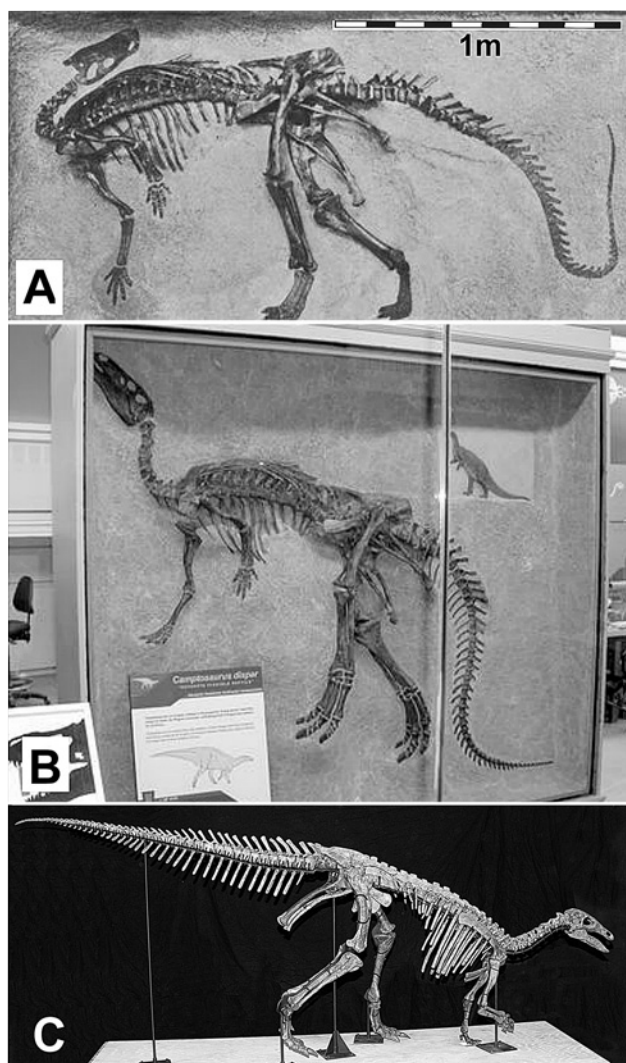


Fig. 4. — *Camptosaurus aphanoeetes* (CM 11337). **A**, as originally mounted in 1922; **B**, as later remounted in 1934; **C**, most recent mount by Phil Fraley Productions.

an extremely old date for the Quarry 9 strata has yet to be independently verified, but if true, *Camptosaurus* (and by extension all other dinosaurs) at Quarry 13 are significantly older than those on the Colorado Plateau (Fig. 2). Considering the age range associated with this date, a younger age is possible, bringing it just within age ranges reported for the Morrison Formation on the Colorado Plateau (Kowallis et al. 1998). Nevertheless, the Q13 *Camptosaurus* is older than that from Dinosaur National Monument. The geologic age for youngest *Camptosaurus* specimens is more problematic. The youngest specimens may be from the Cleveland-Lloyd Quarry, dated at 146.8 ± 1 Ma by Bilbey (1998), or the teeth from the Rainbow Draw microsite on the north side of Dinosaur National Monument. The site is approximately 18.6 m above the level of strata near the Carnegie Quarry dated as 135.2 ± 5.5 Ma

by Bilbey (1998), but 148.97 ± 0.12 Ma by Kowallis et al. (1998).

The long chronological range for *Camptosaurus* raises the question as to whether *C. dispar* low in the Morrison is the same species as high in the Morrison as Galton and Powell (1980), and more recently Foster (2003) suggest. There is growing evidence that the Morrison Formation dinosaur fauna is not homogenous at the species level and, in some cases, even at the generic level (Carpenter 1998; Turner and Peterson 1999; Foster 2003). This conclusion is in contrast to an earlier assessment by Dodson et al. (1980). The changes in dinosaur genera and species do not occur at the same chronostratigraphic horizon, thereby signaling an abrupt faunal turnover. Instead, overlapping first occurrence datum (FAD) and last occurrence datum (LAD) of the various dinosaur taxa mask taxonomic changes within the formation. However, correlating these FADs and LADs regionally has been difficult, because of the lack of suitable time lines such as those present in marine rocks. It was hoped that the clay-change reported by Turner and Peterson (1999) in the Morrison Formation would provide the needed biostratigraphic control over large areas (Turner and Peterson 1999; Foster 2003; Turner et al. 2004). When first presented, this clay change hypothesis was hailed as a major breakthrough in understanding the biostratigraphy of the Morrison Formation. Unfortunately, there is now reason to doubt the uniformity of the clay change over large areas (Trujillo 2006), although it still may have local utility. Radiometric dating remains the most useful tool for plotting quarries (hence their taxonomic content) chronologically (Fig. 2). However, considerably more dates are needed outside the Colorado Plateau to test the hypothesis for the FADs and LADs of the various taxa. As mentioned above, preliminary indications suggest that *C. dispar* from Quarry 13 is significantly older (>156 Ma) than the *Camptosaurus* from Dinosaur National Monument (149 or 135 Ma).

CARNEGIE CAMPTOSAURUS

Several specimens of *Camptosaurus* were found during the 14 years that the Carnegie Quarry was worked (1909–1923; McIntosh 1981). Of these, the most complete was a partial skeleton found on the east end of the quarry in 1922 (Fig. 3). The specimen was briefly described by C.W. Gilmore in 1925 after preparation as a partial-relief panel mount by L.S. Coggeshall and J. LeRoy. The specimen went on exhibition (McGinnis 1982) on Founders Day in 1925 (Fig. 4A). The specimen was partially rearticulated in 1934 with alterations to the neck, limbs, and tail, as well as rotation of the body section (Fig. 4B). The skeleton was removed from the panel mount in 2005–2006 and the bones completely prepared so that a free-standing skeleton could be created (Fig. 4C). This opportunity was taken by us to redescribe and figure the skeleton in greater detail than was done by Gilmore (1925).

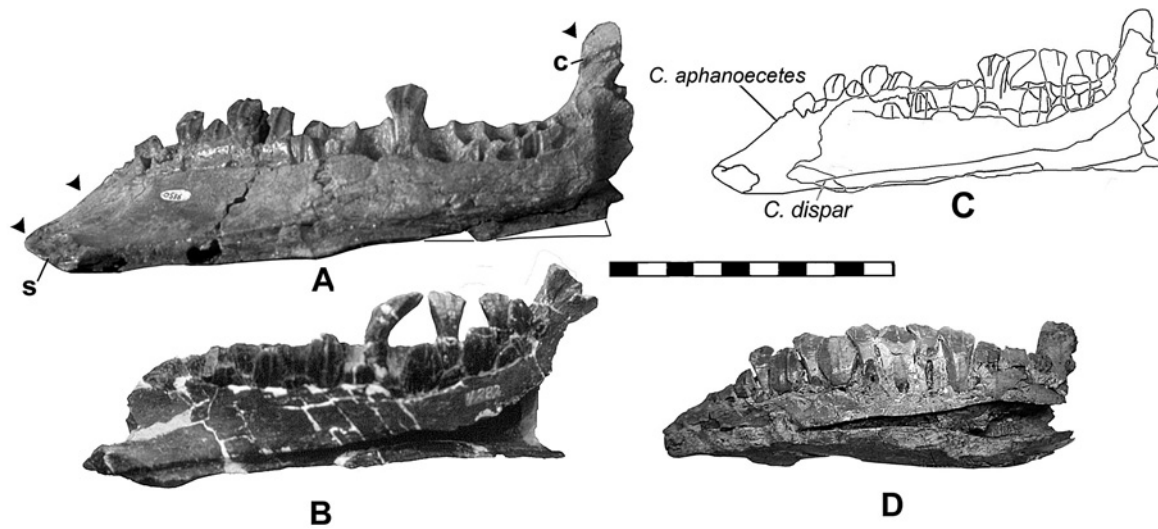


Fig. 5.—Medial views of dentaries. **A**, *Camptosaurus aphanoeccetes* (DINO 0556); **B**, *C. dispar* (USNM 4282, holotype *C. browni*, not to scale); **C**, comparative overlay at same dentary depth; **D**, “*C.*” *hoggii* (holotype BMNH R2998; Lower Cretaceous, England), note arch of tooth row to level of coronoid process and anterior taper. Darts in **A** denote areas of difference between *C. aphanoeccetes* and *C. dispar*. Scale units for **A**, **D** are cm. Abbreviations: c, coronoid process; s, symphysis.

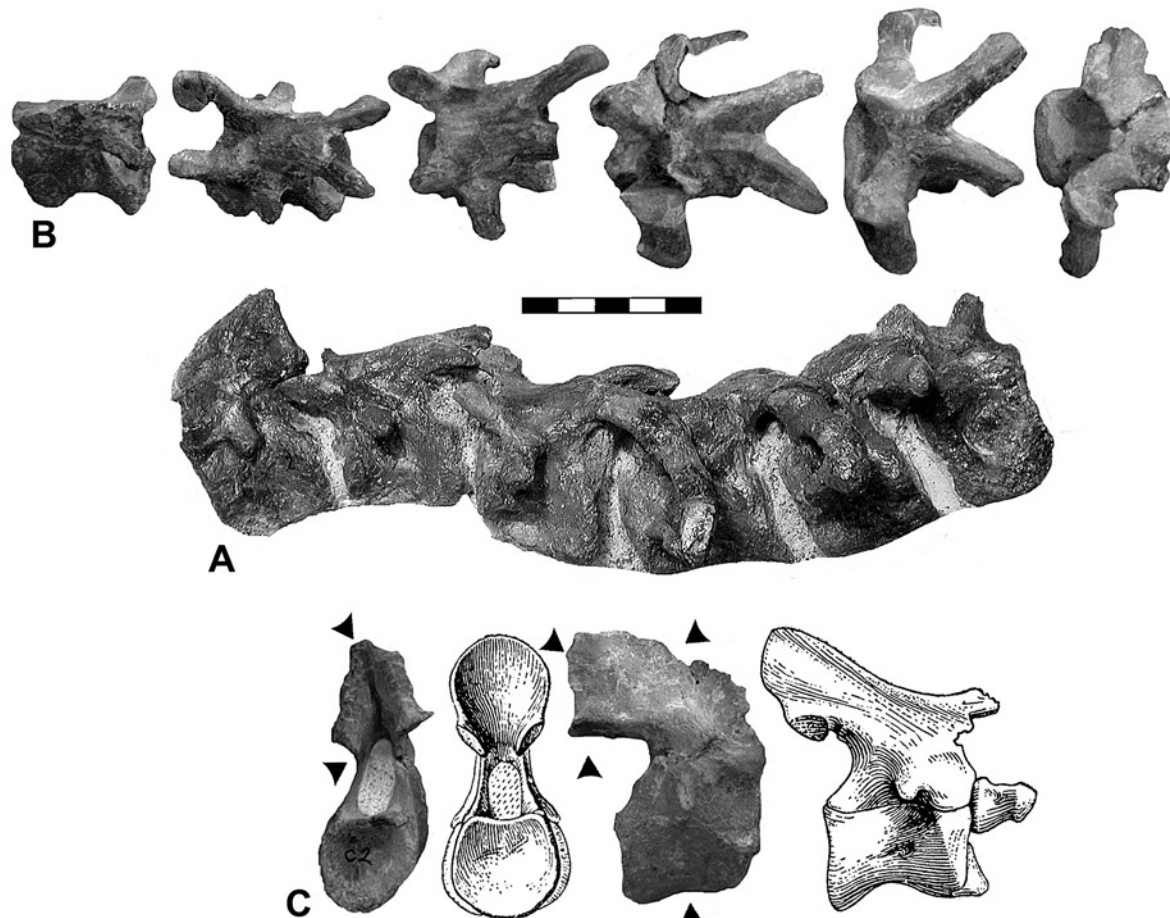


Fig. 6.—Cervical vertebrae 2-7 in left lateral view of *Camptosaurus aphanoeccetes* (CM 11337). **A**, as originally articulated showing the natural curvature with matrix still attached; **B**, dorsal view; **C**, comparison of the axis with that of *C. dispar* (USNM 5473). Darts indicate areas of difference with *C. dispar*. **C** (in part), adapted from Gilmore (1909). Scale units are cm.

Furthermore, owing to the completeness and undistorted nature of the forelimb, it was used in a biomechanical analysis to determine its function. This analysis is modeled after Carpenter (2002) for theropod forelimb biomechanics and uses the same terminology defined there. Muscle terminology is Romerian, following the arguments set forth by Wilson (2006), and is based largely on Meers (2003). Some minor modifications of positional terminology for the muscles of the humerus of *Camptosaurus* are necessary because the humerus is carried in a more vertical orientation than in the alligator. Anterior replaces ventralis, and posterior replaces dorsalis. Thus, the coracobrachialis brevis ventralis is the coracobrachialis brevis anterior in *Camptosaurus*.

MATERIALS AND METHODS

Various specimens of *Camptosaurus* were examined and photographed. All the specimens at the Carnegie Museum of Natural History were excavated from the Carnegie Quarry at what is now Dinosaur National Monument and belong to the new species described below. Other specimens from the quarry are currently housed at the Monument’s headquarters building at Dinosaur, Colorado. Specimens from Quarry 13 all belong to *C. dispar* and are housed at the National Museum of Natural History and the Peabody Museum of Natural History. This material includes individuals of different age groups and probably different gender. Measurements were given by Gilmore (1909, 1925). Articulation and manipulation of the pectoral girdle and forelimb follows that used previously for theropods (Carpenter 2002) and adapted by Senter (2005) and Senter and Robins (2005). Because juvenile specimens of *Camptosaurus* fall within the size range of adult *Dryosaurus* Marsh, 1894, differences used to separate the two taxa are noted below, especially with the appendicular material.

Abbreviations—**AMNH** - American Museum of Natural History, New York, NY; **BMNH** - Natural History Mu-

seum, London, UK. **CM** - Carnegie Museum of Natural History, Pittsburgh, PA.; **DINO** - Dinosaur National Monument, Jensen, Utah; **DMNH** - Denver Museum of Nature and Science, Denver, CO; **LACM** - Natural History Museum of Los Angeles County, Los Angeles, CA; **UMNH** - Utah Museum of Natural History, Salt Lake City, UT; **USNM** - National Museum of Natural History, Washington D.C.; **YPM** - Yale Peabody Museum of Natural History, New Haven, CT

SYSTEMATIC PALEONTOLOGY

Class Ornithopoda Marsh, 1881
Order Ankylopollexia Sereno, 1986
Genus *Camptosaurus* Marsh, 1885

Camptosaurus aphanoeccetes, new species

Etymology.—From *aphanoe-* (Greek) meaning “hidden” and *-cetes* (Greek) meaning “to dwell”, as in to “dwell in plain sight” in reference to the new species having been “hidden in plain sight” because it was on exhibit for over 75 years.

Holotype.—CM 11337 partial, articulated skeleton containing eight cervicals, 16 dorsals, four sacrals, 14 caudals, both scapulae, left coracoid, both humeri, left radius, left ulna, left carpals and manus, both ilia, both pubes, both ischia, both femora, both tibiae, complete and partial fibulae, six cervical ribs, 31 dorsal ribs, and ossified tendons.

Holotype Locality.—East end of Carnegie Quarry at Dinosaur National Monument, Uintah County, Utah.

Holotype Stratigraphic Position.—Middle of the Brushy Basin Member, Morrison Formation (see Fig. 2).

Paratype material.—CM 15780 right femur, tibia, fibula, astragalus, metatarsal; CM 41689 right(?) incomplete sternal plate; CM 79050 left pubis and ischium; DINO 556 right dentary; DINO 1030 left articulated coracoid and scapula; DINO 1032 right scapula;

Referred material.—CM 21707 left tibia; CM 21723 right femur; CM 21724 left partial femur; CM 21725 two metatarsals; CM 21778 distal end of ischium; DINO 499 part of mandible with several teeth; DINO 1021 incomplete portion of right pubis; DINO 1091 left femur; DINO 2457 left metatarsal III; DINO 2461 left metatarsal II; DINO 2558 right

TABLE 1. Measurements of cervical vertebrae 2-7 (in cm) in CM 11337.

	Greatest Centrum Length (mid-centrum)	Centrum Height (posteriorly)	Centrum Width (posteriorly)
cv2	3.3	2.4	2.4
cv3	4	2.2	2.75
cv4	3.6	3.1	2.8
cv5	3.9	3.2	2.7
cv6	3.2	3	3.4
cv7	3.7	3.3	3.3
cv8	4.5	3.8	-
cv9	4.7	3.9	-

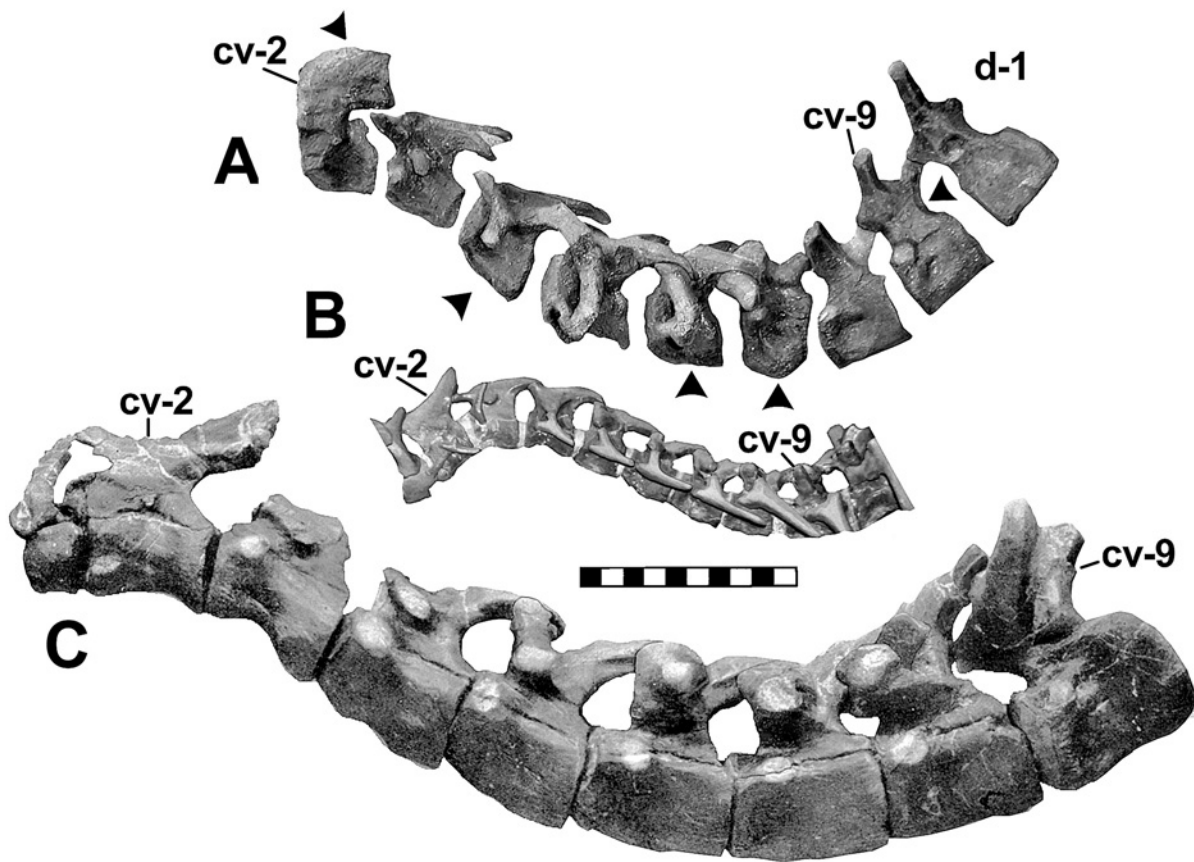


Fig. 7.—Comparisons of the cervical vertebrae in left lateral view for two species of *Camptosaurus* (darts point to regions of major differences). A, *C. aphanoecetes* (CM 11337); B, juvenile *C. dispar* as mounted (USNM 2210, holotype *C. nanus*); C, older *C. dispar* (USNM 5473). Abbreviations: cv, cervical vertebra; d, dorsal vertebra. C modified from Gilmore (1909). Scale units are cm.

partial maxillary; DINO 3831, 3832 and 3908 associated left femur, left tibia, and right tibia (possibly *Camptosaurus*). Other material cataloged under DINO may belong to *C. aphanoecetes* but was either inaccessible or cannot be separated from *Dryosaurus*.

Diagnosis.—Differs from *C. dispar* in the following: mandibular symphysis short and more vertically oriented, coronoid process relatively taller; postzygapophyses of axis extend well beyond posterior face of centrum, axis neural spine above the postzygapophyses laterally compressed, not expanded laterally forming deep pocket; cervical centra shorter compared to height, especially in mid-cervicals; mid- and posterior cervicals amphiplatyan to weakly plati-concave, not opisthocoelous; cervical 7 centrum wedge-shaped in lateral view; neural arches of posterior cervicals very tall; anterior dorsal centra shorter compared to height; anterior caudal centra not angled posteroventrally, mid-caudal centrum with small chevron facet; mid-caudal vertebra neural spine long and slender, with postzygapophysis located high on spine; scapular blade arched in profile, not straight, and distal end steeply sloped; deltopectoral crest a low triangle, not prominent; ilium with more vertical pubic peduncle, dorsal rim arched, prepubic



Fig. 8. — Right cervical ribs in lateral views of *Camptosaurus aphanoecetes* (CM 11337). A, cervical 3; B, cervical 4; C, cervical 5; D, cervical 6; E, cervical 9 (left, reversed). Scale units are cm.

TABLE 2. Measurements of dorsal vertebrae (in cm) in CM 11337.

Dorsal	Greatest Centrum Length (mid-centrum)	Neural Spine Height/Length Top of Spine
1	3.9	-
2	3.8	3/.8
3	3.9	4.1/1.2
4	4.2	5.8/.8
5	4	-.2/4
6	4.5	-.3
7	4	-.3/7
8	4.9	-.3/4
9	4.5	-.3/4
10	4.7	-.DAMAGED
11	4.7	-.>2.5
12	4.6	-.3/5
13	5	-.3/7
14	4.5	-.3/5
15	4.3	-.3/8
16	>3.6	-.3/1
s1	~5.6	-.4/3
s2	4.7	-.4/1
s3	4.9	?
s4	4.3	3/7
s5	3.7	2/8

process proportionally longer, postpubic process lower, with rounded distal end; pubis with posterior projecting iliac peduncle forming large acetabular notch; ischium with small distal foot.

DESCRIPTION AND COMPARISONS

Skull.—The skull of *C. aphanoeectes* is unfortunately unknown, but a few isolated dentaries are known from the Carnegie Quarry. Gilmore (1909) described the cranial material from Reed's Quarry 13, Wyoming, and additional material of *Camptosaurus* is known from Bone Cabin Quarry and Bone Cabin Quarry West, as well as from the Cleveland Lloyd Quarry, Utah. The skull of *Camptosaurus amplius* (Marsh, 1879) used by Gilmore (1909) to correct Marsh's (1894) earlier reconstruction of the skull was shown by Brill and Carpenter (2006) not to be from the Morrison Formation nor to belong to *Camptosaurus*; it was made the holotype of *Theiophytalia kerri* Brill and Carpenter, 2006. The correct skull was shown by Brill and Carpenter (2006: fig. 3.3).

The dentary of *C. aphanoeectes* closely resembles that of *C. dispar* (Fig. 5) as described by Gilmore (1909), except in a few minor but significant details. First, the coronoid process is proportionally taller relative to the depth of the dentary than in *C. dispar* (Fig. 5C). Second, the symphyseal ramus between the first dentary alveolus and symphysis, upon which the prementary articulates, is long and not as steeply angled. Third, the symphysis is short, deep, and angled more anterodorsally. A further possible difference is that the dentary is proportionally longer relative to its depth than *C. dispar*. However, an ontogenetic series for the dentary is unknown for *C. dispar*, and there remains the possibility that the long, slender dentary of *C. aphanoeectes* may be a juvenile condition.

Despite these differences, the dentaries of *C. aphanoeectes* and *C. dispar* are more similar than either is to *Camptosaurus hoggii* (Owen, 1874) from the Lower Cretaceous of England (Fig. 5D). The dentary of *C. hoggii* is deeper relative to its length, its dental margin and tooth row is arched, and the symphyseal ramus longer and lower. We consider these differences too great to refer BMNH R2998 to *Camptosaurus*, contrary to Norman and Barrett (2002). At present, we consider it an unnamed euornithopod.

Cervical Vertebrae.—A nearly complete cervical vertebrae column is known for CM 11337 (measurements given in Table 1). When found, eight cervicals were in articulation (Figs. 3, 6, 7). The spacing of the centra shows how thick the intervertebral disks were

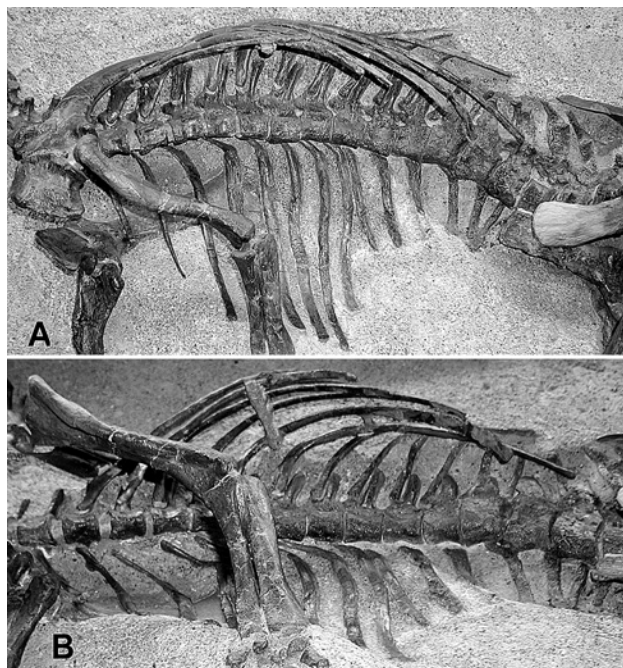


Fig. 9. — Articulated dorsal vertebrae of *Camptosaurus aphanoeectes* (CM 11337). A, lateral; and B, ventrolateral views. Note that the back in A has a slight dorsal curve.

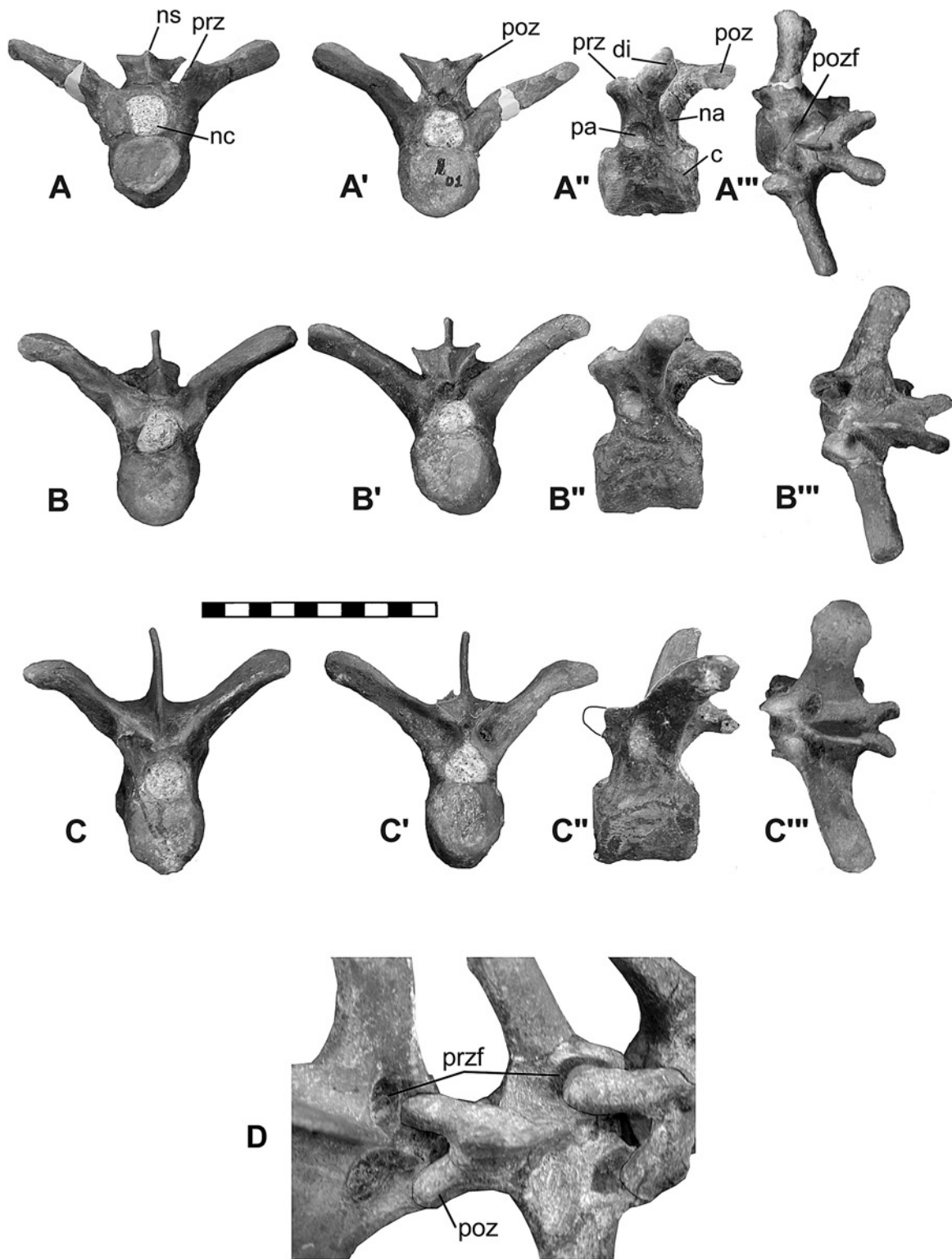


Fig. 10.—Dorsal vertebrae 1-3 of *Camptosaurus aphanoeccetes* (CM 11337). Dorsal 1: **A**, anterior; **A'**, posterior; **A''**, left lateral; **A'''**, and dorsal views. Dorsal 2: **B**, anterior; **B'**, posterior; **B''**, left lateral; **B'''**, and dorsal views. Dorsal 3: **C**, anterior; **C'**, posterior; **C''**, left lateral; and **C'''**, dorsal views. **D**, close-up of dorsals in articulation in dorsal view to show how the postzygapophyses are accommodated by the prezygapophyseal facets located posterodorsal to the prezygapophyses at the base of the neural spine. Abbreviations: c, centrum; di, diapophysis; na, neural arch; nc, neural canal; ns, neural spine; pa, parapophysis; poz, postzygapophysis; pozf, postzygapophysis facet; prz, prezygapophysis; przf, prezygapophysis facet. Scale units are cm.

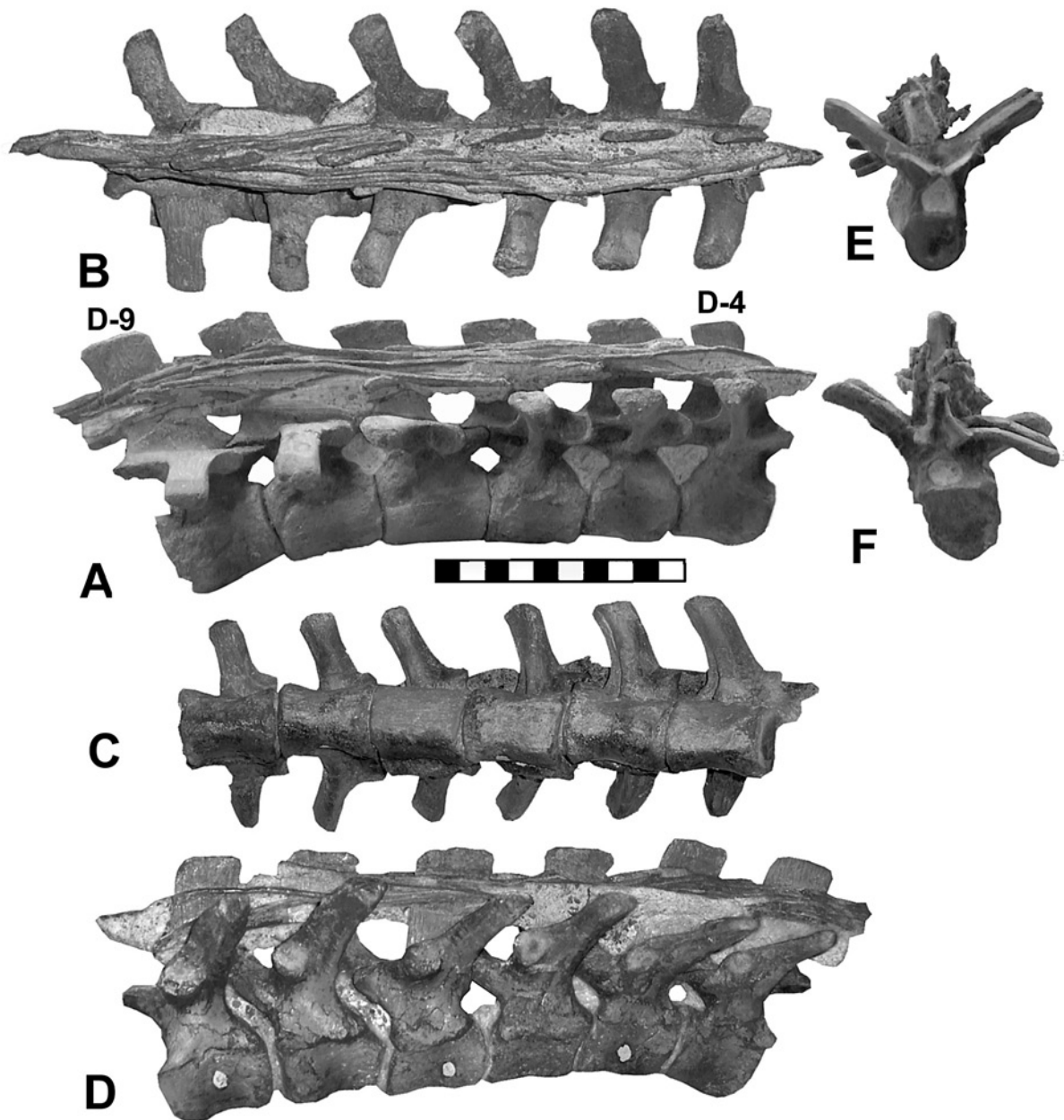


Fig. 11.—Articulated dorsal vertebrae 4-9 of *Camptosaurus aphanoeetes* (CM 11337) held by ossified tendons. A, right lateral; B, dorsal; C, ventral; D, left lateral; E, anterior; and F, posterior views. Scale in cm.

(Fig. 6). Many of the zygapophyses are reconstructed.

The atlas is missing and the axis is incomplete anteriorly, lacking a small vertical section including the prezygapophyses, articular face of the centrum and odontoid (Fig. 6C). This loss may have been due to a joint in the encasing rock. The neural spine of the axis lacks the posterior, cup-like expansion forming a thin, frill-like plate above the postzygapophyses as seen in *C. dispar* (Fig. 6C). Instead, the postzygapophyses, which are more horizontal than *C.*

dispar, are separated by a cleft, and furthermore overhang the centrum more. The neural spine is also anteroposteriorly longer, the top more horizontal and the posterior margin more vertical than in *C. dispar* (Fig. 6C). The axial centrum has a ventral keel, which results in a flatter rather than concave ventral margin in lateral view (Fig. 6C). In *C. dispar*, the ventral side of the centrum is broadly rounded and not keeled.

The post-axis cervical vertebrae of *C. aphanoeetes* are

TABLE 3. Measurements of caudal vertebrae (in cm) in CM 11337.

Caudal	Greatest Centrum Length (mid-centrum)	Centrum Height (posteriorly)	Centrum Width (posteriorly)	Total Height To Top Of Neural Spine (posteriorly)
cd 1	3.8			
cd 2	3.5			
cd 3	3.5	4.9	4.8	14.3
cd 4	3.9	4.5	4.5	13.9
cd 5	4.2	4.4	4.2	13.5
cd 6	3.9	4.3	3.7	13.3
cd 7	4.1	4	3.8	13.1
cd 8	3.9	4.1	3.8	12.2
cd 9	4.1	3.6	3.8	11.6
cd 10	4.1	3.5	3.7	12.2
cd 11				

anteroposteriorly short compared to their height (Figs. 6, 7A). This shortness reaches its maximum in cervical (CV-) 7, where the centrum is anteroposteriorly shorter than it is tall, and is wedge-shaped; the centra of CV-8 and CV-9 are sequentially longer. In contrast, the cervicals of *C. dispar* (Fig. 7B, C) are significantly longer than tall and show no reduction in length even in juveniles (USNM 2210, holotype of *C. nanus*), which are essentially smaller versions of the larger individuals. The anterior centra of *C. aphanoecetes* are slightly opisthocelous and the middle and posterior ones amphiplatyan. In contrast, the anterior centra are platycoelous in *C. dispar* and the middle and posterior ones opisthocelous as noted by Gilmore (1909). Ventrally, there is a prominent ventral keel on all the cervicals of *C. aphanoecetes*, which gives the ventral margin a straight edge. This ridge becomes wider in each subsequent cervical beginning with CV-4. The ridge projects ventrally in CV-7 mimicking a hypophyseal, although it is not one. The anterior face of CV-3 and CV-4 is angled posteroventrally, but especially CV-4, which causes the neck to angle slightly ventrally. None of the cervicals, except for the axis, has the low neural spine as seen in *C. dispar*. Nor do the diapophyses lengthen in more posterior vertebrae as described by Gilmore (1909) for *C. dispar*. Rather, they remain the same length from CV-3 to CV-7, and only increase in CV-8.

Cervical ribs of *C. aphanoecetes* are mostly preserved on the right side. These are elongate (Fig. 8) and oriented parallel to the centrum, except for the last, which angles posteroventrally. The tuberculum faces dorsally to articulate with the diapophysis, and the capitulum faces medially to articulate with the parapophysis. The lateroventral edge of the rib near the capitular process is keeled.

Dorsal Vertebrae.—The 16 dorsal vertebrae of CM 11337 were found in articulation (Figs. 3, 9); measurements are given in Table 2. Many of the neural spines are reconstructed, as are some of the transverse processes. Overall, the dorsal vertebrae closely resemble those of *C. dispar* except in a few points. The first three dorsals were separated and cleaned (Fig. 10). As with the cervicals, the anterior dorsal centra are proportionally shorter compared to their height than in *C. dispar*. The actual amount varies depending on position, but its height/length is roughly 66% in CM 11337 and 50% in *C. dispar*, including juveniles. The centrum of the first dorsal is very slightly opisthocelous, whereas it is more strongly developed in *C. dispar* (Gilmore 1909). Whereas the neural spine of the first dorsal is low in *C. dispar*, it is barely developed in *C. aphanoecetes*. In dorsal vertebra (D-) 2, the centrum is amphiplatyan in *C. aphanoecetes*, but weakly opisthocelous in *C. dispar*. There is a pair of deep facets near the anterior base of the neural spine beginning with D-2 to accommodate the postzygopophysis of the preceding vertebrae when the body curves laterally (Fig. 10D). D-4 to D-16 are bound by ossified tendons and were left in two segments (Figs. 11, 12). Unlike *C. dispar*, all of the centra retain a weak keel on the ventral side (Figs. 11C, 12C).

CM 11337 retains all of the ossified tendons in situ and these form two layers (Figs. 11, 12). They begin at the D-3–D-4 junction and extend to the sacrum. They may have extended onto the caudals, although none was found during the new preparation. Overall, the ossified tendons of the anterior dorsal vertebrae are more slender than the posterior ones. The individual tendons are flattened near their ends, with bifurcated anterior ends and dorsoventrally flared posterior ends. The anterior ossified

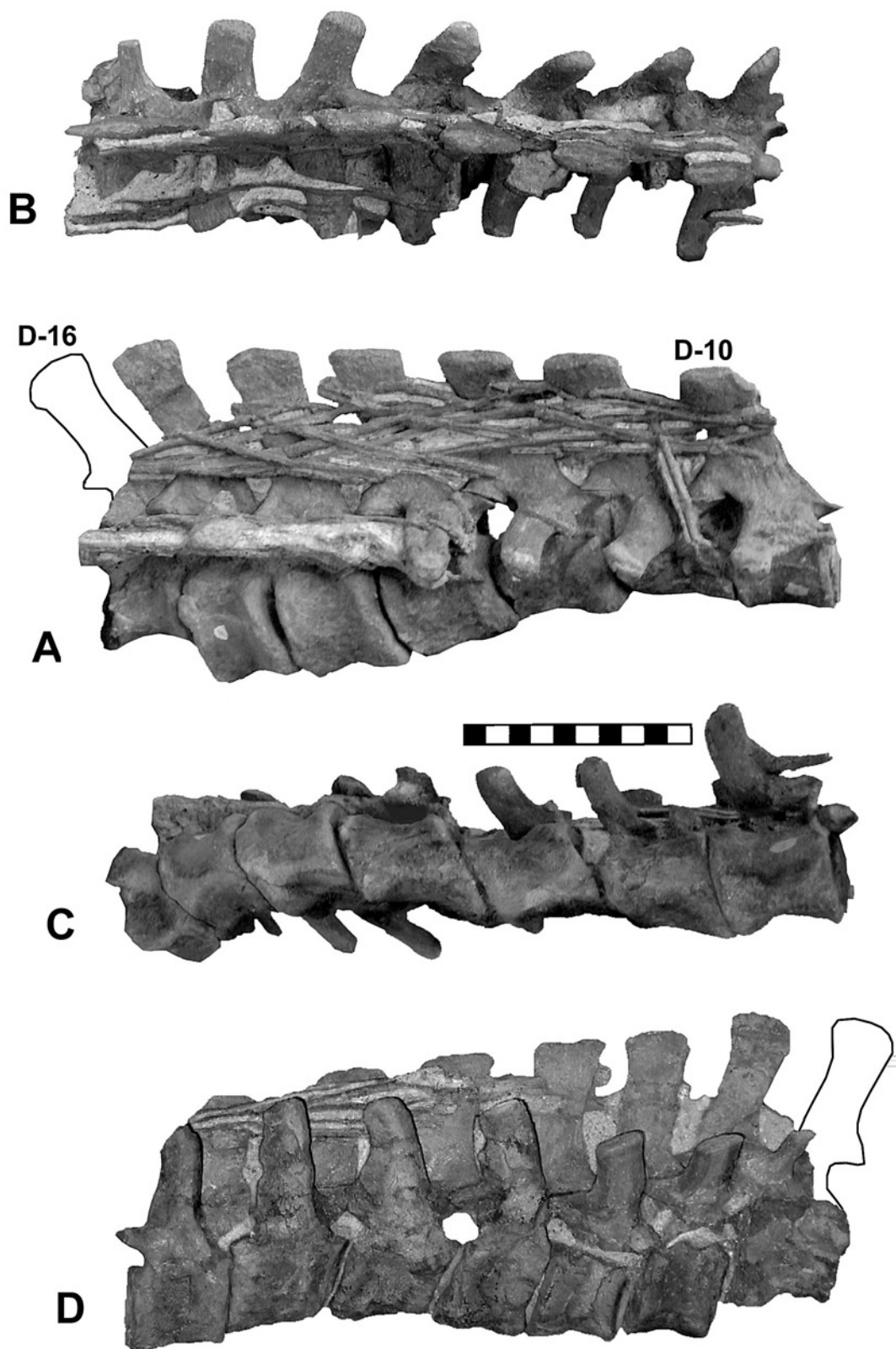


Fig. 12. — Articulated dorsal vertebrae 10-16 of *Camptosaurus aphanoeetes* (CM 11337) held by ossified tendons. A, right lateral; B, dorsal; C, ventral; and D, left lateral views. Scale units are cm.

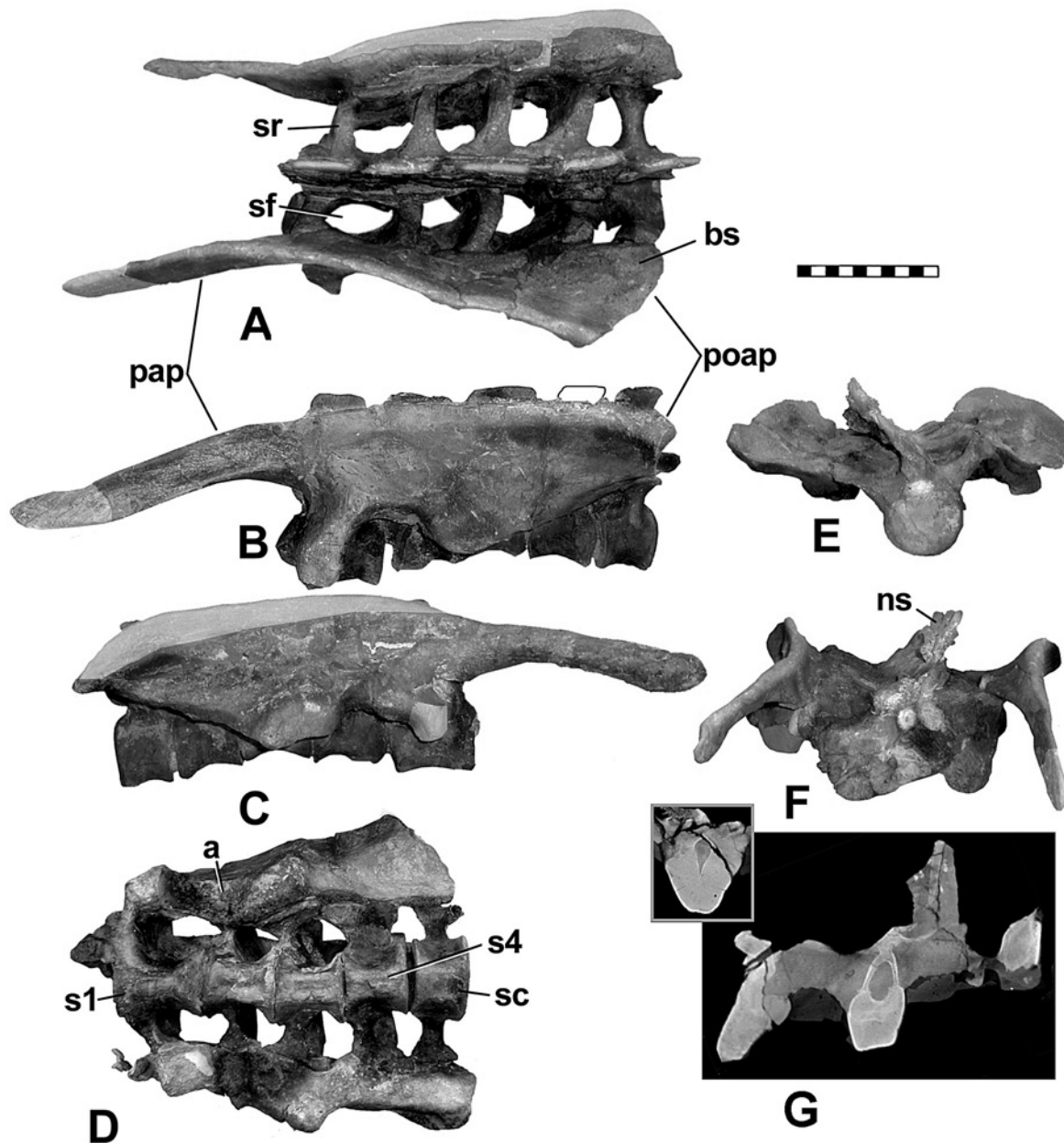


Fig. 13.—Sacrum and attached ilia of *Camptosaurus aphanoecetes* (CM 11337). **A**, dorsal; **B**, left lateral; **C**, right lateral; **D**, ventral (without preacetabular processes); **E**, posterior; and **F**, anterior views. **G**, Computed Tomography shows the enlarged, vertically ellipsoid neural canal in the anterior sacrum (s2?); inset shows the ventral slit into the posterior sacral centrum (s4?). Abbreviations: a, acetabulum; bs, brevis shelf; ns, neural spine; pap, preacetabular process of ilium; poap, postacetabular process of ilium; s1, sacral 1; s4, sacral 4; sc, sacro-caudal (=caudal 1); sf, sacral fenestra; sr, sacral rib. Scale units are cm.

tendons are longitudinally arrayed from D-3 to D-10, at which point a rhombohedral lattice forms. The longitudinal tendons are imbricated in that they originate low and adjacent to the neural spines and extend postero dorsally over succeeding vertebrae; none of them is fused to the neural spines. Some of these longitudinal tendons extend at least across five vertebrae, possibly six. The lattice pat-

tern begins at the D-9–D-10 juncture and extends to the sacrum, at which point there are fewer of them and these are arranged longitudinally; this same longitudinal pattern on the sacra is seen in the *Camptosaurus* sp. from Bone Cabin Quarry (illustrated in Gilmore 1909: pl. 19). The lattice tendons are more steeply arrayed than the longitudinal ones, consequently they are shorter and extend across only

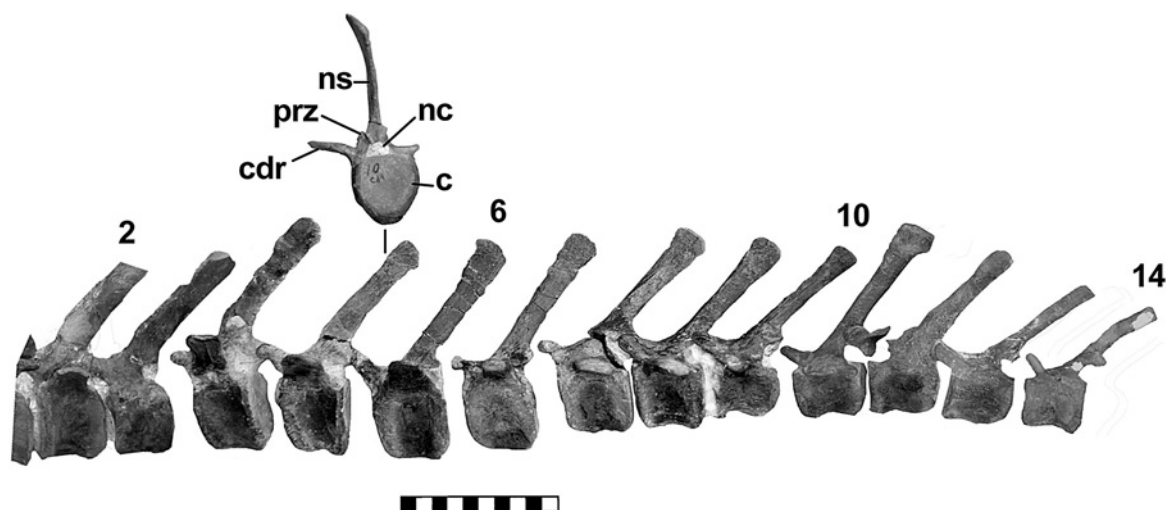


Fig. 14.—Caudal vertebrae 2-14 in left lateral view of *Camptosaurus aphanoeccetes* (CM 11337). Abbreviations: c, centrum; cdr, caudal rib; nc, neural canal; ns, neural spine; prz, prezygapophysis. Scale units are cm.

three or at most four neural spines. Organ (2006) notes that the longitudinal array is plesiomorphic for ornithischians, whereas the rhomboidal array is the derived condition seen in iguanodontoids.

The dorsal ribs resemble those of *C. dispar*, as well as those of other medium-sized ornithopods.

Sacral Vertebrae.—The sacrum of CM 11337 is complete, although slightly distorted and some of the neural spines are damaged (Fig. 13). Nevertheless, the overall morphology is similar to *C. dispar*. There are four unfused sacral vertebrae as in *C. dispar* as defined by the sacral ribs (Fig. 13D). These sacral ribs are attached more on the anterior portion of the centra than intervertebrally as in *C. dispar*. The centrum of sacral (S-)1 is slightly keeled ven-

trally, whereas it is flatter and broad in the rest. Centra 3 and 4 have a slight trough on the ventral side. There is a sacro-caudal (=caudal 1) as in *C. dispar*, but it is loosely attached to the sacrum; the dorso-sacral (D-16) is not attached to the sacrales unlike the specimen described by Gilmore (1909). The diapophysis of the sacrales is partially or completely fused to the top of the sacral ribs producing an "I" cross-section. The diapophyses and sacral ribs are expanded distally against the ilium, but are not coalesced into the iliac yoke seen in older ornithopods individuals for bracing the ilium medially. The first pair of sacral foramina are anteroposteriorly elongated rather than circular as described by (Gilmore 1909) for *C. dispar*. The neural canal in the anterior sacrales (e.g., S-2) is vertically expanded (Fig. 13G), whereas it is smaller but ventrally tapering into the centrum body in the posterior sacral (S-4?).

Caudal Vertebrae.—There were 14 caudals in articulation when CM 11337 was found (Figs. 3, 14). The first caudal (CD-), or sacro-caudal, forms part of the sacrum; measurements are given in Table 3. However, the lack of a diapophysis extending above its rib characterizes the vertebra as a caudal. Distally, the caudal rib braces the postacetabular process of the ilium (Fig. 13D, E). As with the other vertebrae, the caudals resemble those of *C. dispar* except in some details (Fig. 15). First, the neural spines remain tall relative to the centrum height at CD-14, the postzygapophyses are situated higher on the spine, and the chevron facets are small relative to the centrum size. The chevron facets are best developed on the posterior end of the centra, with the first appearing on CD-2 (Fig. 14). Chevrons are missing in this specimen.

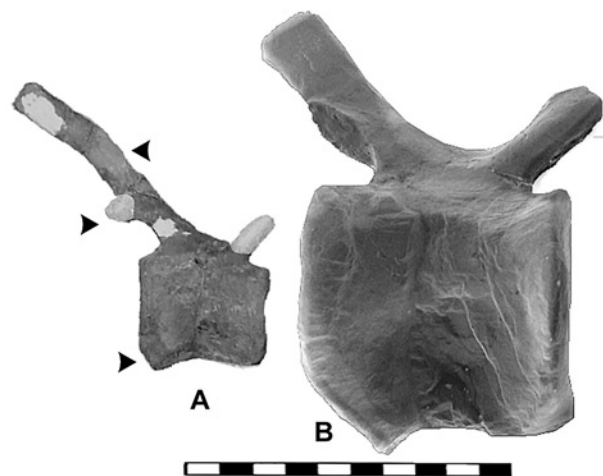


Fig. 15.—Comparison of caudal vertebra 13 in two species of *Camptosaurus* (darts point to regions of major differences). A, *C. aphanoeccetes* (CM 11337); B, *C. dispar* (USNM 4282, holotype *C. browni*). Scale units are cm.

Pectoral Girdle—The left scapula is attached to the coracoid in the holotype, although the two are not completely fused (Fig. 16); a right scapula is also present, but not its

coracoid. Overall, the scapula and coracoid resemble that of *C. dispar* (Fig. 17), including on the medial side the posteriorly extended groove from the coracoid foramen mentioned by Gilmore (1909). One feature of *Camptosaurus* not discussed by Gilmore (1909) is a prominent, cup-like depression, here called the supraglenoid fossa, that is present on the lateral surface of the scapula, just dorsal to the glenoid (Fig. 16A). This fossa is present in both *C. aphanoecetes* and *C. dispar* regardless of age. A similar, although less prominent fossa is present in other iguanodontoids, such as the hadrosaur *Edmontosaurus* Lambe, 1920 (DMNH 1493). Medially, the scapula is thickened near its joint with the coracoid, a prominence called the medial buttress. The scapula of *C. aphanoecetes* is usually arched in lateral view, whereas it is always straight in *C. dispar* in both juvenile and adult specimens (Fig. 17). Furthermore, the distal portion of the scapular blade typically tapers posteroventrally and is not abruptly terminated as in *C. dispar*. A small, triangular facet is present on the anterior edge of the acromion (Fig. 16D), which Gilmore (1909) suggested might be for a clavicle, a point Dodson (1980) seems to accept. This bone has never been found in an ornithischian, and it seems more probable that this scar marks the origin for the middle head of the supracoracoideus (s. intermedius). The coracoid of *C. aphanoecetes* lacks any distinguishing features that separate it from *C. dispar*. It is tall and anteroposteriorly narrow, and has a thickened anterodorsal margin. The scapula of a juvenile *C. aphanoecetes* can be separated from that of *Dryosaurus* in that the latter is considerably more expanded distally.

The partial right (?) sternal plate is damaged along its thin medial and posterior (?) borders (Fig. 18). The lateral border is straighter than in other *Camptosaurus* specimens described by Dodson and Madsen (1981), but is otherwise similar.

Forelimb.—Both humeri are present in CM 11337. Compared with the femur, these are short, slender bones as in *C. dispar*. The shaft is relatively straight in anterior view and slightly sigmoid in profile (Fig. 19; 20A, B). However, the humeral shaft is variable in *C. dispar* (Fig. 20C-G), making this character of dubious taxonomic utility. One

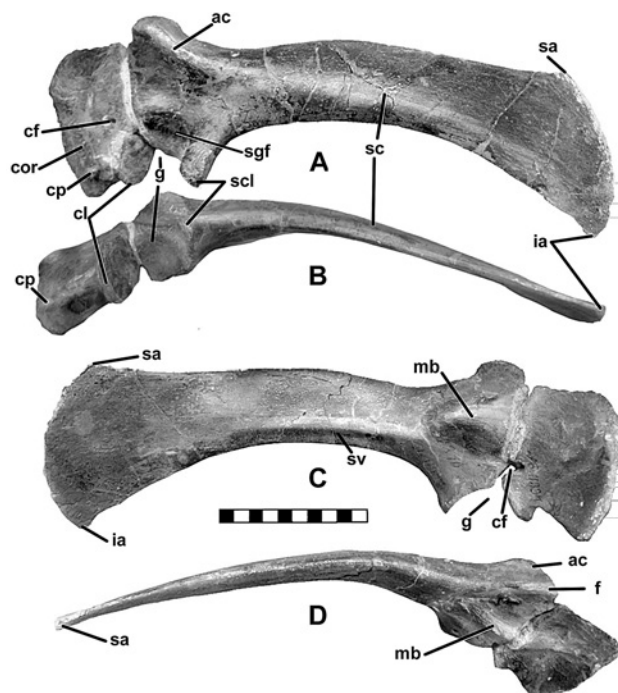


Fig. 16.—Left scapula and coracoid of *Camptosaurus aphanoecetes* (CM 11337). A, lateral; B, ventral; C, medial; and D, dorsal views. Abbreviations: ac acromion process; cf coracoid foramen; cl coracoid labrum; cor coracoid; cp coracoid protuberance; f “facet”; g glenoid cavity; ia inferior angle; mb medial buttress; sa superior angle; sc scapula; scl scapular labrum; sgf supraglenoid fossa; sv ridge for the *M. serratus ventralis*. Scale units are cm.

point of difference may be in the lateral profile of the deltopectoral crest. The crest of *C. dispar* projects abruptly from the shaft and has an elongate anterior margin in both the juvenile and adult specimens (cf. Fig. 20D, G). In contrast, the crest in *C. aphanoecetes* is less prominent and more rounded in profile (Fig. 20B). The humerus of a juvenile *C. aphanoecetes* differs from that of *Dryosaurus* in being considerably more robust at mid-shaft for its length.

The holotype of *C. aphanoecetes* includes a complete left radius and ulna (Fig. 21) and associated manus (Fig. 22). Overall, the ulna and radius resemble those of

TABLE 4. Relative lengths as ratios of metacarpals in CM 11337 and USNM 4277 from Quarry 13 (longest metacarpal in the denominator).

Metacarpals	CM 113371	USNM 4277
MC-I/MC-II	0.29	0.43
MC-II/MC-III	0.78	0.80
MC-IV/MC-III	0.91	0.79
MC-V/MC-IV	0.54	0.67
MC-I/MC-V	0.45	0.65

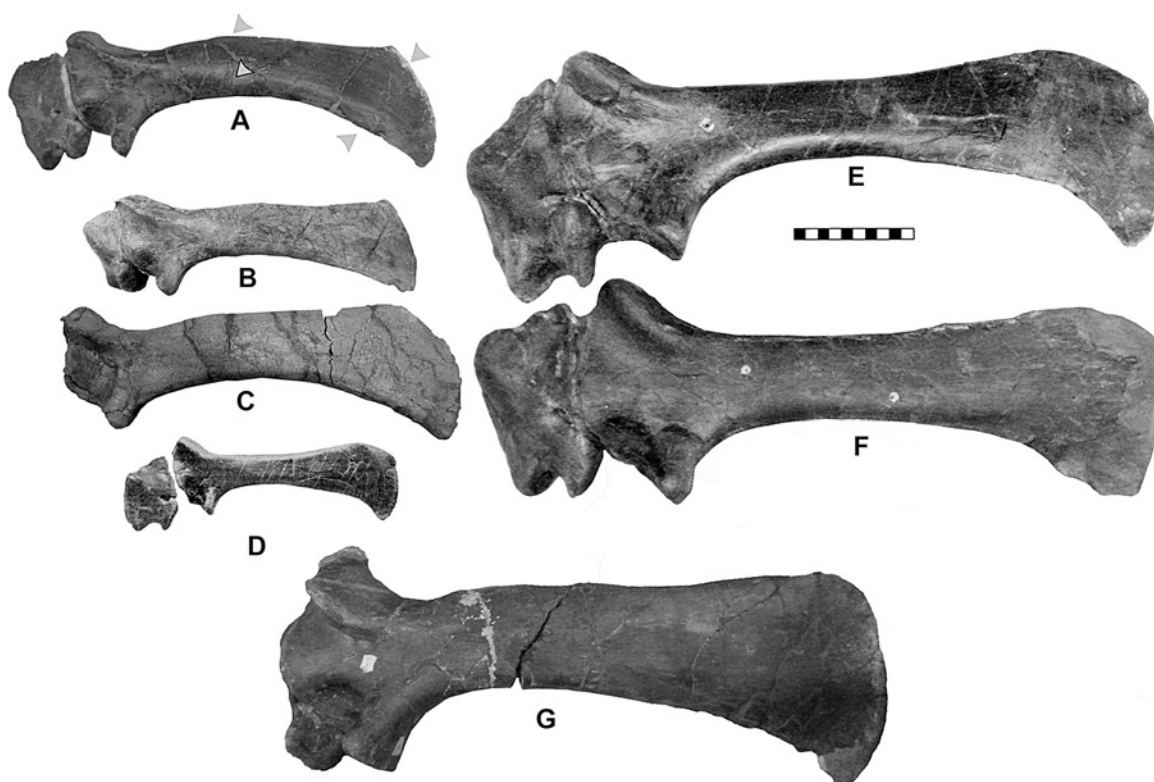


Fig. 17. — Comparison of the scapula in two species of *Camptosaurus* (black darts point to regions of major differences, grey dart points to a region of uncertain taxonomic value). *C. aphanoecetes*: A, (CM 11337); B, (DINO 1030); C, (DINO 1032 reversed). *C. dispar*: D, juvenile (USNM 2210, holotype *C. nanus*); E, (USNM 4282, holotype *C. browni*); F, (USNM 4282 reversed, holotype *C. browni*); G, (USNM 5473 reversed). Scale units are cm. B adapted from Gilmore (1909).

C. dispar. The moderately developed olecranon is similar to that of the juvenile *C. dispar* (Gilmore 1909: fig. 41), but the olecranon is variably developed in *C. dispar* (cf. Gilmore 1909: figs. 27, 41). Therefore, the olecranon size in *C. aphanoecetes* is not considered taxonomically sig-

nificant. The ulna of *Camptosaurus* has a more prominent lateral process for the radius than does *Dryosaurus*.

The manus of *C. aphanoecetes* is mostly intact and remarkably retains the carpals in situ: a proximal row formed by the radiale, intermedium, and ulnare, and a distal row formed by carpals 2-5 (Fig. 22). The ulnare is a complex wedge shape, being thicker on the palmar side than on the extensor side (10.5 mm vs 2.5 mm, Fig. 22A, C), and, on the extensor side, being thicker above metacarpal V than above metacarpal IV (Fig. 22A). Overall, the morphology of the manus is similar to that of *C. dispar*, including the degree of proximal carpal fusion (Fig. 22). When found the distal row of carpals was held in place by matrix; thus, their orientation and positions relative to one another are certain (Fig. 22). They were not closely packed together, being separated by synovial capsules and cartilage. The carpals show some differences from the specimens from Quarry 13, such as the lack of distal carpal (DC-) 1 (cf. Figs. 22C, 23E). Its absence in CM 11337 is not taphonomic, because no space is present for it between metacarpal (MC-) II and the radiale as there is in the Quarry 13 specimens. It is possible that it co-ossified with either MC-II or the radiale, although no trace of it remains despite the traces between other fused elements of the manus being visible. DC-2 is only visible on the palmar side where it is fused along its

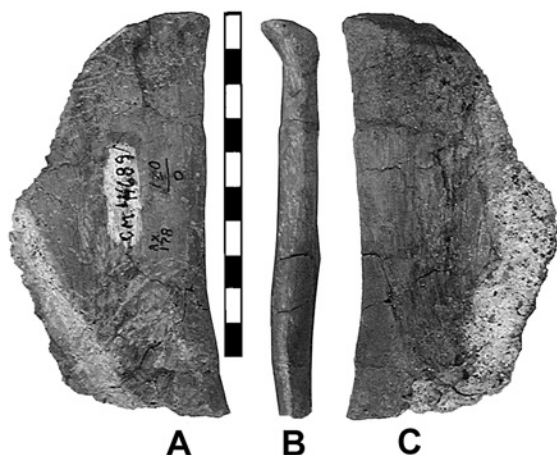


Fig. 18.—Partial sternal plate of *Camptosaurus aphanoecetes* (CM 41689). A, dorsal (?); B, medial; and C, ventral (?) views. Scale units are cm.

dorsal surface to the palmar side of the radiale (Fig. 22C). The diamond shape of DC-2 and its location are very different from that of the Quarry 13 specimens in which it is a broad, thin element capping MC-II (Fig. 23B, E). DC-3 partially underlies DC-2 in CM 11337 (Fig. 22C). It has a complex shape being elongated in the extensor-palmar direction, and thicker on the palmar side than the extensor side. The DC-3 described by Gilmore (1909) is situated between the radiale and the intermedium where it may also fuse to those bones (Fig. 23D, E). DC-4 of CM 11337 is also more complex in shape. It is wider and flatter on the extensor side than the palmar, where it is also rounded (Fig. 22A, C). In the Quarry 13 specimens, DC-4 is a large element that sits atop MC-IV (Fig. 23A, D, E). Finally, DC-5 in CM 11337 has a rounded wedge shape, thicker on the palmar side, between MC-5 and the ulnare (Fig. 22A); this is the only carpal similar to that of the Quarry 13 specimens (Fig. 23B, E). Due to fusion, manual manipulation of the prepared specimen showed that movement between the two carpal rows was restricted to a few degrees between the intermedium and DC-3, and between the ulnare and DC-4 and DC-5.

MC-I is fused to the radiale, although a trace of the suture is still visible. The proximal ends of the other metacarpals are rounded somewhat to accommodate the distal carpals and to allow some movement of about 5–10° between the two groups of bones. Only MC-V is concave proximally, whereas Gilmore (1909) reports that it is concave in both MC-IV and MC-V in the Quarry 13 specimens. The

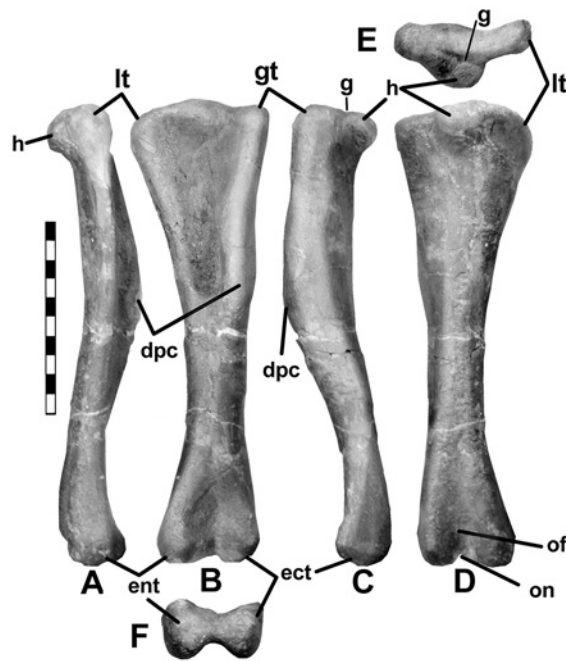


Fig. 19.—Left humerus of *Camptosaurus aphanoecetes* (CM 11337). A, medial; B, anterior; C, lateral; D, posterior; E, proximal; and F, distal views. Abbreviations: dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; g, groove separating head from diaphysis; gt, greater tuberosity; h, head; lt, lesser tuberosity; of, olecranon fossa; on, olecranon notch. Scale units are cm.

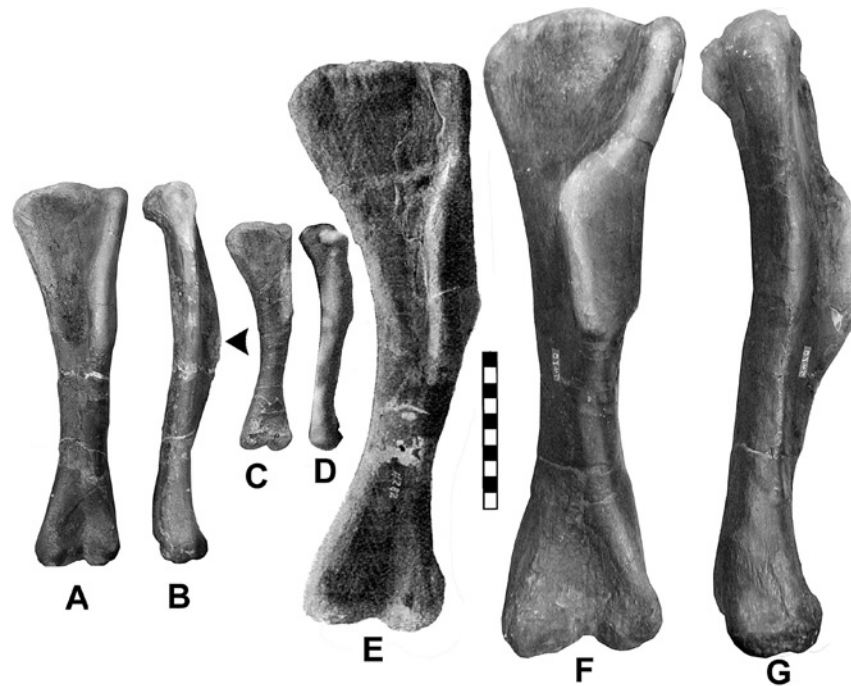


Fig. 20.—Comparison of the humerus in two species of *Camptosaurus* (dart points to region of major difference): A, B, *C. aphanoecetes* (CM 11337); C, D, juvenile *C. dispar* (USNM 2210 reversed, holotype *C. nanus*); E, *C. dispar* (USNM 4282, holotype *C. browni*); F, G, *C. dispar* (USNM 5473 reversed). Scale units are cm. C and E adapted from Gilmore (1909).

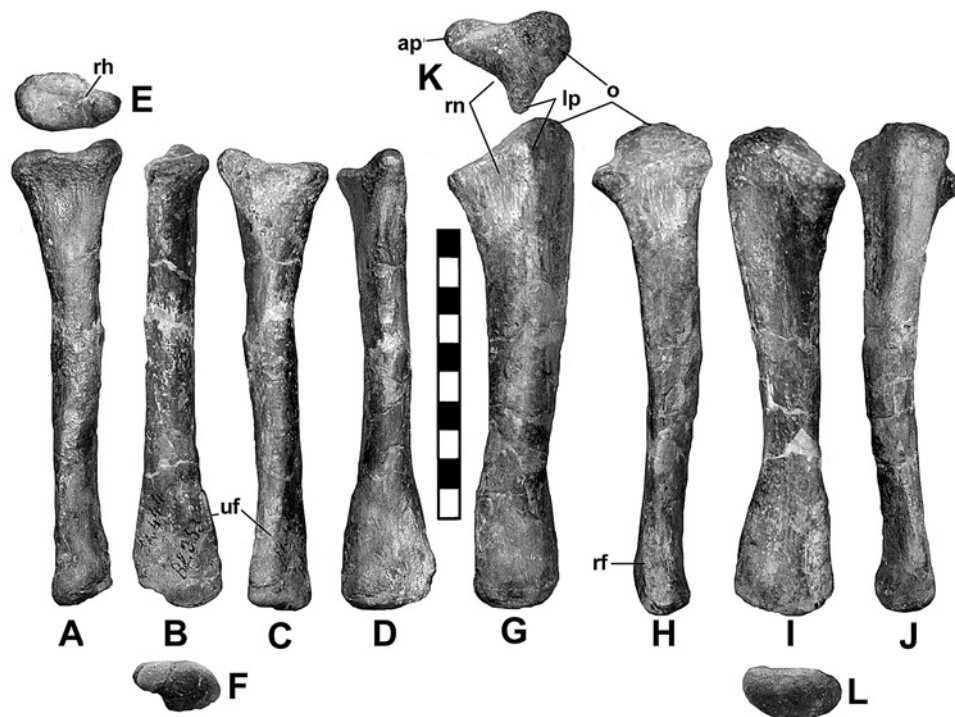


Fig. 21.—Left ulna and radius of *Camptosaurus aphanoeetes* (CM 11337). Radius: **A**, lateral; **B**, anterior; **C**, medial; **D**, posterior; **E**, proximal; and **F**, distal views. Ulna: **G**, lateral; **H**, anterior; **I**, medial; **J**, posterior; **K**, proximal; and **L**, distal views. Abbreviations: ap, anterior process; lp, lateral process; o, olecranon; rf, radial facet; rh, radial head; rn, radial notch; uf, ulnar facet. Scale units are cm.

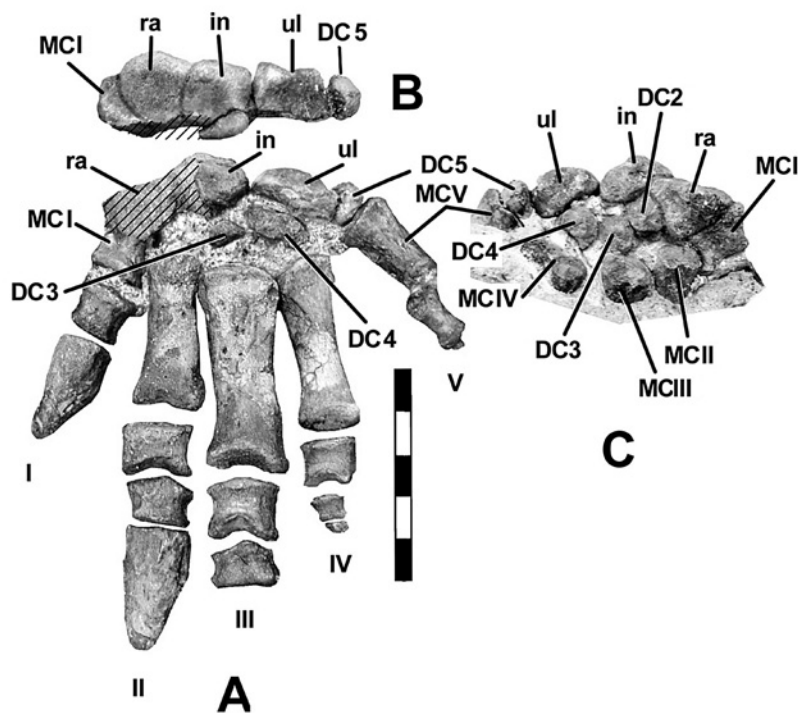


Fig. 22.—Left manus of *Camptosaurus aphanoeetes* (CM 11337) as found (note the matrix supporting the carpals). **A**, extensor side; **B**, carpals in proximal view; **C**, carpals in palmar view. Hatched area is damaged. Abbreviations: I, II, III, IV, V, digits I, II, III, IV, V; DC 2, 3, 4, 5, distal carpal 2, 3, 4, 5; in, intermedium; MC I, II, III, IV, V, metacarpal I, II, III, IV, V; ra, radiale; ul, ulnare. Scale units are cm.

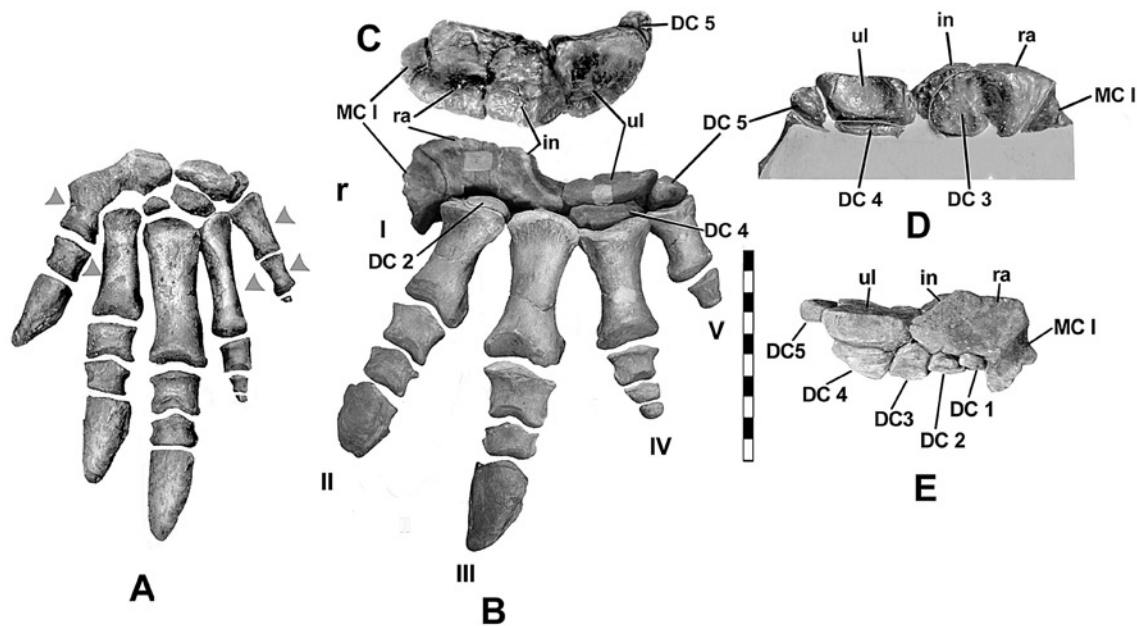


Fig. 23.—Comparison of the manus in two species of *Camptosaurus* (darts point to regions of major differences). *C. aphanoeetes* (CM 11337): A, restored manus. *C. dispar* (USNM 4277 reversed): B, extensor side; C, proximal; D, carpals in palmar view. *C. dispar* (USNM 4282; holotype *C. browni*): E, carpals in palmar view showing variation of carpals compared with D. Abbreviations: I, II, III, IV, V, digits I, II, III, IV, V; DC 1, 2, 3, 4, 5, distal carpal 1, 2, 3, 4, 5; in, intermedium; MC I, II, III, IV, V, metacarpal I, II, III, IV, V; ra, radiale; ul, ulnare. Scale units are cm.

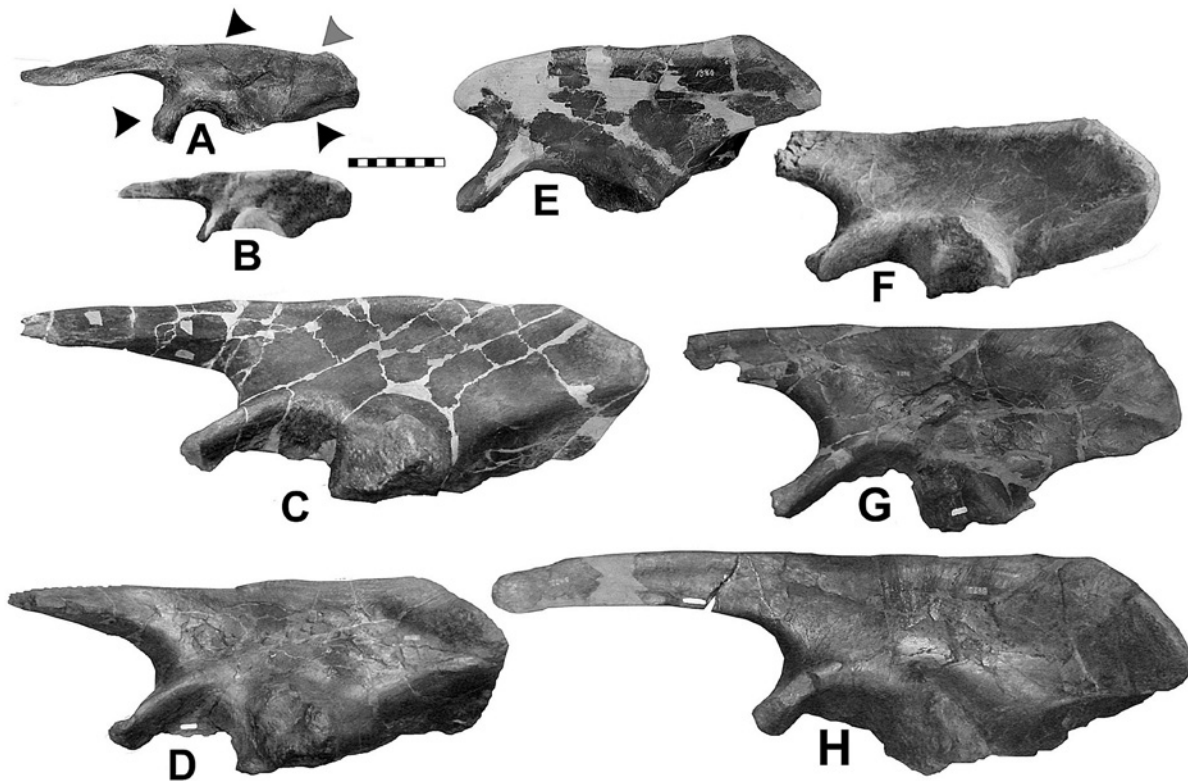


Fig. 24.—Comparison of the ilium in two species of *Camptosaurus* (black darts point to regions of major differences, grey dart points to a region of uncertain taxonomic value). A, *C. aphanoeetes* (CM 11337). *C. dispar*: B, juvenile (USNM 2210 with femoral head, holotype of *C. nanus*); C (USNM 7631 reversed); D (USNM 5818 reversed); E (YPM 1880, holotype of *C. medius*); F (YPM 1880, holotype of *C. medius* reversed); G (USNM 5959 reversed); H (USNM 5473 reversed). Scale units are cm. E courtesy of Walter Joyce and the Peabody Museum of Natural History; F adapted from Gilmore (1909).

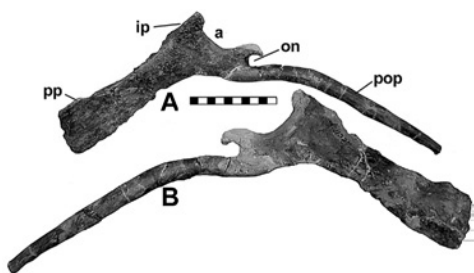


Fig. 25.—Left pubis of *Camptosaurus aphanoeetes* (CM 11337). A, lateral; and B, medial views. Abbreviations: a, acetabulum; ip, ilium peduncle; on, obturator notch; pop, postpubic process; pp, prepubic process. Scale units are cm.

phalangeal count of CM 11337 is the same as that reported by Gilmore (1909) for the Quarry 13 specimens. The unguals appear to be longer and narrower than in the specimens described by Gilmore (1909; Fig. 23). However, there is so much restoration of them that this proportionally greater length is not certain.

The significance of the differences in the manus of the two species of *Camptosaurus* is difficult to assess due to the lack of juvenile material of *C. dispar* for comparison with the adult manus. Thus, the significance of the proportionally smaller carpals and their looser arrangement in *C. aphanoeetes* as compared with *C. dispar* (cf. Figs. 22A, C, 23) may reflect the immaturity of the individual, or may reflect real differences. The same may be true of the proportionally more slender metacarpals compared to their length (Table 4), or the proportionally longer phalanx V-1 (Fig. 23A). Among larger specimens of *C. dispar*, there is considerable variation in the relative sizes and shapes of the carpals, especially the distal ones (e.g., Fig. 23D, E). This situation complicates understanding the significance of the difference in the wrist region in *C. aphanoeetes*.

Pelvic Girdle—Both ilia were found attached to the sacrum (Figs. 3, 13). There is some damage to the dorsal margin of the right ilium and to the preacetabular blade of the left ilium. Overall, the ilia resemble those of *C. dispar* (Fig. 24), although some differences are evident. As Gilmore (1925) noted, the ilium is low compared to its length, which was one character he used to refer the specimen to *C. medius*. However, the ilium in the juvenile *C. dispar* is also low (Fig. 24B); therefore, this character is not taxonomically significant. On the other hand, the more arched dorsal margin, and proportionally longer and lower postacetabular process are features that do not change ontogenetically in *C. dispar*. In addition, the pubic process is angled anteroventrally more in *C. dispar* regardless of age than is the case for *C. aphanoeetes*. Finally, one feature of questionable taxonomic value is the prominent notch along the dorsal margin of the postacetabular process. Although not as prominent, it does appear in YPM 1880 (Fig. 24E).

Both pubes are known for *C. aphanoeetes* (Fig. 25). The blades of the holotype are straight, whereas they are

bowed in the referred specimen (cf. Fig. 26A, B). The distal end of the postpubic process is unknown for any specimen, but otherwise the pubes resemble those of *C. dispar* (Fig. 26), except for a few points: the peduncle for the ilium is very prominent, having an elongate surface that extends into the acetabulum. Also, the acetabular notch is very large in proportion to the pubic body. There is an obturator notch rather than an obturator foramen. In *C. dispar* the foramen is formed by the union of a process extending ventrally from near the acetabular portion of the pubis and another process extending dorsally from the postpubic process (Fig. 26D). In the juvenile *C. dispar* (USNM 2210), the two processes are not co-ossified. Possible closure of the obturator notch by cartilage in *C. aphanoeetes* is discussed further below.

The ischia of *C. aphanoeetes* include two partial ones of the holotype (Fig. 27), and a nearly complete one belonging to the paratype specimen (Fig. 27C, D). These are all straight shafted in contrast to the usual bent shaft of *C. dispar* (Fig. 28D-G). However, the shaft is straight in the juvenile of *C. dispar* (Fig. 28C); therefore, the straight shaft may reflect the immaturity of the specimens of *C. aphanoeetes*. Two characters do appear to distinguish the two species: the large obturator process forming a deep obturator notch and the small, distal foot of the shaft (Fig. 28A, B), rather than simply a distal expansion.

The pelves of *C. aphanoeetes* and *C. dispar* are compared in Figure 29. As may be seen, the acetabulum of *C. aphanoeetes* is proportionally larger than it is in *C. dispar*. However, the femoral head is not expanded, thus leaving a large amount of space. Presumably, this space is

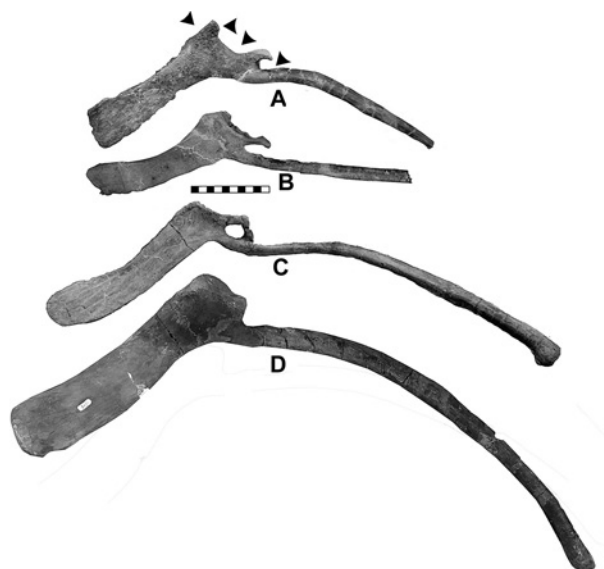


Fig. 26. —Comparison of the pubis in two species of *Camptosaurus* (black darts point to regions of major differences). *C. aphanoeetes*: A, (CM 11337); B, (CM 79050, B in reverse). *C. dispar*: C, (YPM 1880 holotype); D, (YPM 1878 holotype). Scale units are cm. D courtesy of Walter Joyce and the Peabody Museum of Natural History; C adapted from Gilmore (1909).

partially filled with cartilage as it is in extant birds (pers. obs.), as well as articular cartilage around the femoral head. The articulated pelvis does show that the obturator notch of the pubis is closed by the ischium, and possibly by cartilage as well. The cartilaginous area may be indicated on the postpubic shaft by a rugose area, which is seen on all the specimens. This rugose area occurs where the dorsally extending process occurs in *C. dispar*. Furthermore this scar is large and encompasses the ischial contact with the postpubic process (Fig. 29C, D). Thus, the cartilage probably included part of the ischium as well.

Hindlimb.—Both femora of the holotype are present, but are moderately to slightly crushed (Fig. 30), as are their associated tibiae and fibulae (Fig. 31). The proximal end of the right femur (Fig. 30G-J) is distorted, but it is not known if this is pathological or preservational. The femur, tibia, and fibula of the paratype specimen, CM 15780, are not crushed (Figs. 30, 31) and show that the hindlimb material resembles that of *C. dispar*. The astragalus of *C. aphanoecetes* (Fig. 32; CM 15780) resembles that of *C. dispar*, although the ascending process is more prominent. The referred metatarsals (Fig. 33) are similar to those of *C. dispar*.

The femur, tibia, and fibula of a juvenile *Camptosaurus* can be differentiated from those of *Dryosaurus* in their much greater robustness, especially at midshaft. In addition, the anterior trochanter of the femur of *Dryosaurus* projects to the top of the greater trochanter, whereas it is lower in *Camptosaurus*. The anteriorly located intercondylar groove is more prominent in *Camptosaurus* than in *Dryosaurus*. On the tibia, the lateral distal malleolus for the fibula and calcaneum extends ventrally in *Camptosaurus*, whereas it is significantly shorter in *Dryosaurus* (see

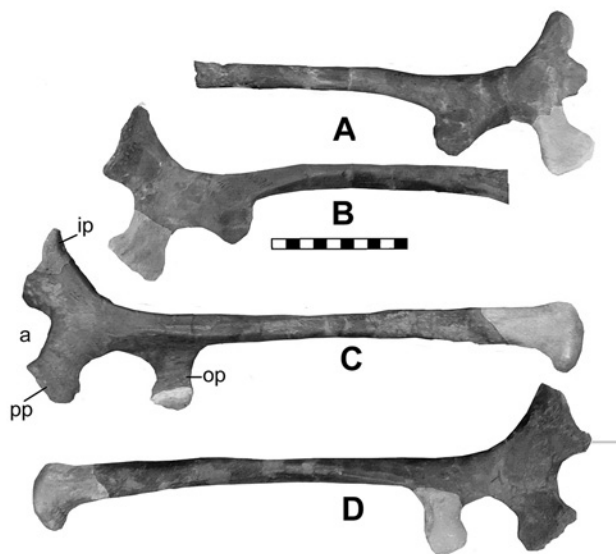


Fig. 27.—Ischia of *Camptosaurus aphanoecetes*: (CM 11337). Right ischium: A, lateral; and B, medial views; left ischium: C, lateral; and D, medial views. Abbreviations: a, acetabulum; ip, iliac peduncle; op, obturator process; pp, pubic peduncle. Scale units are cm.

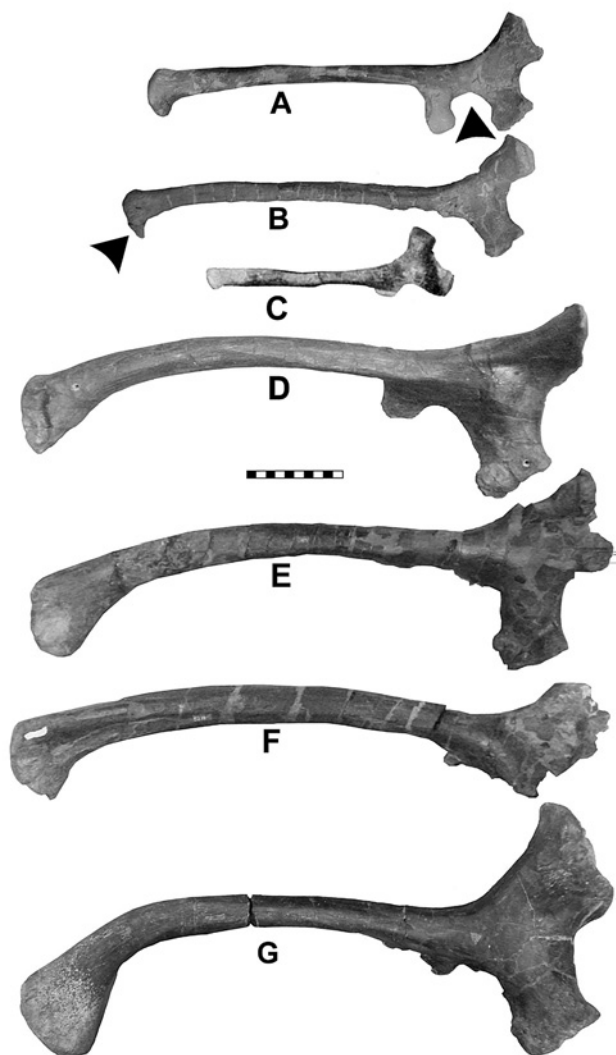


Fig. 28.—Comparison of the ischium in two species of *Camptosaurus* (black darts point to regions of major differences, grey dart points to regions of uncertain taxonomic value). *C. aphanoecetes*: A, (CM 11337); B, (CM 79050). *C. dispar*: C, (USNM 2210); D, (USNM 4282, holotype of *C. browni*); E, (USNM 5818 reversed); F, (USNM 5818); G, (USNM 4697 reversed). Scale units are cm.

Galton 1981: fig. 16).

Skeletal reconstructions of the two species of *Camptosaurus* are presented in Figure 34. The stance and mode of locomotion shown by the two species is discussed further in the next section.

BIOMECHANICS OF THE FORELIMB

The holotype of *C. aphanoecetes* has an uncrushed left forelimb with manus, and this allowed an analysis of forelimb mechanics in a medium-sized ornithopod. The forelimb is analyzed using functional complexes or units as defined by Bock (1974:121): "I have chosen the

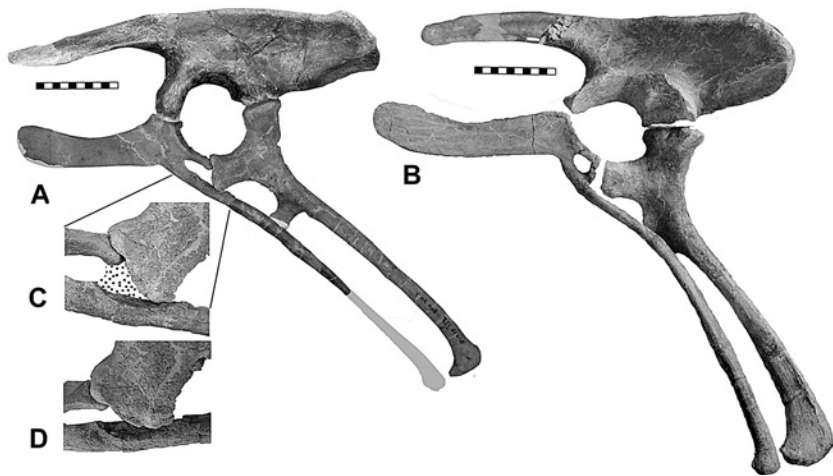


Fig. 29.—Comparison of the pelvis in two species of *Camptosaurus*. **A**, *C. aphanoeetes* (composite); **B**, *C. dispar* (based on holotype of *C. medius*). **B** modified from Gilmore (1909). Closeup of pubis articulation with ischium in **C**, lateral; and **D**, dorso-lateral oblique views. Note the facet on the postpubic process for the ischium. The obturator notch of the pubis is closed off by the ischium and possibly by cartilage (stipple area in **C**). Scale units are cm.

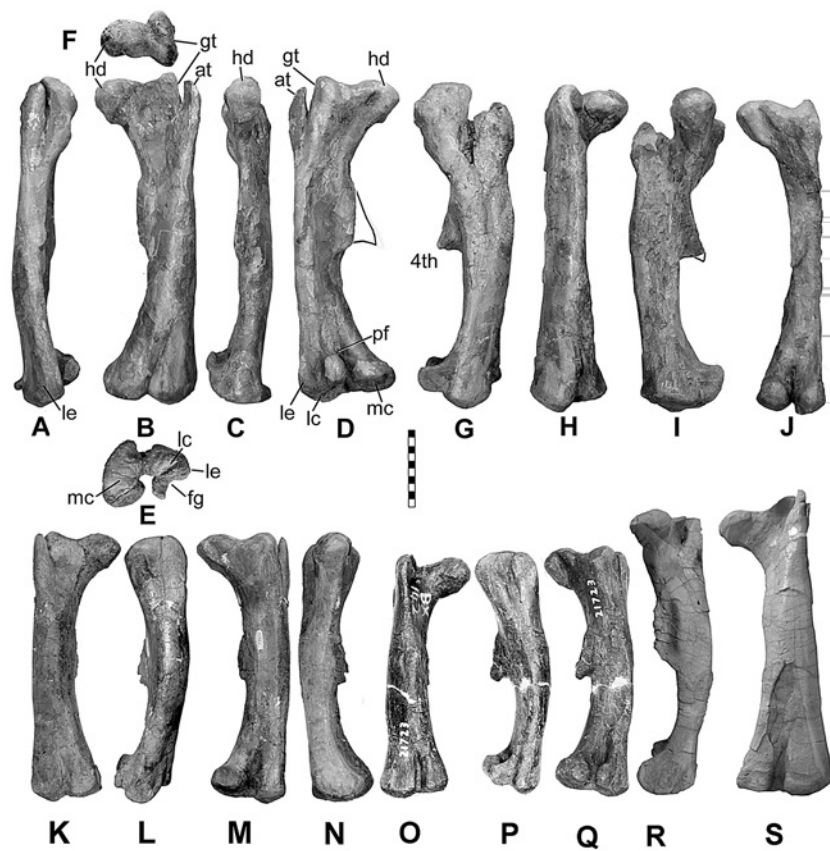


Fig. 30.—Femora of *Camptosaurus aphanoeetes*. CM 11337 left femur: **A**, lateral; **B**, anterior; **C**, medial; **D**, posterior; **E**, distal; and **F**, proximal views; right femur (pathological?): **G**, lateral; **H**, anterior; **I**, medial; and **J**, posterior views. CM 15780 right femur: **K**, anterior; **L**, lateral; **M**, posterior; and **N**, medial views. CM 11723 right femur: **O**, anterior; **P**, lateral; **Q**, and posterior views. DINO 1091 right femur: **R**, medial; and **S**, anterior views. Abbreviations: 4th, fourth trochanter; at, anterior trochanter; fg, fibular groove; gt, greater trochanter; hd, head; lc, lateral condyle; le, lateral epicondyle; mc, medial condyle; pf, popliteal fossa. Scale units are cm.

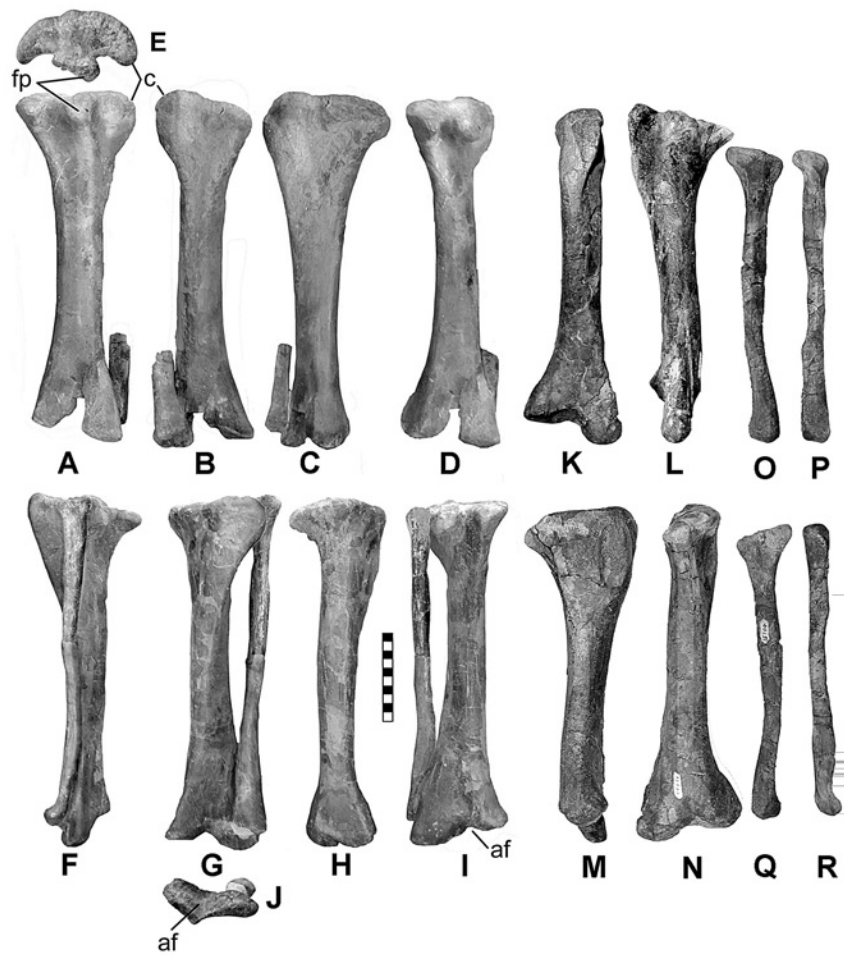


Fig. 31.—Tibia and fibula of *Camptosaurus aphanoeetes*. CM 11337 right side: **A**, lateral; **B**, anterior; **C**, medial; **D**, posterior; and **E**, proximal views; left side: **F**, lateral; **G**, anterior; **H**, medial; **I**, posterior; and **J**, distal views. CM 15780 left tibia: **K**, anterior; **L**, lateral; **M**, medial; and **N**, posterior views. CM 15780 left fibula: **O**, lateral; **P**, anterior; **Q**, medial; and **R**, posterior views. The distal end of the right tibia (**A**-**D**) had previously been cut and expanded and filled with plaster in an attempt to restore it. Abbreviations: af, astragular facet; c, cnemial crest; fp, fibular process. Scale units are cm.

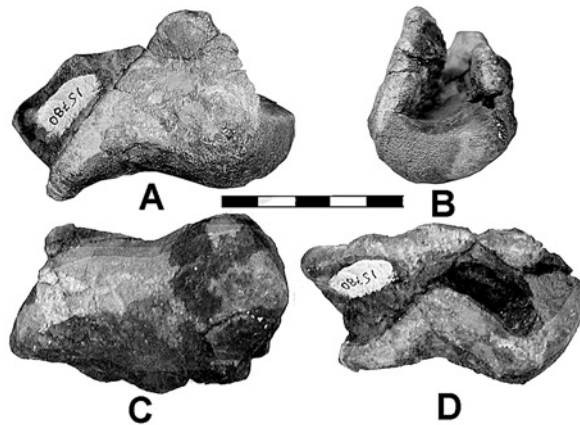


Fig. 32. — Right astragalus of *Camptosaurus aphanoeetes* (CM 15780). **A**, anterior; **B**, lateral; **C**, ventral; and **D**, dorsal views. Scale units are cm.

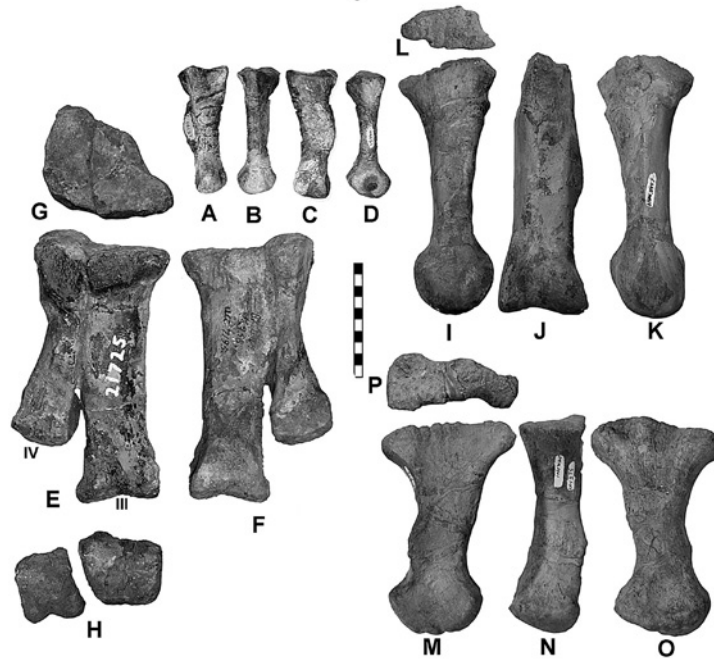


Fig. 33.—Metatarsals of *Camptosaurus aphanoeetes*. CM 15780 left metatarsal IV: **A**, anterior; **B**, lateral; **C**, posterior; and **D**, medial views. CM 21725 right metatarsals III and IV: **E**, anterior; **F**, posterior; **G**, proximal; and **H**, distal views. DINO 2457 left metatarsal III: **I**, medial; **J**, anterior; **K**, lateral; and **L**, proximal views. DINO 2461 left metatarsal II: **M**, medial; **N**, anterior; **O**, lateral; and **P**, proximal views. Scale units are cm.

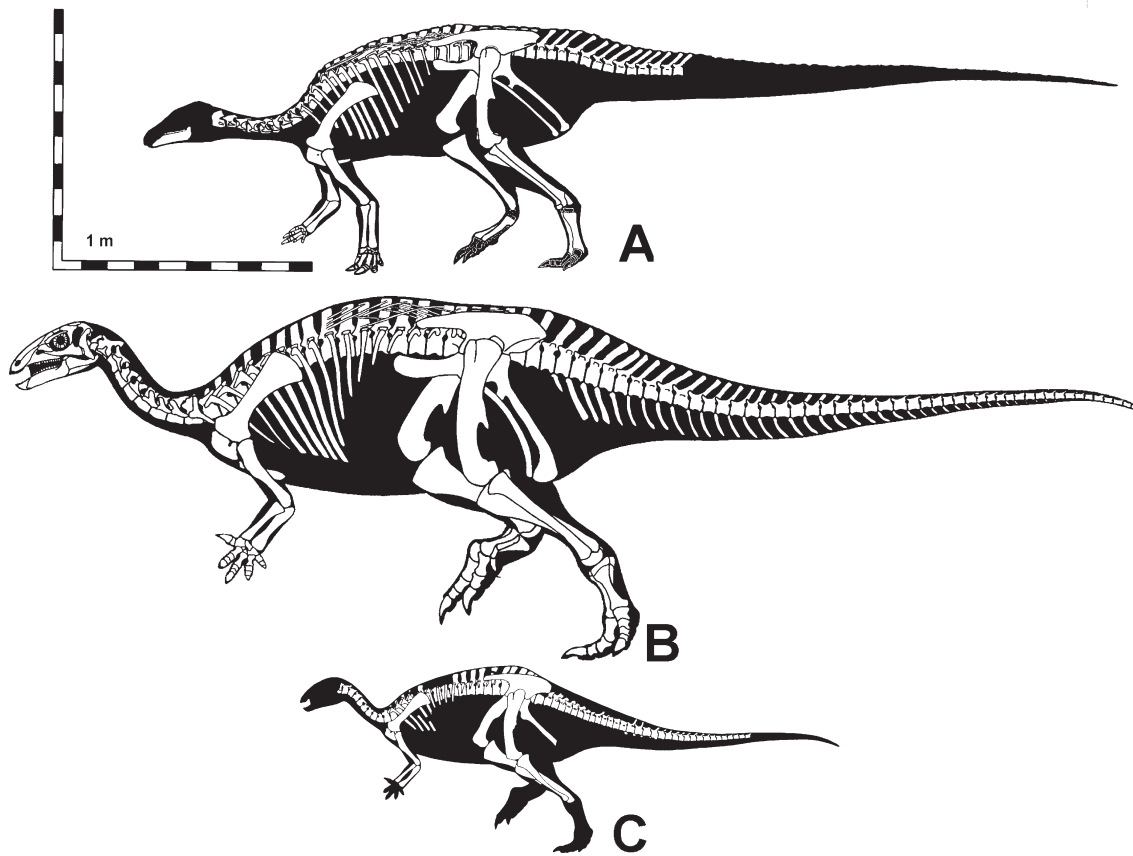


Fig. 34.—Skeletal reconstructions of *Camptosaurus*. **A**, *C. aphanoeetes*; **B**, *C. dispar* (adult); **C**, *C. dispar* (juvenile based on USNM 2210, holotype *C. nanus*). **B**, **C** courtesy of Gregory Paul.

TABLE 5. Effects of soft tissue on the range of motion in *Gallus* (extension is 90°-0°, flexion 91°-180°). In most cases the range of motion is the most restricted with the skin still in place. Shoulder is measured relative to the axis of the scapula, hips relative to the ilium, elbow relative to the long axis of the humerus, and knee relative to the long axis of the femur.

Functional Unit	Skin On	Skin Off	Skin & Muscle Off
shoulder	50°-100°	20°-110°	0°-160°
elbow	30°-95°	25°-145°	20°-180°
hips	15°-105°	0°-115°	360°
knee	35°-135°	35°-135°	35°-170°

alternative scheme of treating the skeletomuscular system as a unit in the belief that the skeletomuscular system comprises a unified adaptive system whose function and adaptational properties and whose evolutionary and systematic significance can be comprehended far better as a single interwoven complex than is possible if these systems are considered separately.” Carpenter (2002) applied the concept of functional complexes to define points of movement as determined by joints and associated muscle regardless of whether the skeletomuscular system involves one-joint muscles or two-joint muscles. The one-joint complex involves two bones connected across a joint by a muscle acting to move one of the bones rotationally relative to the other. For example, the *teres major*, which originates on the scapula and inserts on the humerus, moves the humerus relative to the scapula at the glenoid-humeral articulation. In contrast, the two-joint complex involves a muscle that spans two joints between its origin and insertion, with rotation of two adjacent bones possible. The *triceps longus lateralis* originates on the scapula and inserts on the olecranon process of the ulna; thus, it acts as a retractor for the humerus and an extensor of the ulna.

To better understand the biomechanics of the forelimb in *Camptosaurus*, it is necessary to reconstruct the musculature. Traditionally, reconstruction of the musculature for extinct animals has relied heavily on presumed muscle origin-insertion scars, as well as those of ligaments (e.g., Gregory and Camp 1918). More recent studies have used phylogenetic bracketing to identify these muscles (e.g., Dilkes 2000; Jasinowski et al. 2006). But limb movement is more than muscles. It also involves limitations imposed by the joints and by the skin. The limitation of the joints in extinct vertebrates can be determined from the smooth surfaces at the bone ends that are separated from the diaphysis by a rim or abrupt textural transition (Carpenter and Smith 2001; Carpenter 2002). Studies by Carpenter (2002) and Senter (2006), for example, show the full range of motion hypothetically possible at various joints. Their methodology works for hinge joints, but is less reliable for certain ball and socket joints, e.g., femoral head and acetabulum where 360° of rotation is possible. The influence of both skin and muscle in the hinge studies have generally not been considered, because these soft tissues are absent in

fossils. Nevertheless, the limitations exerted by soft tissue on limb mobility can be illustrated by *Gallus gallus* (Linnaeus, 1758) in Figure 35 and with measurements in Table 5. The range of motion with skin and muscle is 25% -75% (0 = 42%) than for bone only.

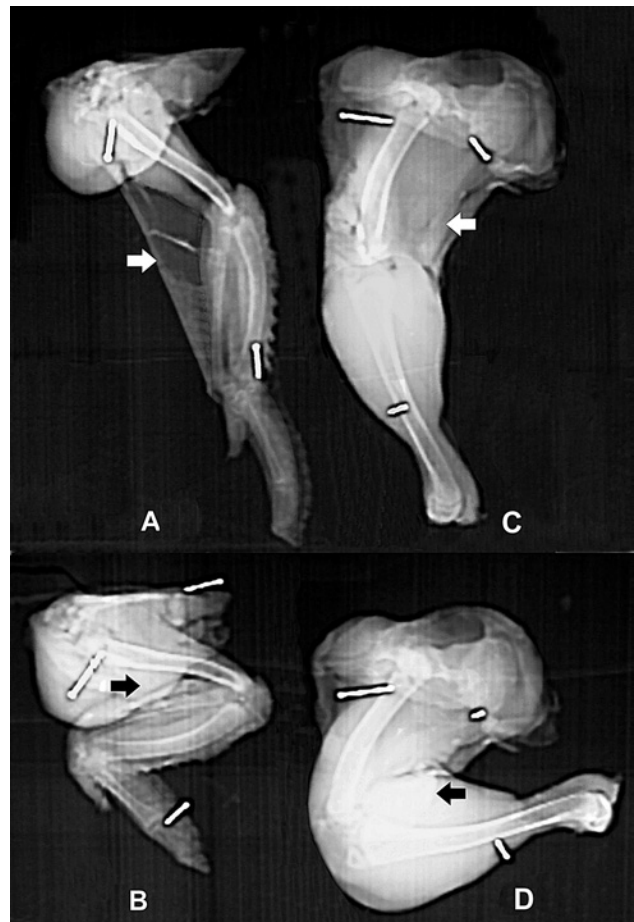


Fig. 35.—X-ray images showing range of motion restricted by soft tissue in left limbs of *Gallus gallus*. **A**, protracted forelimb, extended forearm; **B**, retracted forelimb, flexed forearm; **C**, retracted thigh, extended lower limb; **D**, protracted thigh, retracted lower limb. Main causes of soft tissue restriction shown by arrows: **A**, patagium; **B**, impediment by forelimb muscles; **C**, retractors; **D**, impediment by muscle masses of hindlimb.

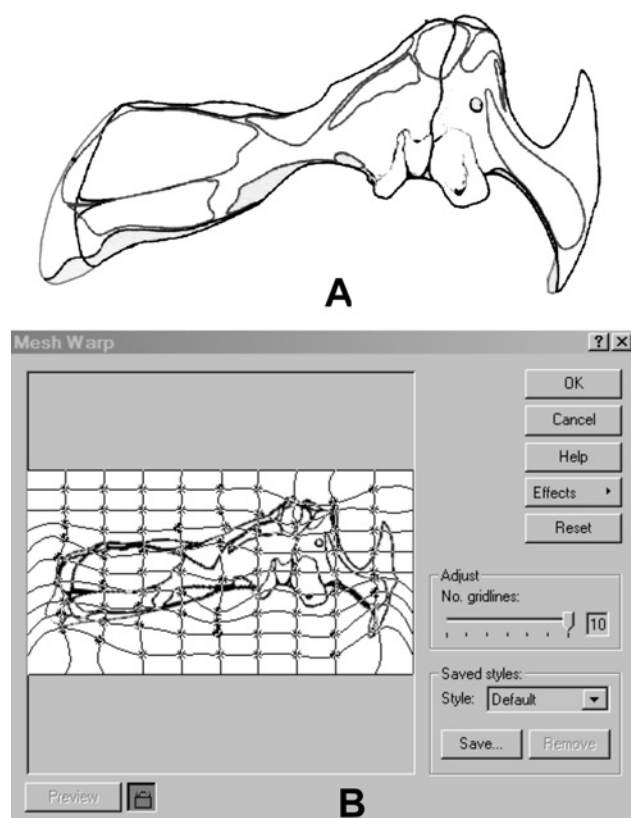


Fig. 36.—Deformation of the scapulocoracoid of the alligator. **A**, uses the “Mesh Warp” feature of Corel PhotoPaint 7 (Bezier grid deformation of Photoshop) using a 10 x 10 grid; **B**, moving the nodes moves the contents of the surrounding cells.

Reconstructing muscles, however, can be difficult because not all muscles leave scars (Bryant and Seymour 1990). This problem is exacerbated in young animals, such as the holotype of *C. aphanoeetes*, because scars are even less developed than they are in adults. A testable method developed for reconstructing the forelimb of *Tyrannosaurus* (Lipkin and Carpenter in press) is used to reconstruct the forelimb musculature in *Camptosaurus*. The basic premise is if it were possible to make the forelimb bones of a crocodilian and of a bird resemble those of *Camptosaurus*, which of the two would most show similar muscle scar patterns to the *Camptosaurus*? The method deforms the pectoral girdle (e.g., Fig. 36A) and forelimb elements of both a crocodilian (*Alligator* Daudin, 1809) and bird (*Gallus*) into the shape of those elements for *Camptosaurus*. The results can then be used to create a musculature map as a testable hypothesis. The technique does not involve morphing of a bone of one taxon into that of another taxon, because the bones of the two taxa are not used as the end points of a continuum. Standard morphing produces a gradation sequence of composites based on changing ratios of one taxon relative to another (e.g., composite humerus based on 25% of alligator and 75% of

Camptosaurus). Furthermore, although the new technique uses a Cartesian grid (Fig. 36B), it does not attempt to explain homologous points of two forms in the manner used by Thompson (1961).

The deformation of the scapulocoracoid and the humerus uses the “Mesh Warp” feature of Corel PhotoPaint 7 (Bezier grid deformation of Photoshop) using a 10 x 10 grid. By manually moving each intersect of the gridlines (“node”), a small area of each bone could be deformed. The deformation was smooth, meaning that no sharp angles and lines resulted, thus approximating changes in a biological structure. Nodes were moved until the outline of the bone closely approximated the size and outline of the same bone in *Camptosaurus*. As used, “Mesh Warp” is not mathematically as rigorous as the thin plate spline of Bookstein (1991), because measuring the change in landmark position is irrelevant.

The results of the deformations are shown in Figures 37 and 38. Except for the scapular blade, the muscle map for both the deformed scapulocoracoid (Fig. 36B) and humerus (Fig. 38B, G) of the alligator is more similar to the muscle maps for *Camptosaurus* (Figs. 37E, 38C, H) than is that for the bird (Fig. 37D, 38E, J). The matches are far from exact and the differences highlight several important points. First, for example, the scapular blade of *Camptosaurus* has two large beveled surfaces on the lateral surface (Fig. 16A) that would seemingly suggest the presence of only two muscles, the rhomboideus superficialis and teres major (Fig. 37E) as in the bird. But it is also possible that more muscles were present as predicted by the deformed alligator scapula, which shows that several closely placed muscles could have been present (Fig. 37B) on the scapula of *Camptosaurus*. It is possible, then, that closely placed adjacent muscles may appear to be a single muscle if the origin or insertion scars separating them are not well defined. An example is seen on the humerus of *Camptosaurus* where the supracoracoideus complex and pectoralis form a single large scar on the deltopectoral crest. Second, the differences between the muscle maps of the deformed alligator and *Camptosaurus* indicate that the musculature in *Camptosaurus* is not derived from that of the alligator, although the similarities do suggest a common ancestry. For example, the coracobrachialis brevis posterior (c.b. dorsalis of the alligator) for the *Camptosaurus* is located below the acromion process and the supracoracoideus intermedius on the acromion. Another example is that rather than a shared insertion for the teres major and latissimus dorsi as on the humerus of the alligator (Fig. 38F), the two have separate insertions in *Camptosaurus* (Fig. 38H). Vectors for some major muscles are shown in Figure 39. A full description of the musculature will be presented elsewhere (Carpenter in prep.).

The pectoral girdle and forelimb used in the biomechanical analysis is shown in Figure 40, and the four functional complexes for the kinematics are shown in Figure 41. The position of the pectoral girdle is dictated in part by the ribcage (represented here by D-3 and associated

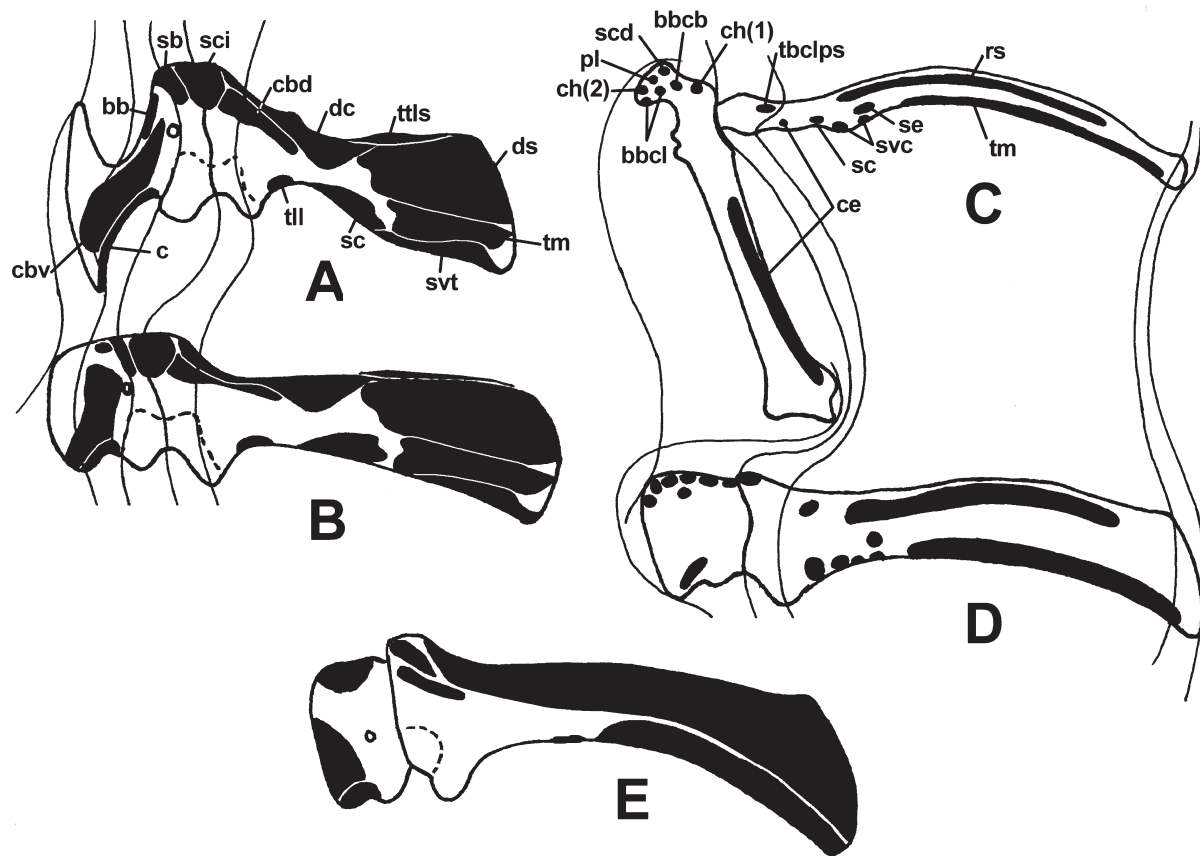


Fig. 37.—“Mesh Warp” deformation of a crocodilian and avian scapula and coracoid to approximate that of *Camptosaurus*. Wavy vertical lines serve as visual aid showing direction and degree of deformation. This method allows for the prediction of the position and shape of various muscles on the scapulocoracoid of *Camptosaurus*. **A**, original muscle map of *Alligator*; **B**, deformed muscle map of *Alligator*; **C**, original muscle map of *Gallus*; **D**, deformed muscle map of *Gallus*; **E**, muscle map of *Camptosaurus* based on muscle scars. Note that the muscle map more closely resembles that of the *Alligator* than *Gallus* suggesting that the muscle map of *Alligator* should be used to reconstruct muscles that do not leave distinct scars. Abbreviations: bb, M. biceps brachii; bbcb, M. biceps brachii caput breve; bbcl, M. biceps brachii caput longum; c, M. costocoracoideus; cbd, M. coracobrachialis brevis dorsalis; cbv, M. coracobrachialis brevis ventralis; ce, M. coracobrachialis externus; ch, M. coracohumeralis; dc, M. deltoideus clavicularis; ds, M. deltoideus scapularis; pl, M. prepatagialis longus; rs, M. rhomboideus superficialis; sb, M. supracoracoideus brevis; sc, M. scapulohumeralis cranialis; scd, M. scapulohumeralis caudalis; sci, M. supracoracoideus intermedius; se, M. subscapularis externus; svc, M. subscapularis ventralis cranialis; svt, M. serratus ventralis thoracis; tbclps, M. triceps brachii, caput longum pars scapularis; tll, M. triceps longus lateralis; tm, M. teres major; ttls, M. trapezius + levator scapulae. Terminology for alligator adapted from Meers (2003); terminology for *Gallus* adapted from Yasuda (2002).

ribs) and by the position of the right scapula. As noted by Gilmore (1925), the right scapula was preserved in situ relative to the vertebral column (Fig. 3). In this position, the axis of the scapula is approximately -17° relative to the axis of the anterior dorsal vertebrae (Fig. 42). However, because the anterior part of the vertebral column curves ventrally (Figs. 11A, 34), the axis of the scapula is approximately -53° below horizontal, which is close to the -60° seen in theropods (Carpenter 2002). As a result of being in this position, the glenoid faces ventroposteriorly. As with other articulated dinosaur skeletons, the first dorsal rib bisects the scapula just anterior to the scapular neck, the dorsoventrally narrowest portion of the blade (Fig. 42). As noted elsewhere (Carpenter 2002), the coracoids of dinosaurs are typically closely set, if not in con-

tact. This has been clearly established for ornithopods with the three-dimensional hadrosaurs including “mummies” (e.g., AMNH 5060) and skeletons (e.g., LACM 23502). In *Camptosaurus*, this placement would put the distal ends of the scapulae approximately 30 cm apart separated by the ribcage, and the coracoids well under the chest (Fig. 40) as noted by Gilmore (1909). To accommodate this positioning of the coracoid, the longitudinal axis of the scapula and coracoid is twisted ventromedially so that a portion of the medial side of the scapula and coracoid are visible in dorsal view (Fig. 16D). The extensor (“dorsal”) side of the manus faces anterolaterally in a manner similar to that seen in the manus track of *Anomaepus* Hitchcock, 1848 (Lull 1953 fig. 61).

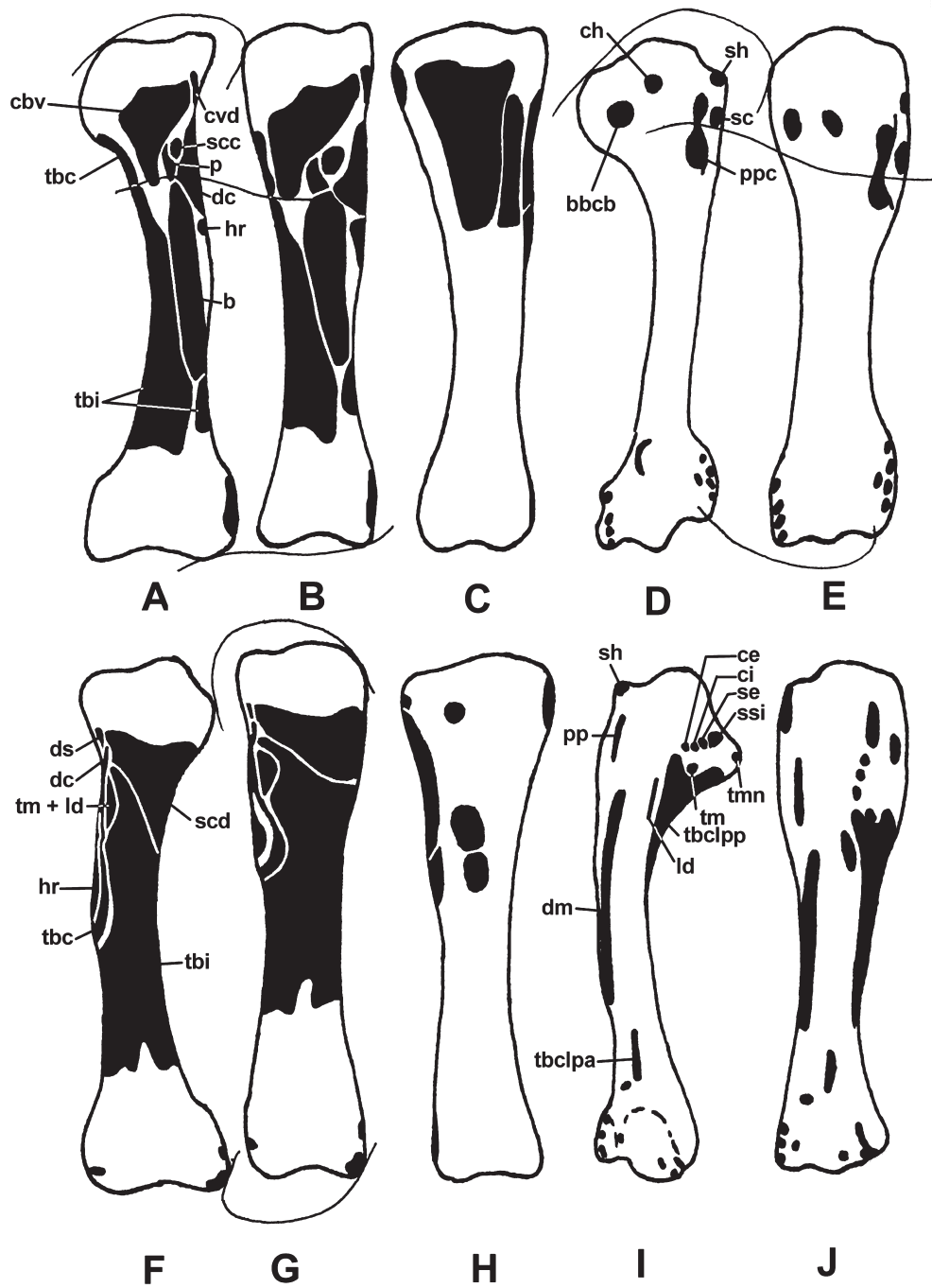


Fig. 38.—“Mesh Warp” deformation of a crocodilian and avian humeri. Top row shows anterior surface: **A**, original muscle map of *Alligator*; **B**, deformed muscle map of *Alligator*; **C**, muscle map of *Camptosaurus* based on muscle scars; **D**, original muscle map of *Gallus*; **E**, deformed muscle map of *Gallus*. Bottom row shows posterior surface: **F**, original muscle map of *Alligator*; **G**, deformed muscle map of *Alligator*; **H**, muscle map of *Camptosaurus* based on muscle scars; **I**, original muscle map of *Gallus*; **J**, deformed muscle map of *Gallus*. Note that the muscle map for *Camptosaurus* more closely matches that of *Alligator* than *Gallus*. Some differences include separate latissimus dorsi and teres major insertions in *Camptosaurus*. Abbreviations: b, M. brachialis; bbcb, M. biceps brachii caput breve; cbv, M. coracobrachialis brevis ventralis; ce, M. coracobrachialis externus; ch, M. coracohumeralis; ci, M. coracobrachialis intermedius; cvd, M. coracobrachialis brevis dorsalis; dc, M. deltoideus clavicularis; dm, M. deltoideus major; ds, M. deltoideus scapularis; hr, M. humeroradialis; ld, latissimus dorsi; pp, M. supracoracoideus pars sternobrachialis; ppc, M. pectoralis pars claviculobrachialis; sc, M. supracoracoideus; scc, M. scapulohumeralis cranialis; scd, scapulohumeralis caudalis; se, M. subscapularis externus; sh, M. scapulohumeralis; ssi, M. subscapularis internus; tbc, M. triceps brevis caudalis; tbc, lpa, M. triceps brachii, caput laterale, pars accessorius; tbc, lpp, M. triceps brachii, caput laterale, pars principalis; tbi, M. triceps brevis intermedius; tm, M. teres major; tmn, M. teres minor. Terminology for alligator adapted from Meers (2003); terminology for *Gallus* adapted from Yasuda (2002).

Shoulder Complex (Fig. 41, #1; Fig. 43)—The shoulder complex is defined as those structures involved in the moving of the humerus (and by extension the entire arm), including both hard and soft tissues (Carpenter 2002). The hard tissues in *Camptosaurus* are the scapula, coracoid, and humerus. The sternal plate contributes to the shoulder complex in that it provides an origination for the pectoralis, a major humeral adductor and retractor.

The scapula and coracoid are treated together because they are joined along their synchondrodial joint into a single, non-moving functional unit which serves as a platform for the origin of many forelimb muscles (Fig. 39). There is a narrow, V-shaped gap between the coracoid and scapula within the glenoid (Fig. 16C), a feature also seen in large, presumably adult *C. dispar* (e.g., USNM 5473). In extant sea turtles, for example, *Chelonia mydas* (Linnaeus, 1758) USNM 222598, a similar gap occurs, which appears to lock the glenoid cartilage in place. Presumably a similar function occurred in *Camptosaurus* (Fig. 43C). The acromion process extends laterally over the humerus putting the supracoracoideus intermedius dorsal to the humerus where it can function as a humeral abductor and retractor (Fig. 39). In this position, the supracoracoideus intermedius passes over the coracobrachialis posterior, which originates below the acromion. A longitudinal ridge on the medial side of the scapular blade above its ventral margin probably marks the insertion of the serratus ventralis (Fig. 16C). The coracoid forms about one-third of the glenoid and the scapula the remainder. The glenoid is very deep, because of the development of a prominent lip or margin at the anterior edge of the glenoid and an even more developed one at the posterior lip (Fig. 16A). The scapular margin projects ventrolaterally to brace the humeral head posteriorly (Fig. 16C). The scapular portion of the glenoid is not horizontal lateromedially, but relative to the medial surface of the scapula, it angles approximately $+30^\circ$ (Fig. 43A). The glenoid faces ventrolaterally when the scapula is in anatomical position, resulting in the humerus angling ventrolaterally as well, with the elbows slightly splayed (Fig. 40), the significance of which is discussed below. The proximal and distal ends of the humerus are in the same plane (Fig. 43A) rather than angled relative to one another as is seen in many dinosaurs, such as theropods (Carpenter 2002). There is a slight groove atop the head that almost separates it from the proximal end of the humerus (Fig. 18E). This groove probably served to increase the surface area for the attachment of the joint cartilage. The humeral head and glenoid form a hemi-sellar joint as in many dinosaurs. The maximum range of abduction-adduction is about 20° (Fig. 45A) and of protraction-retraction is about 35° (Fig. 45B).

Elbow Complex (Fig. 41, #2)—The elbow complex is formed by the distal end of the humerus and proximal ends of both the radius and ulna (Figs. 41, 44A). Nevertheless, movement was a simple hinge, because the ulna and radius move together. The distal condyles of the humerus

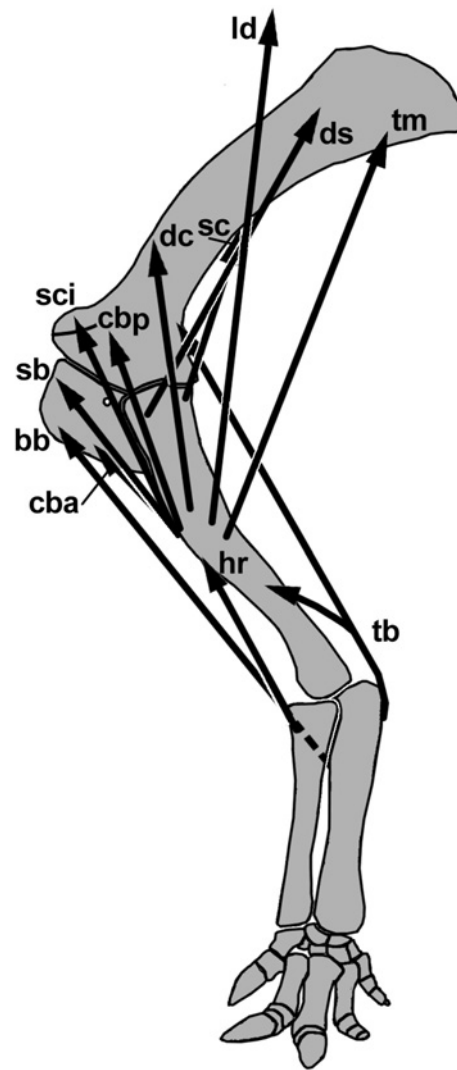


Fig. 39.—Vector map for major forelimb muscles of *Camptosaurus*. Abbreviations: bb, M. biceps brachii; cba, M. coracobrachialis anterior; cbp, M. coracobrachialis posterior; dc, M. deltoideus clavicularis; ds, M. deltoideus scapularis; hr, M. humeroradialis; ld, M. latissimus dorsi; sb, M. supracoracoideus brevis; sc, M. scapulohumeralis; sci, M. supracoracoideus intermedius; tb, M. triceps brevis; tm M. teres major.

face slightly anteriorly, but do not extend onto the flexor surface as in extant birds and *Deinonychus* Ostrom, 1969 (Carpenter 2002: fig. 6). This absence restricts the arc of flexion-extension to about 75° (Fig. 45B); it could not normally assume the 120° rotation shown by Gilmore (1925: fig. 2), where the radial head is shown to be abutted against the humeral shaft. The radius has a broad contact with the ulna proximally (Fig. 44A) as is typical for dinosaurs; thus, human-like pronation-supination of the forearm is not possible (Carpenter 2002). This restriction results, as Gilmore (1925) noted, in the palmar surfaces of the manus facing

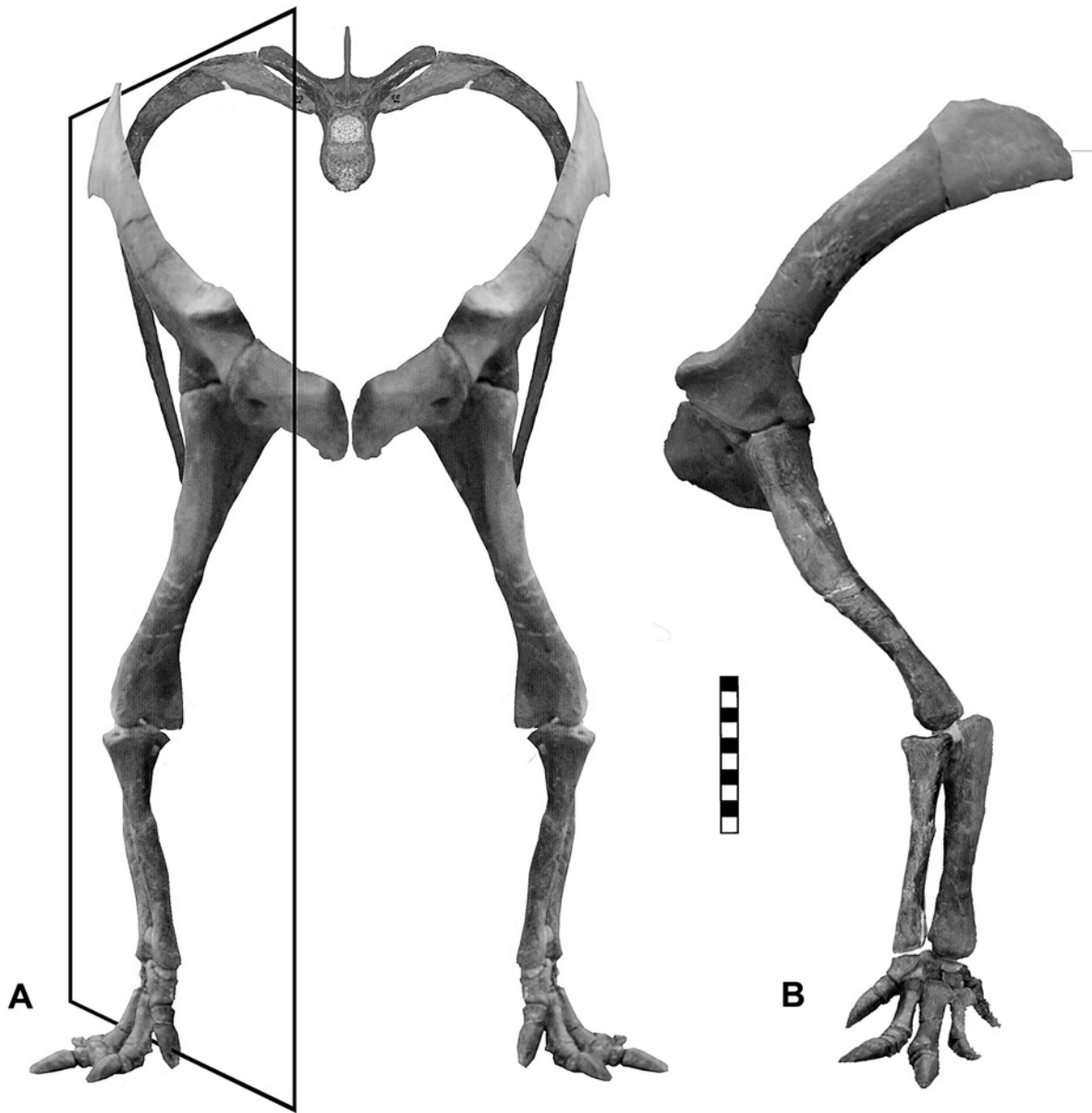


Fig. 40.—Restored pectoral girdle, dorsal vertebra 3, and forelimb of stationary *C. aphanoecetes*. **A**, anterior; and **B**, left lateral views (anatomical right side mirrored from complete left side). The forelimbs are slightly sprawled, because the glenoid faces ventrolaterally. This insures that the upper arm clears the chest during retraction. With the near contact of the coracoids, the chest assumes a heart-shape cross-section that is narrowest ventrally. Plane in which the forelimb moves denoted by outline. Lateral facing manus is in the same position as seen in resting *Anomoepus scambus* Lull, 1953 (Lull 1953: fig. 61). Scale units are cm.

medially when the *Camptosaurus* is in a bipedal stance (Fig. 34B); the same condition occurs in theropods (Carpenter 2002). Retraction and protraction of the elbow is not in a plane parallel to the vertebral column, but in an anteromedial-posterolateral plane (Fig. 40A). This allows the elbow to clear the chest during retraction and brings the manus near the midline of the body during protraction.

Wrist Complex (Fig. 41, #3)—The wrist complex of

Camptosaurus is well preserved in CM 11337 and consists of the distal ends of the ulna and radius, the carpals in two rows, and the proximal ends of the metacarpals (Fig. 41). Decay of the soft tissue, followed by slight compaction of the sediments, has placed all of the elements of the manus in the same plane (Fig. 22). The manus elements have been removed from the matrix and rearticulated (Fig. 46) for the mounted skeleton. The correct anatomical position for metacarpals is for them to form a slight arc so that the

proximal ends are in contact with one another (Fig. 46B). The wedge-shaped MC-IV (Fig. 46B) causes the greatest amount of divergence of digit IV relative to III (Fig. 46A). Both the radiale and ulnare have facets on their proximal surfaces for the radius and ulna, respectively (Fig. 22B). These facets extend partially onto the intermedium so that, when articulated with the ulna and radius, a small wedge forms between them (Fig. 40B). This wedge stabilizes the wrist by preventing rotation. The range of flexion between the forearm and the proximal row of carpals is about 40° and extension is about 30° (Fig. 47). No radial adduction-ulnar flexion could occur owing to the anterior-posterior elongation of the wrist (Fig. 44).

Manus (Fig. 41, #4)—The manus complex (Fig. 41) is short and compact, because the phalanges are short and wide (Fig. 46). Digit I was practically rigid, because the joint surfaces between metacarpal I and its phalanx are flat (Fig. 22A). This rigidity is a precursor to the immobile thumb of *Iguanodon* Mantell, 1825. The long axis of MC I is about 30° relative to the horizontal axis of the wrist, whereas Gilmore (1909) reported about 45° in USNM 4277. The distal condyles of the metacarpals are moderately developed and allow the greatest range of motion for the digits (Fig. 48). In contrast, the distal condyles of the phalanges are poorly developed, not well separated, and do not wrap very far around onto either the palmar or extensor sides. Thus, although there is a considerable range of motion between the metacarpals and the first phalanges, interdigital flexion and extension was limited (Fig. 48). This loss of digital mobility and flexibility relative to the primitive ornithischian condition, for example, *Lesothosaurus* Galton, 1978 (Thulborn 1970; Sereno 1991), is due to changes in the phalanges: short and broad shallow joints, loss of midline ridge on the proximal articular surface, loss of collateral ligament pits, and hoof-like unguals. These modifications of the manus are analogous to changes seen in the pes of subunguligrade ornithopod dinosaurs, such as hadrosaurs (see Moreno et al. 2007), and demonstrate that the manus of *Camptosaurus* was primarily weight bearing.

DISCUSSION

During this study, it was necessary to re-evaluate the various species referred to *Camptosaurus*. Galton and Powell (1980) put much emphasis on the relative size of the intramaxillary cavity to separate *Camptosaurus dispar* from *Camptosaurus prestwichii* (Hulke, 1880) (Upper Jurassic, England). Unfortunately, the maxilla for *C. aphanoecetes* is unknown, thus the reliability of this character cannot be tested. Some characters, such as the small rounded distal end of the ischium in *C. prestwichii*, are more similar to that of the small ischial foot seen in *C. aphanoecetes* than to the large ischial foot seen in *C. dispar*. Furthermore, *C. aphanoecetes* has a wider brevis shelf than *C. prestwichii*. As shown above, the dentary of *C. hoggii* shows

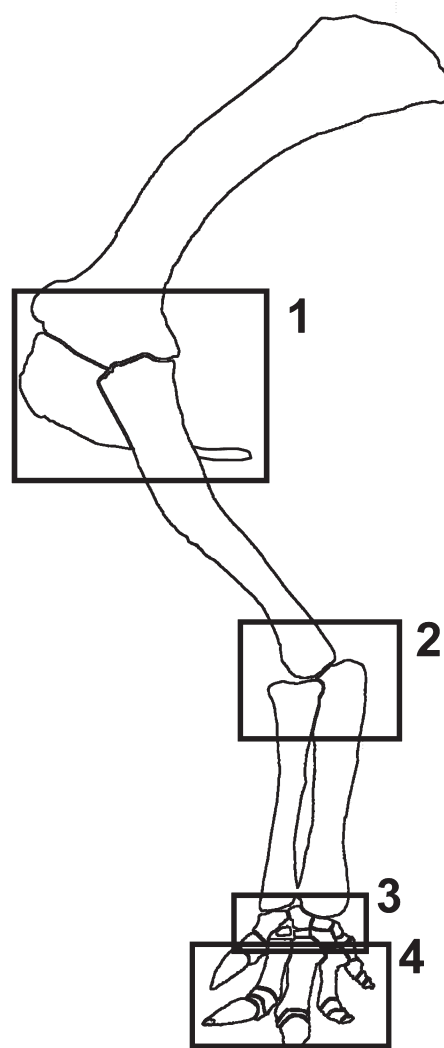


Fig. 41.—Functional complexes of the *Camptosaurus* forelimb includes: 1, shoulder complex (scapula, coracoid, sternal plate, proximal end of humerus, and associated muscles and tendons); 2, elbow complex (distal end of humerus, proximal ends of ulna and radius, and associated muscles and tendons); 3, wrist complex (distal ends of ulna and radius, carpals, proximal ends of metacarpals, and associated muscles and tendons); 4, manus complex (metacarpals, phalanges and associated muscles and tendons).

that it differs too much from that of *C. aphanoecetes* and *C. dispar* to belong to *Camptosaurus*. It seems very doubtful that the differences can be explained as due to crushing of *C. hoggii* as suggested by Norman and Barrett (2002), because in the approximately dozen crushed dentaries of the iguanodontoid *Eolambia* Kirkland, 1998 (Lower Cretaceous, Utah), none shows arching of the dental margin or tooth row (K.C. pers. obs.). *C. hoggii* is here considered an unnamed euornithopod. *C. depressus* Gilmore, 1909 (Lower Cretaceous, South Dakota) is also moved from *Camptosaurus* to the genus *Planicoxa* DiCroce and Carpenter, 2001 (Lower Cretaceous, Utah), as *Planicoxa de-*

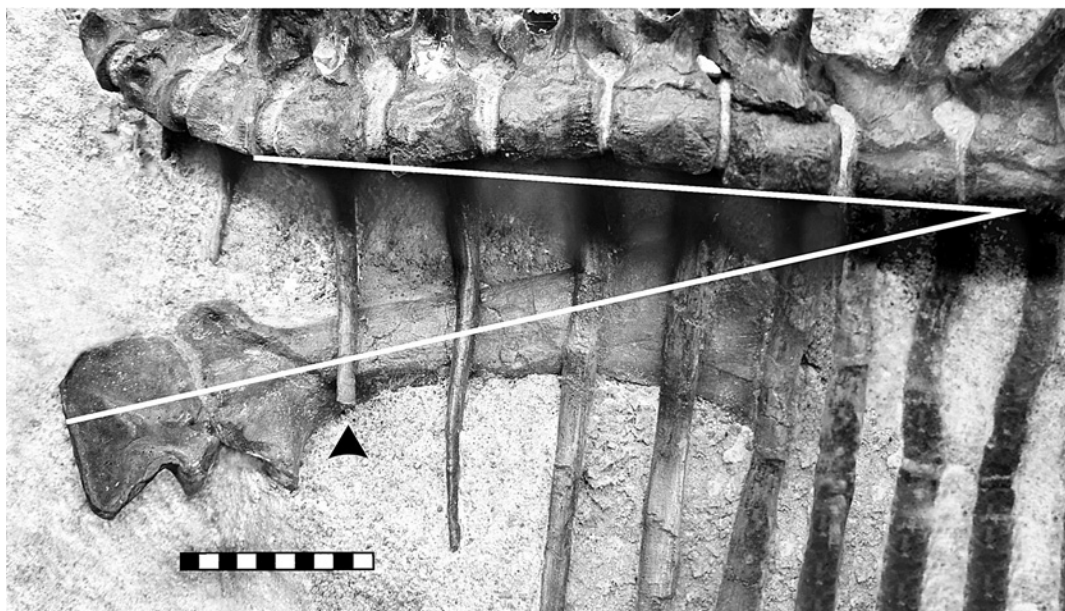


Fig. 42.—Right scapula of *Camptosaurus aphanoeetes* (CM 11337) preserved in situ (-17° relative to vertebral column). Note that the first dorsal rib (arrow) bisects the scapula at its narrowest point. Scale units are cm.

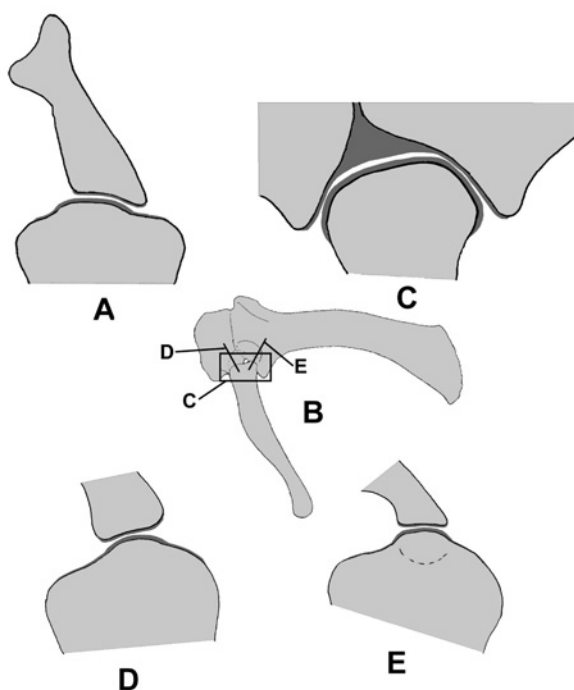


Fig. 43.—Cross-sections of the shoulder complex (dark grey represents approximation of cartilage based on scars). The acromion is located dorsal to the greater tuberosity, on the dorso-lateral corner of the humerus. This gives the deltoideus a nearly vertical orientation (A). Location map for the other cross-sections (B). Sagittal section showing the humeral head in the glenoid (C). Cross-section of humeral head and coracoid (D). Cross-section of humeral head and scapula (E).

pressa. In naming *C. depressus*, Gilmore (1909:293) cited the “narrowness or depressed nature of the ilium.” The ilium resembles *Planicoxa venenica* DiCroce and Carpenter, 2001, in the horizontally directed postacetabular blade of the ilium; both are also Barremian in age (DiCroce and Carpenter 2001). The horizontal ilium is not due to crushing as seen by the absence of fractures on the medial side, as well as the lack of sacral rib facets on the folded portion. In addition, the beginning of the fold is also seen on the fragment of the right ilium. *P. depressa* differs from *P. venenica* in the non-arched profile, proportionally shorter and more robust preacetabular blade relative to ilium length, shallower acetabular notch, and proportionally narrower brevis shelf relative to ilium length (Fig. 49). In a rush to judgment, Kirkland and Madsen (2007) synonymized *Cedrorestes* Gilpin, DiCroce, and Carpenter, 2007, with *Planicoxa* on the erroneous assumption that the horizontal postacetabular process of *Planicoxa* was due to distortion. However, the two specimens of *Planicoxa* clearly show that the short, truncated, horizontal postacetabular process is normal as noted by Gilmore (1909), and cannot be produced from the elongate, tapered, vertical postacetabular process of *Cedrorestes*.

The biomechanical analysis suggests that the primary mode of locomotion in *Camptosaurus* was quadrupedal, rather than bipedal. Marsh (1894), being greatly influenced by the skeleton of *Iguanodon*, assumed that *Camptosaurus* was tripodal, using its tail as a prop. Gilmore (1909:302), however, concluded from “the compact, ossified carpus, with smooth, well defined, articulating surfaces, which is supported by comparatively short and stout metacarpals, [that the] function was that of support rather than

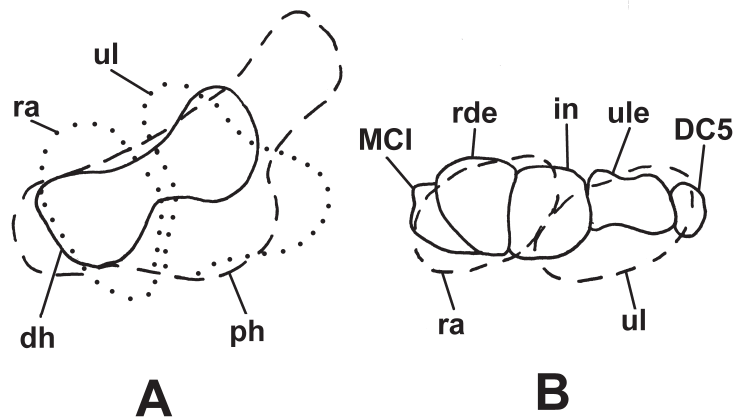


Fig. 44.—Overlays of the proximal and distal ends of the humerus relative to the ulna and radius. **A**, overlay of the distal ends of the ulna and radius; **B**, proximal ends of the wrist. A and B are in correct relative position to one another showing that the humerus is rotated towards the midline of the body. This is due to the position of the glenoid and the curvature of the scapula-coracoid. Abbreviations: DC5, distal carpal 5; dh, distal end of humerus; in, intermedium; MCI, metacarpal I; ph, proximal end of humerus; ra, radius (proximal end in A, distal end in B); rde, radiale; ul, ulna (proximal end in A, distal end in B); ule, ulnare.

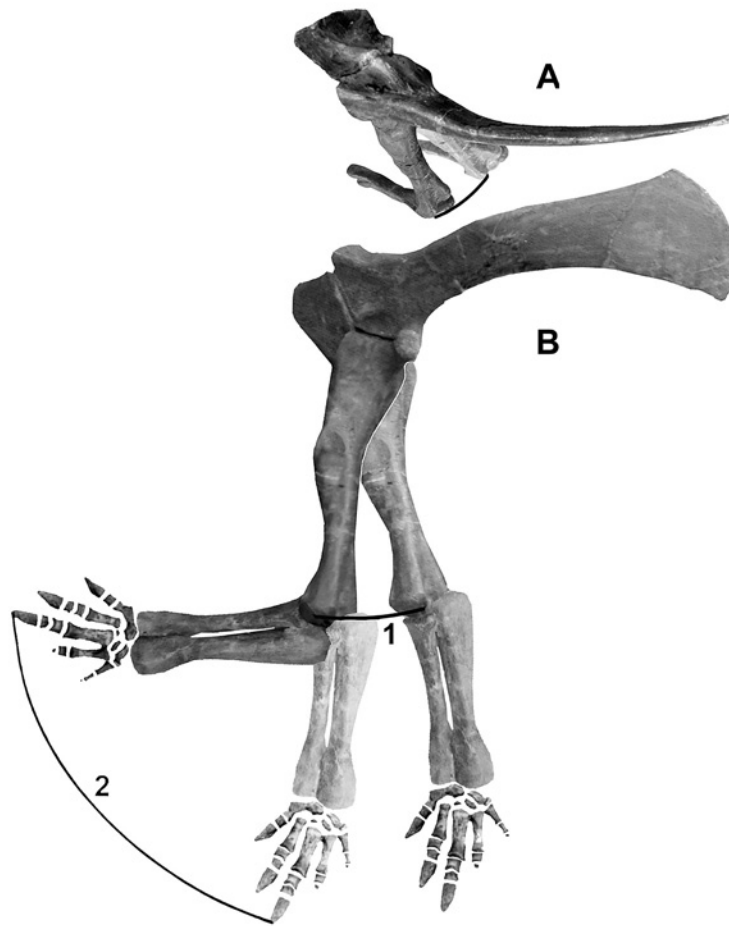


Fig. 45.—Range of motion for forelimb of *Camptosaurus aphanoeetes*. **A**, humeral abduction-adduction (32°) in dorsal view; **B**, forearm movement in lateral view; 1, humeral protraction-retraction (20°); 2, forearm flexion-extension (78°).

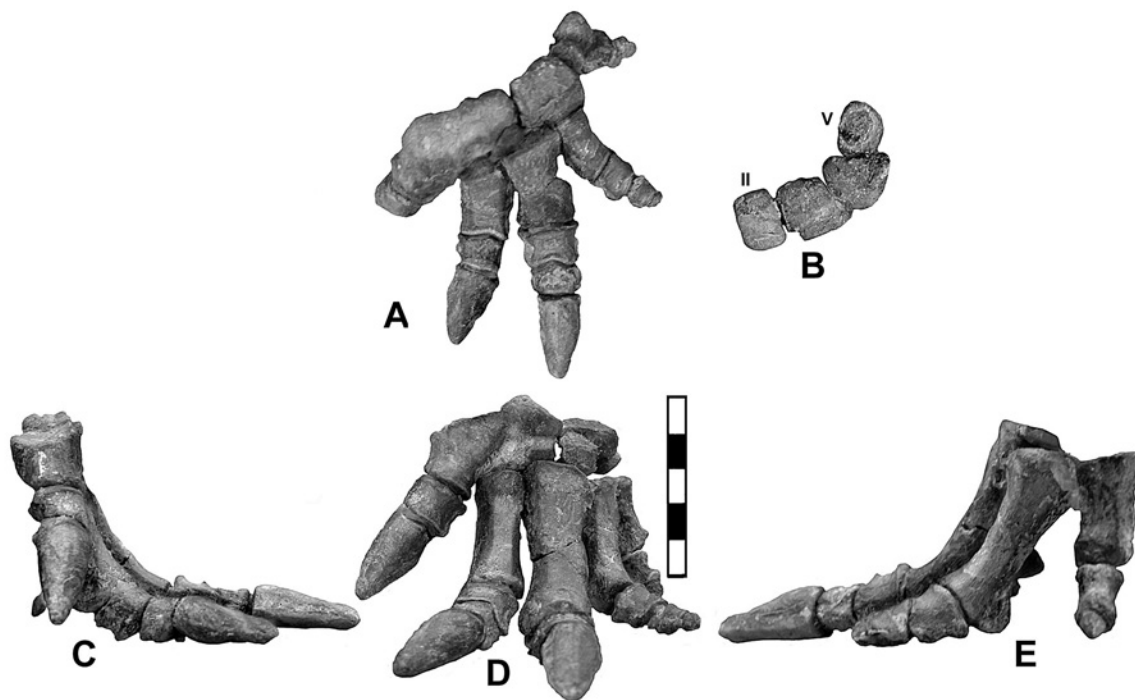


Fig. 46.—Reconstructed manus and wrist of *Camptosaurus aphanoeetes*. A, dorsal view; B, dorsal view of metacarpals in articulation (metacarpal I is fused to the radiale and is not included); C, medial view; D, extensor side; E, lateral view. Note the divergence of digit IV relative to digit III caused by the wedge shape of metacarpal IV in B. Scale units are cm.

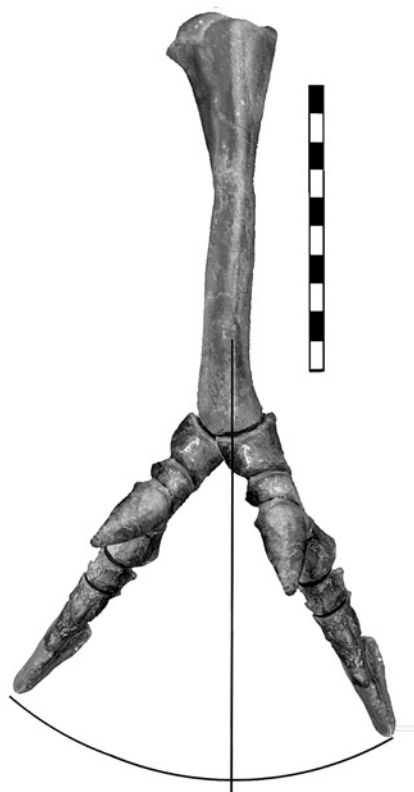


Fig. 47.—Manus range of motion ($\sim 70^\circ$) relative to the ulna and radius in anterior view. Scale units are cm.

prehension" (repeated again in Gilmore 1912). He notes a great disparity between the lengths of the fore- and hindlimbs as a possible objection to quadrupedal locomotion, but he considered this disparity was reduced some by bowing of the femur (Gilmore 1909:302). Gilmore (1912) also thought the stoutness of the manus was a precursor for the short, stout manus in stegosaurs and ceratopsians. Although he considered *Camptosaurus* as primarily quadrupedal, he also considered it likely that it could occasionally walk bipedal as well using the tail as a counterbalance: "The tail was long ... and in life it probably served as a balancing organ when upright bipedal posture was assumed" (Gilmore 1909:302). The tail also may have been important in quadrupedal locomotion by shifting the center of gravity posteriorly so as to reduce the weight on the manus.

The shift from the plesiomorphic bipedal locomotion seen in *Lesothosaurus* to quadrupedal locomotion may be correlated with an enlargement of the gut signifying an increase residence time of food in the hindgut (Carpenter 2006). *Camptosaurus* does indeed seem to represent the transitional stage as Gilmore (1909) surmised. Although the manus shows modification for weight bearing, other parts of the skeleton still retain a more primitive condition. Neither the coracoid nor the acromion on the scapula is enlarged as seen in stegosaurs, ceratopsians, or ankylosaurs. The deltopectoral crest of the humerus is small, lacking the enlarged surface for insertion of protractors and retractors seen in quadrupedal ornithischians. The humeral condyles

are not well developed, nor do they extend onto the anterior face of the humeral shaft. Furthermore, the olecranon is very short, unlike stegosaurs, ankylosaurs, and ceratopsians. Overall then, the elbow lacked the mobility seen in quadrupedal ornithischians and the insertion for the triceps is proportionally smaller as well. The wrist, however, is rather stiff and is more similar to that of *Stegosaurus* Marsh, 1877, than to that of ankylosaurs or ceratopsians. This is rather surprising considering that *Camptosaurus* (up to 1000 kg, Russell in Erickson 1988) did not reach the body mass of *Stegosaurus* (estimated at 2,610 kg, Seebacher 2001) and thus did not need to fuse the wrist for locomotion as was suggested by Gilmore (1909, 1912). Erickson (1988) does report on a very large specimen of *Camptosaurus* for which he gave an estimated mass of over 2000 kg. The manus for this specimen is incomplete, but does show greater co-ossification than seen in specimens of *C. dispar* (USNM 4277 and YPM 1877).

CONCLUSIONS

Camptosaurus was a Late Jurassic medium to large-sized ornithopod from the Morrison of the United States and Lower Kimmeridge Clay of England; it may also be present in coeval strata of Portugal, although the material is

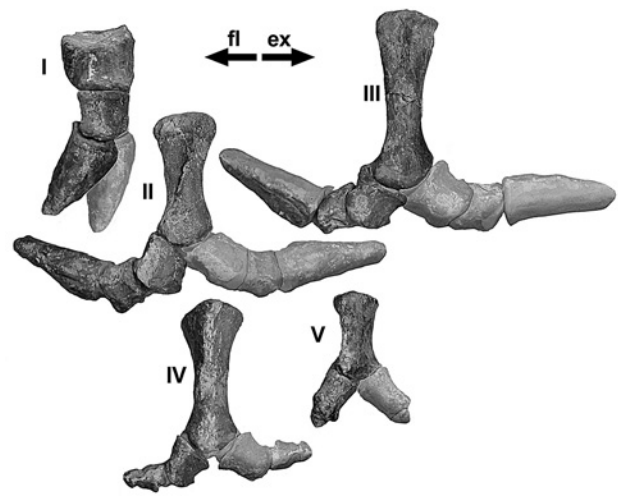


Fig. 48.—Range of motion of the ungual tip relative to the axis of the metacarpal: Digit I ~33°, digit II ~210°, digit III ~212°, digit IV ~181°, digit V ~74°. Abbreviations: ex, extension; fl, flexion.

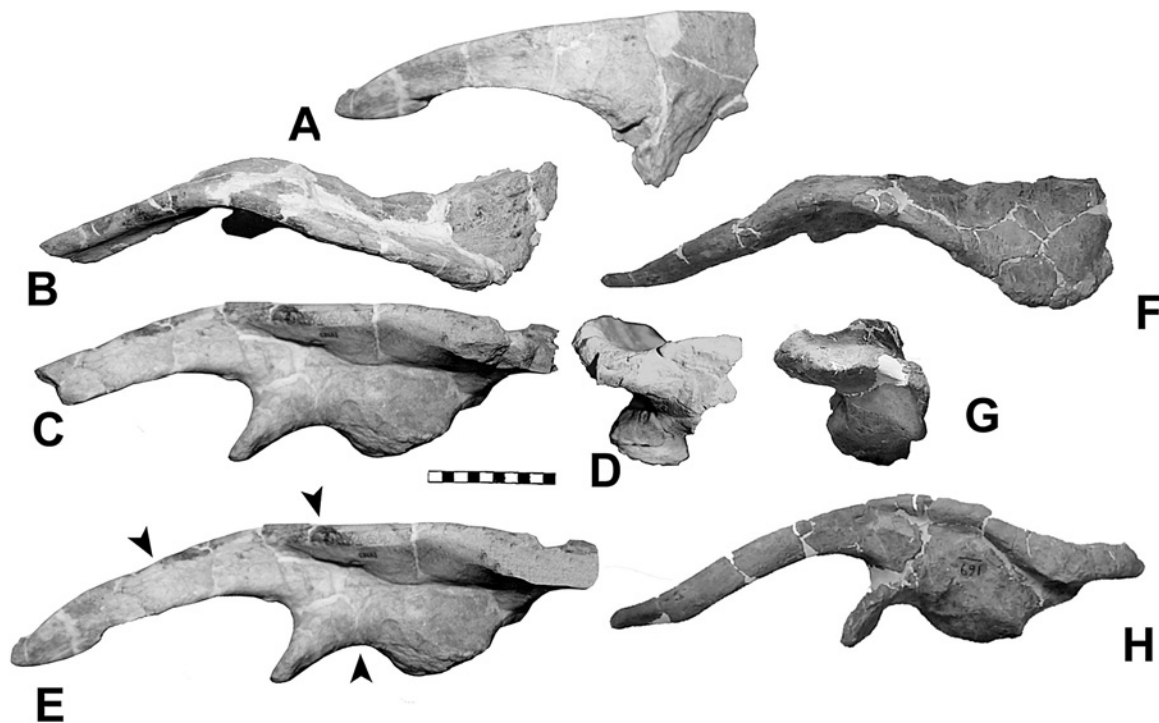


Fig. 49.—Ilium of *Planicoxa depressa* formerly *Camptosaurus depressus* (Lower Cretaceous, South Dakota,) compared with that of *Planicoxa venenica* (Lower Cretaceous, Utah). *Planicoxa depressa* (USNM 4753): A, medial side of right ilium; B, dorsal view of left ilium; C, lateral view of left ilium; D, posterior view of left ilium; E, composite reconstruction of left ilium in lateral view (darts show areas of difference with *P. venenica*). *Planicoxa venenica* (DMNH 42504) holotype left ilium: F, dorsal; G, posterior; and H, lateral views. Scale units are cm.

fragmentary (Galton 1980). Only three species are recognized from this study: *Camptosaurus dispar*, *C. aphanoeetes*, and *C. prestwichii*. The two Lower Cretaceous *Camptosaurus* species can no longer be referred to that genus: "*C.*" *hoggii* is considered an unnamed euornithopod, whereas *C. depressus* is now *Planicoxa depressa*, new combination.

The biomechanical study of *Camptosaurus*, based on *C. aphanoeetes*, shows that it was primarily quadrupedal. The manus is extensively modified and has limited interphalangeal movement. In addition, movement at the wrist was limited as well.

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