



# GEOLOGY OF THE INTERMOUNTAIN WEST

*an open-access journal of the Utah Geological Association*

ISSN 2380-7601

Volume 5

2018

## A PHOTO DOCUMENTATION OF BIPEDAL ORNITHISCHIAN DINOSAURS FROM THE UPPER JURASSIC MORRISON FORMATION, USA

Kenneth Carpenter and Peter M. Galton



Theme Issue

An Ecosystem We Thought We Knew—  
The Emerging Complexities of the Morrison Formation  
SOCIETY OF VERTEBRATE PALEONTOLOGY

*Annual Meeting, October 26 – 29, 2016*

*Grand America Hotel*

*Salt Lake City, Utah, USA*



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*Camptosaurus aphanoecetes* (CM 11337, holotype)  
as displayed at the Carnegie Museum of Natural History,  
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## A Photo Documentation of Bipedal Ornithischian Dinosaurs from the Upper Jurassic Morrison Formation, USA

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### ABSTRACT

Bipedal ornithischian dinosaurs from the Upper Jurassic Morrison Formation are rare, forming only about 15% of the dinosaur specimens. Nevertheless, one of them was among the first dinosaurs named from what was then the "Atlantosaurus Beds" of Colorado. Collecting and restudy for 140 years has increased the diversity from the initial 1877 discovery to the currently valid four genera and six species, viz., *Fruitadens haagaroum*, *Nanosaurus agilis*, *Camptosaurus dispar*, *C. aphanoecetes*, *Dryosaurus altus*, and *D. elderae*, which we briefly review. We demonstrate that the enigmatic *Nanosaurus agilis* is the senior name for *Drinker nisti*, *Othnielosaurus consors*, and *Othnielia rex*. In addition, a new species, *Dryosaurus elderae* is proposed for the *Dryosaurus* specimens from Dinosaur National Monument that are characterized by elongate cervical vertebrae and a long, low ilium among other features.

### INTRODUCTION

The first bipedal ornithischian dinosaur to be named and described (very briefly) from the Morrison Formation (Upper Jurassic) was *Nanosaurus agilis* by Othniel Charles Marsh in 1877. The Morrison Formation consists of non-marine sediments that were deposited across a broad, comparatively flat land that was formerly covered by the Middle to early Late Jurassic Sundance Seaway. The northeastward withdrawal of this seaway coincided with subduction and uplift to the west, which was accompanied by volcanism that spread ash downwind (figure 1; Armstrong and Ward, 1993; Kowallis and others, 2001; Christiansen and others, 2015; Schweickert, 2015). Radiometric dates from the ashes range from  $156.84 \pm 0.59$  Ma to  $150.0 \pm 0.52$  Ma (Christiansen and others, 2015; Trujillo and Kowallis, 2015).

The axis of the Morrison depositional basin extended across  $12^\circ$  to  $15^\circ$  of latitude (figure 1), with generally seasonal drier conditions to the south and wetter conditions to the north (Demko and others, 2004). It is in this generalized setting that a variety of bipedal ornithischians lived. The record for these dinosaurs is better for the eastern half of the basin than the western half (figure 2). Whether this has paleoecological significance or is the result of happenstance of collecting history needs to be further explored.

The first bipedal ornithischian found in the Morrison Formation was on the surface of a fine-grained sandstone block. Ormel Lucas discovered the specimen during the summer of 1877 high on a bluff in Garden Park, north of Cañon City, Colorado. Lucas passed the specimen to Benjamin Mudge, a fossil collector for

Citation for this article.

Carpenter, K., and Galton, P.M., A photo documentation of bipedal ornithischian dinosaurs from the Upper Jurassic Morrison Formation, USA: *Geology of the Intermountain West*, v. 5, p. 167–207.

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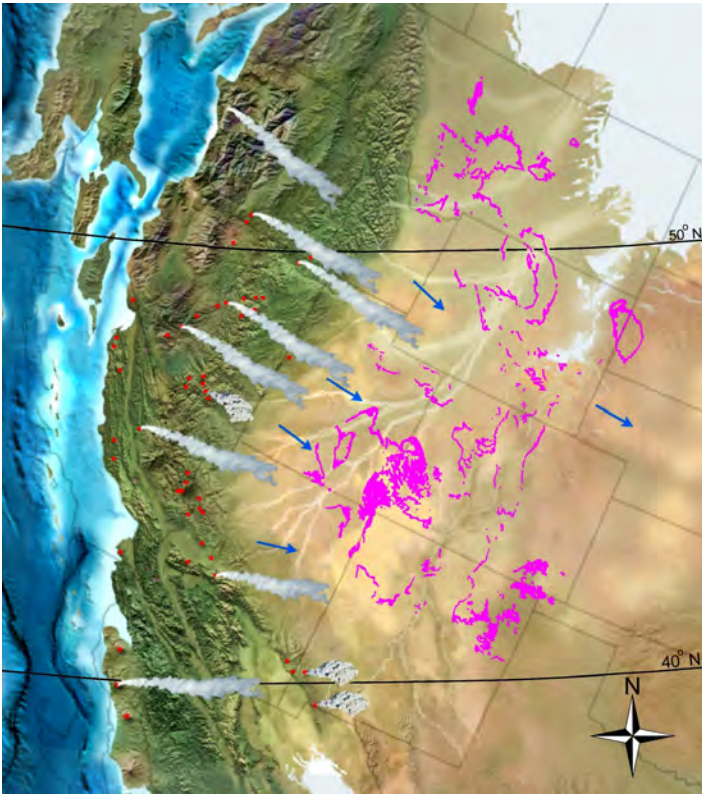


Figure 1. The Morrison depositional basin during the Late Jurassic, with North America rotated so that the paleopole north is at the top. The 50th and 40th parallels are extrapolated from Kent and others (2015, figure 7), which places the Morrison basin farther north than Christiansen and others (2015). The present distribution of the Morrison Formation is superimposed in red-violet. Distribution of felsic plutons, hence possible volcanic centers, shown as red dots (adapted from Christiansen and others, 2015, figure 33) and volcanic ash eruptions aligned downwind based on wind directions shown as blue arrows (adapted from Parrish and Peterson, 1988, figure 16). The widespread, downwind distribution of ash across the basin was hypothesized by Turner and Peterson (1999) as marking an abrupt change from non-smectitic to smectitic clays. When first proposed, it was hoped that this marker bed could be used to place dinosaur localities in their relative stratigraphic positions. Subsequent work, however, has shown that the stratigraphic position of the clay change is not uniform beyond a local region (Trujillo, 2006), in a large part due to the dispersal pattern of ash clouds. The base map from the commercial version of Ron Blakey's Paleogeography of Western North America licensed to the Prehistoric Museum. Placement of geographical features are representational, not exact.

Othniel Charles Marsh of the Peabody Museum of what was then Yale College. Mudge shipped the specimen to Marsh and followed with a letter noting that he thought the specimen might be bird, but even if not, "it looks to me to be new, and valuable..." (Mudge letter to Marsh August 15, 1877). Mudge visited the site with Lucas at Marsh's request, but no further fragments were found (Mudge letter to Marsh, August 26, 1877). The specimen was "from the sandstone about ten feet above the big saurian [i.e., *Camarasaurus supremus*] he [Oramel Lucas] is now taking out, and in the same geological horizon as our Morrison [Colorado] specimens" (Mudge letter to Marsh August 15, 1877). This places the locality at a small hill now called "Cope's Nipple." The specimen was briefly described and named *Nanosaurus agilis* as the smallest known dinosaur by Marsh in September 1877. It was not identified as ornithischian until May 1881 when Marsh presented the first classification of Jurassic dinosaurs. At that time, *Nanosaurus*, *Camptonotus* (later renamed *Camptosaurus*), *Diracodon* (now *Stegosaurus*), and *Laosaurus* were placed into

the Family Camptonotidae in the Suborder Ornithopoda (Marsh, 1881; raised to Order in Marsh, 1882).

In the 140 years since the naming of *Nanosaurus agilis*, almost 24 species of bipedal ornithischians were named from the Morrison Formation, but these have been distilled by us to six species among four genera. Below, we present a photo documentation of these valid taxa as a guide to identifying these rather rare components of the Morrison ecosystem. We also take the opportunity to illustrate many of the holotypes and present illustrations previously made under the direction of O.C. Marsh. The four valid genera are shown on the simplified phylogenetic tree (figure 3) modified from Boyd (2015). These ornithischian genera can be identified by teeth (figure 4) as reviewed by Galton (2007).

## INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History, New York, New York; BYU: Brigham Young University, Provo, Utah; CM: Carnegie Museum of Natural History

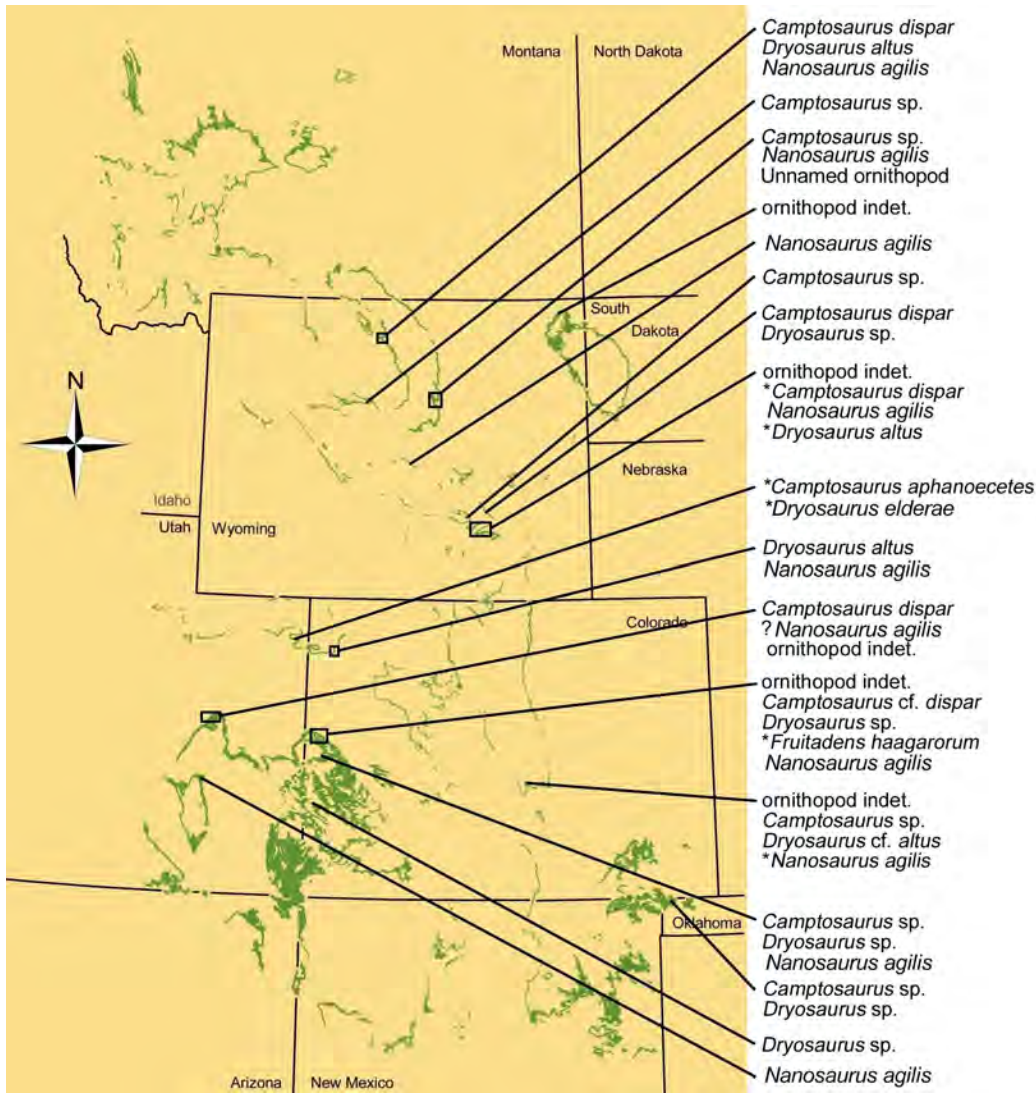


Figure 2. Major occurrences of bipedal ornithischians in the Morrison Formation (green pattern). Holotypes in right column are denoted with asterisk. Black boxes encompass areas with numerous closely associated localities.

ry, Pittsburgh, Pennsylvania; DINO: Dinosaur National Monument, Jensen, Utah; DMNH: Denver Museum of Natural History, Denver, Colorado; LACM: Los Angeles County Museum, Los Angeles, California; MWC: Museums of Western Colorado, Fruita, Colorado; NAMAL: North American Museum of Ancient Life, Lehi, Utah; SMA: Saurier Museum, Aathal, Switzerland; SMM: Science Museum of Minnesota; USNM: National Museum of Natural History, Washington, D.C.; UW: University of Wyoming, Laramie, Wyoming; YPM: Division of Vertebrate Paleontology, Yale University, Peabody Museum of Natural History, New Haven, Connecticut; YPM-PU: Princeton University Collection at Yale University, Peabody Museum of Natural History, New Haven, Connecticut.

## SYSTEMATIC PALEONTOLOGY

### Ornithischia

#### Heterodontosauridae

*Fruitadens haagarorum* Butler and others, 2009

Figures 4 and 5

*Echinodon* sp. Callison, 1987

*Echinodon* sp. Galton, 2002

*Fruitadens* is the most primitive ornithischian dinosaur from the Morrison Formation. It is a late surviving member of the basal ornithischian clade Heterodontosauridae. *Fruitadens* is represented by four fragmentary individuals (Butler and others, 2012) from the Fruita Paleontological Area (FPA) in western Colorado (fig-

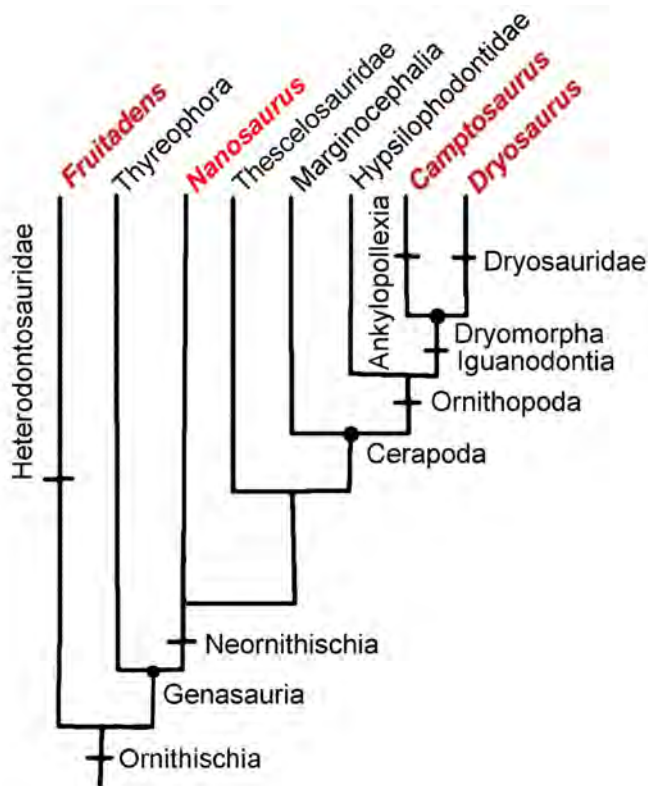


Figure 3. Simplified phylogenetic tree showing the four valid genera (in red) of bipedal ornithischians from the Morrison Formation. Major ornithischian subclades are labeled either along branches (stem-based definitions) or at nodes (node-based definitions) as per Boyd (2015).

ure 2; see Kirkland, 2006; Kirkland and others, 2005, for discussion of FPA geology). The specimens come from low in the Brushy Basin Member of the Morrison Formation. They differ from the other Morrison neornithischians in (1) the presence of three premaxillary teeth and a caniform dentary tooth preceded by a small peg-like tooth, (2) a ventrally projecting midline parhypophysis on the posterior cervical centrum, (3) the high position of the deltopectoral crest on the humerus, (4) the slenderness of the hind limb and an elongate tibia with an anteromedial flange distally, (5) an astragalus with ascending process as a separate ossification and with two foramina anteriorly, and (6) fusion of the distal tibia, fibula, astragalus and calcaneum with a pulley-like transversely narrow distal articular surface (figures 5A to 5D, 5G, 5M, 5N, 5CC, 5MM, 5NN, and 5PP). *Fruitadens* was a very lightly built small animal about 1 m long.

## Genasauria

### Neornithischia

*Nanosaurus agilis* Marsh, 1877

Figures 4 and 6 to 18

*Nanosaurus agilis* Huene and Lull, 1908

*Nanosaurus rex* Marsh, 1877

*Laosaurus consors* Marsh, 1894b

*Othnielia rex* (Marsh, 1877) Galton, 1977

*Drinker nisti* Bakker and others, 1990

*Othnielosaurus consor* (Marsh, 1894b) Galton, 2007

It is rather unfortunate that the first named ornithischian from the Morrison Formation, *Nanosaurus agilis* Marsh, 1877, should be based on such an incomplete immature specimen (YPM VP 1913). The specimen has long been enigmatic, but we believe we have finally resolved the problem. The specimen was first mentioned in a letter to O.C. Marsh by Benjamin Mudge, who incidentally reported on the type locality: "I have just received from Mr. O.W. Lucas some bones which look to me like bird's... This specimen is from the sandstone about ten feet above the big saurian [holotype of *Camarasaurus supremus*] he is now taking out, and in the same geological horizon as our Morrison specimens" (Mudge letter to Marsh, August 15, 1877). The type locality places the stratigraphic level as one of the thin sandstone lenses near the top of Cope's Nipple (a.k.a. "Saurian Hill" of Cope), and thus very high in the Morrison Formation (Carpenter, 1998).

The species was very briefly characterized by Marsh in September 1877. He noted its diminutive size compared to other dinosaurs, that the teeth were laterally compressed and set in sockets (i.e., thecodont teeth), the femur had a "third" trochanter (= fourth trochanter), and the femur was shorter than the tibia. He later claimed that "the greater portion of the skull" was present (Marsh, 1896). Marsh (1894b) also assigned it to the Ornithopoda on the basis of the ilium. A short diagnosis of the genus was given, which was a mix of *N. agilis* and *N. rex*, a name created for a femur collected 1 km south and about 70 m lower at the Felch Quarry 1; the specimen was collected by Benjamin Mudge and Samuel Williston in 1877 as they opened the Felch Quarry.

The badly damaged material of *Nanosaurus agilis* was described in detail for the first time by Huene

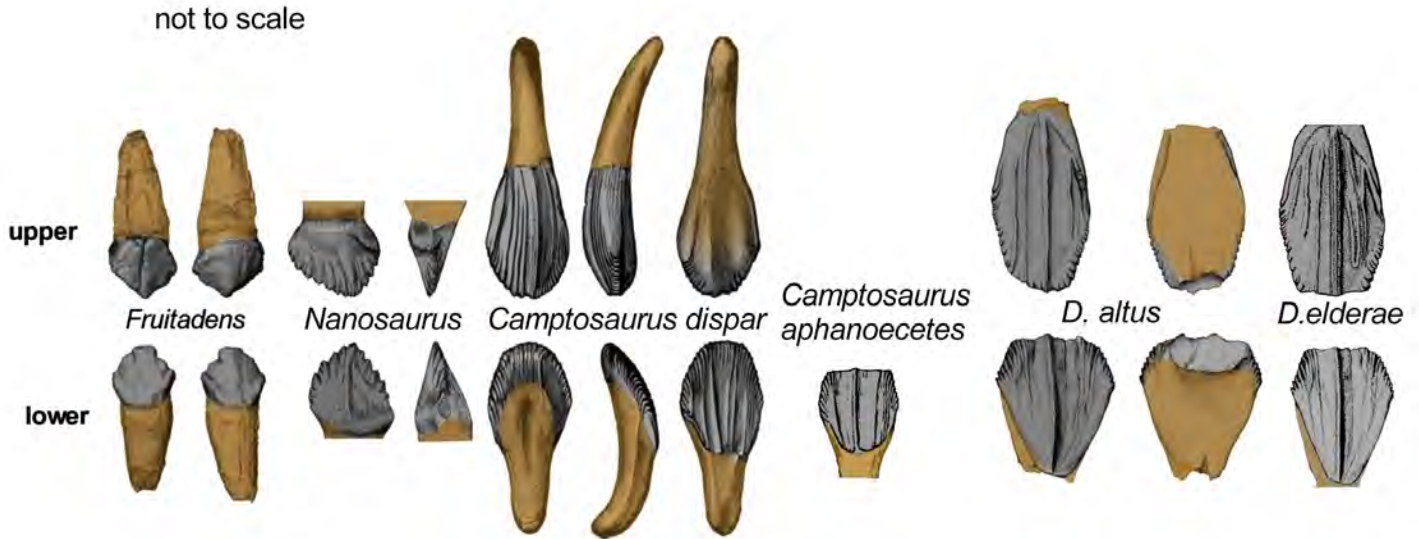


Figure 4. Bipedal ornithischians from the Morrison Formation can be separated by their teeth as seen in this simplified illustration (for additional figures see figures 10, and 28DD to 28FF Galton, 1983, 2007; Butler and others, 2010). *Fruitadens* and *Nanosaurus* have premaxillary teeth that are not present in *Camptosaurus* and *Dryosaurus*. The cheek teeth of *Fruitadens* are characterized by symmetrical, low crowns lacking a primary central ridge on either the lingual or labial sides. In addition, the marginal denticles (seven or less) also lack ridges extending downwards on the crown face (adapted from Butler and others, 2012). In the teeth of *Nanosaurus* (see also figure 10) the crowns are typically asymmetrical, with the crown apex posteriorly offset relative to the vertical midline, the primary ridge is only slightly larger than the secondary ridges, which are of variable lengths (adapted from Bakker and others, 1990). Juvenile teeth have smaller accessory denticles on either side of the marginal denticles making them bi- or tri-cuspid, i.e., multi-cuspid (figures 10H and 10L). This feature is not reliable taxonomically as was pointed out Scheetz (1999), who noted that USNM 5829 has both multi-cuspid and non-multi-cuspid teeth (see figures 10O and 10P). In more mature teeth (figures 10E to 10G, 10J, and 10K; YPM VP 1882), the enamel surface is rough textured. The maxillary teeth may have an enlarged denticulate ridge on the basal, posterior lingual part of the crown. This feature may be dependent on tooth position. In *Camptosaurus dispar* the maxillary tooth has a very prominent primary ridge on the labial surface and several secondary ridges (from Marsh, 1896); these ridges are poorly developed on the lingual surface (the condition in *C. aphanoecetes* is unknown). On the dentary teeth of *C. dispar*, the development of these surfaces is reversed and there is no primary ridge but two well-developed secondary ridges on the lingual surface; ridging is poorly developed on the labial surface. The dentary teeth of *C. aphanoecetes* have a prominent primary ridge and poorly developed secondary ridges. The *Dryosaurus altus* maxillary teeth have a weak primary ridge and only a few secondary ridges labially and practically no ridges lingually (from Galton, 1983). However, dentary teeth have a very prominent primary ridge and a few weak secondary ridges on the lingual surface and practically no ridges labially. The maxillary teeth of *Dryosaurus elderae* have a broad midline ridge that occasionally also supports one and up to three fine longitudinal ridges. Adjacent, secondary ridges are more numerous than in *D. altus* and *D. lettowvorbecki* (not illustrated). In both *Dryosaurus* species, the enamel on the labial surface of crowns of the maxillary teeth and the lingual surface of the dentary teeth is much thicker than that of the opposite side as in *Camptosaurus*. In anterior view opposing teeth curve towards each in both *Camptosaurus* and *Dryosaurus* so that tooth-to-tooth wear surfaces are formed during occlusion with the vertical ridges of the thick convex enamel layer forming cutting edges on the leading edge of the teeth. In the other ornithischians the crowns are uniformly enameled on both sides, the teeth are less asymmetrical in anterior view, and wear facets are less developed and are usually tooth-to-food. Some of the teeth of *Nanosaurus* may also show slightly oblique tooth wear, although this is nowhere nearly as well developed as in *Dryosaurus* and *Camptosaurus*.

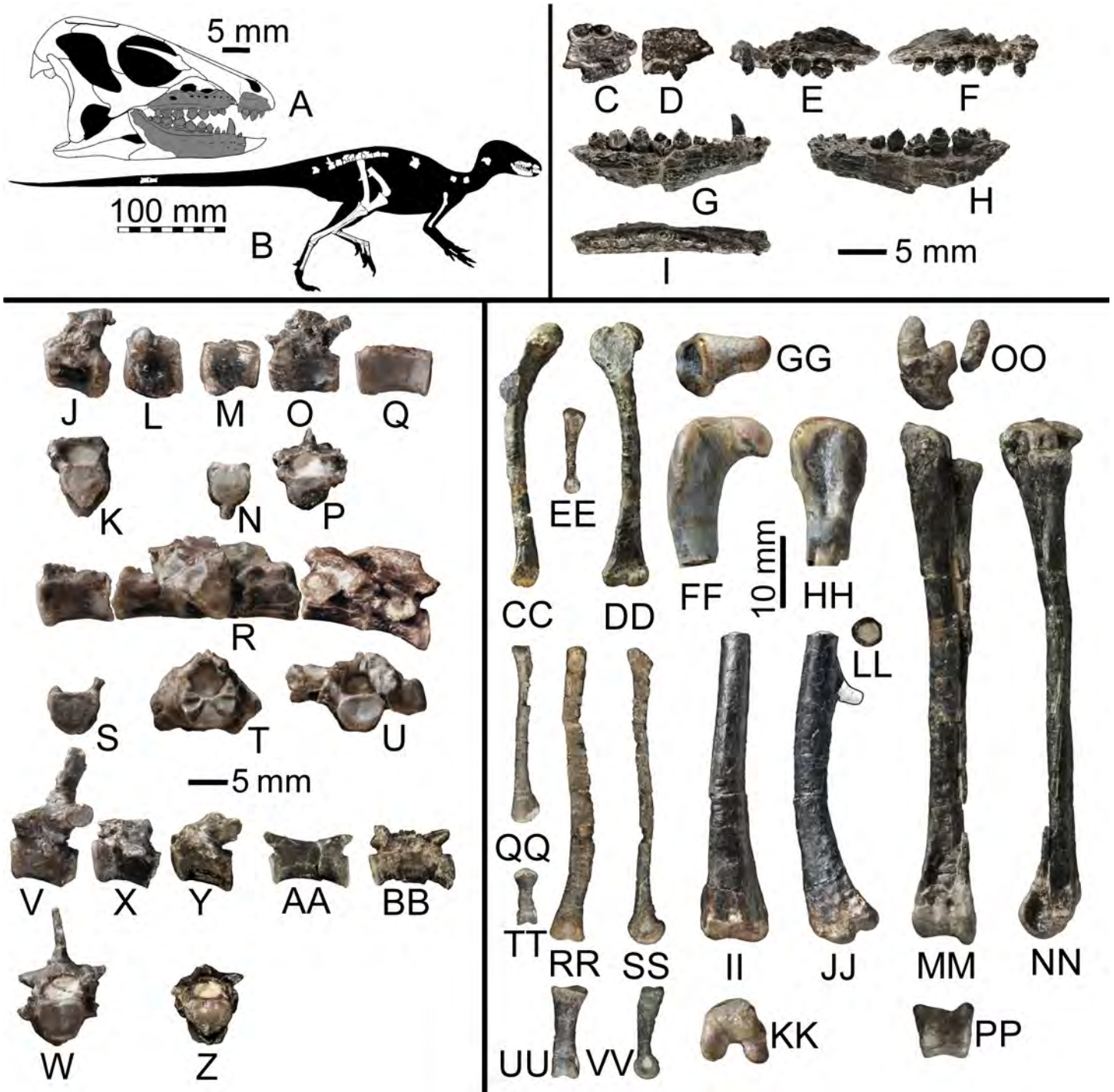


Figure 5. Caption is on the following page.

and Lull (1908) (figures 6A and 6B). They noted that the skeleton was disarticulated and the bones scattered. Also, that much of the bone was missing, leaving only impressions from which wax casts were made. Galton (1978) described latex peels of the bone impressions af-

ter the bone debris was removed (figures 6C and 6D). This gave a better understanding of the exterior bone morphologies, although only from one side. Galton interpreted the specimen in light of other primitive “fabrosaurs.” However, *Nanosaurus* may not be close to



Figure 5 (figure is on the previous page). *Fruitadens haagarorum* Butler and others, 2010. (A) the skull is incompletely known; the missing parts are based on the complete skull of *Heterodontosaurus*. (B) composite skeletal reconstruction, with known bones in white, shows a small, 1-m-long individual. Cranial parts (LACM 128258) are represented by: a right premaxillary fragment in (C) occlusal and (D) lateral views. Partial left maxilla in (E) labial (lateral) and (F) lingual (medial) views. Partial left dentary with restored canine (now broken) in (G) labial (lateral), (H) lingual (medial), and (I) occlusal views. The vertebral column (LACM 115747) is represented by: anterior cervical in (J) left lateral and (K) anterior views. Posterior cervical centrum in (L) left lateral view. Anterior dorsal or posterior-most centrum in (M) left lateral and (N) anterior views. Note the ventrally projecting hypapophysis, a structure that is unusual among ornithischians, but is known on the posterior cervical vertebrae of the primitive iguanodontid *Lurdusaurus* (Taquet and Russell, 1999), as well as some theropods, such as the oviraptorid *Anzu* (Lamanna and others, 2014, figure 4). Dorsal vertebra in (O) lateral and (P) anterior views. Sacrum in (R) left lateral view; sacral centrum 1 in (S) anterior view; sacral vertebra 2 in (T) anterior view; sacral vertebra 6 and sacral ribs of sacral vertebra 5 in (U) posterior view. Caudal vertebrae include caudal 2(?) in (V) left lateral and (W) anterior views; anterior caudal centrum in (X) left lateral view; anterior caudal vertebra in (Y) left lateral and (Z) anterior views; distal caudal vertebrae in (AA) and (BB) left lateral views. The forelimb is incompletely known and is represented by a left humerus (LACM 120478) in (CC) lateral and (DD) anterior views. The now missing deltopectoral crest is restored from an older photograph. A probable metacarpal II (LACM 120602) based on the lateral articular surface of the proximal end in (EE) medial view. The absence of a cotyle for the metatarsal shows that this cannot be phalanx I-1 as identified by Butler and others (2012). Hind limb material includes the proximal end of a right femur (LACM 115727) in (FF) anterior, (GG) proximal, and (HH) lateral views. The anterior trochanter is not well separated from the greater trochanter. The distal two-thirds of a left femur (LACM 120478) in (II) anterior, (JJ) lateral, (KK) distal, and (LL) shaft cross-sectional views. The tab-like fourth trochanter is restored from a drawing of the femur before it was damaged. The lower part of the leg is known from a complete left tibia, fibula, astragalus, and calcaneum (LACM 120478) in (MM) anterior, (NN) lateral, (OO) proximal, and (PP) distal views. The feet are incompletely known and are represented (LACM 120602) by (QQ) right metatarsal I in medial view; metatarsal II or III in (RR) anterior, and (SS) lateral (?) views. Pes phalanges include (TT) a phalange in dorsal view and III-1 in (UU) dorsal and (VV) lateral views. (A) and (B) modified after Butler and others (2009) and (C) to (VV) from Butler and others (2012).

*Lesothosaurus* and other “fabrosaurs” as once thought, especially in light of the recent description of the heterodontosaurid *Fruitaden haagarorum* by Butler and others (2009; see also Butler and others, 2012) and the discovery of a very immature bipedal ornithischian 2 km southeast of *Nanosaurus*. This “*Nanosaurus*”-like neornithischian skeleton is also represented by bone impressions (DMNH 21716; figure 6E) in several maroon-colored fine-grained sandstone blocks and it was described from latex peels by Brill and Carpenter (2001). The matrix is very similar to the block containing the type of *N. agilis*, although lighter in color. This unusual matrix for Garden Park suggests that it came from near the same stratigraphic level as YPM VP 1913.

This new specimen represents an individual a little larger than the type of *N. agilis* and includes the frontals, portion of an articulated vertebral column with separate neural arches and centra, and parts of both limbs. Unlike the type of *N. agilis*, however, the bone impressions are crisper and better delineated, so they are more

informative (compare figure 6C with 6E). The humerus, femur and tibia are morphologically similar to those of the type of *N. agilis*, suggesting that *Nanosaurus* is a neornithischian, rather than a more primitive ornithischian. This is borne out by the lower jaw (figures 7A to 7C), which is more similar to those of *Othnielosaurus* (figure 7D, 7G to 7K) and *Drinker* (figure 7E to 7F), rather than to those of the other bipedal ornithischians known from the Morrison Formation, including *Fruitadens* (figure 7L), *Dryosaurus* (figure 7M), and *Campyosaurus* (figure 7N). Shared characters with *Othnielosaurus* and *Drinker* include anteriorly tapering dentary, dentary with gently convex ventral margin, slightly procumbent anterior dentary teeth, unusual widely spaced posterior teeth, tooth roots well exposed, teeth that extend almost to the symphysis, triangular crowns wider than the roots, and the coronoid process is in line with the tooth row, rather than off set laterally. One ontogenetic change of note is that the lower margin of the dentary becomes less curved or arced in larger, hence more

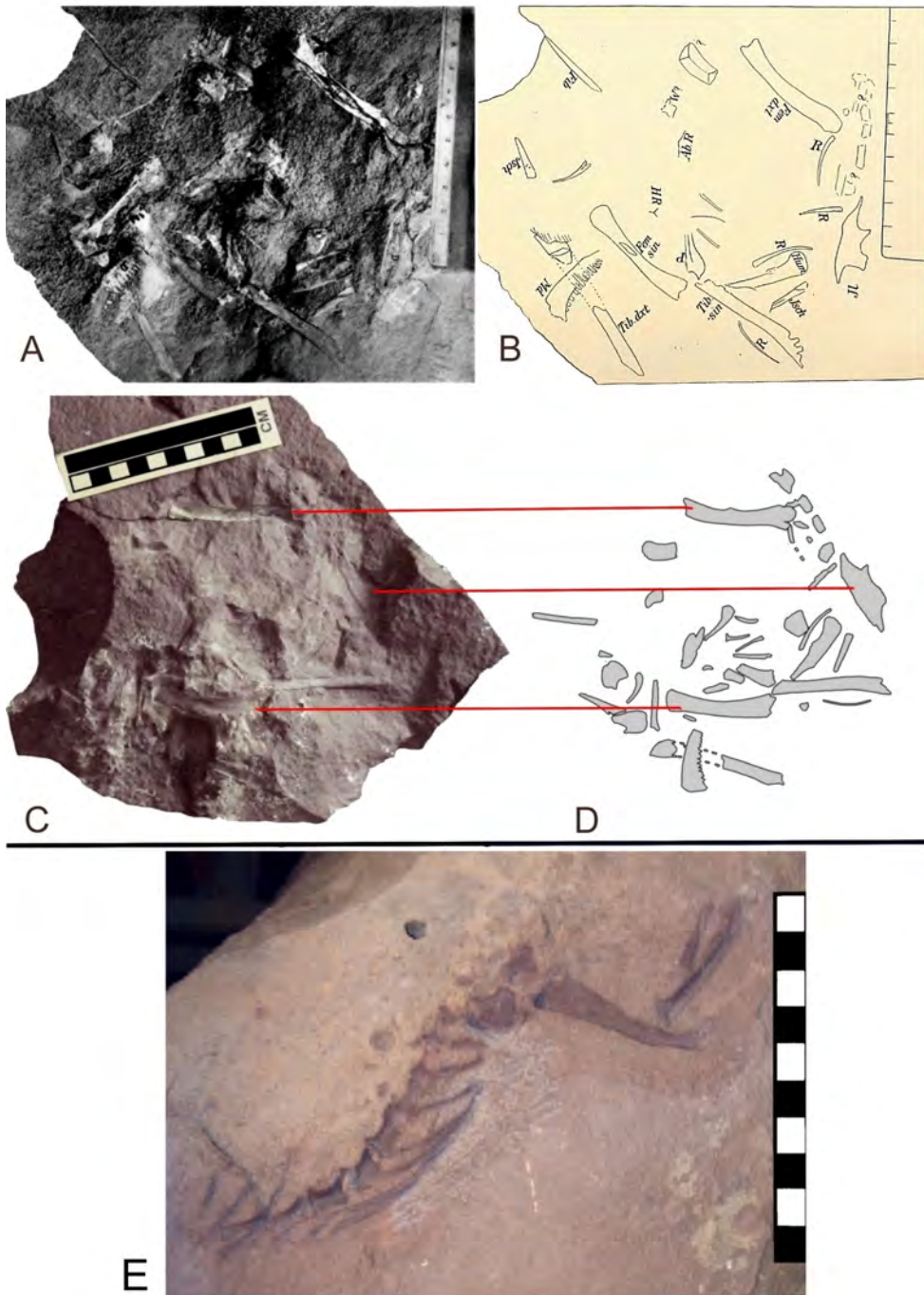


Figure 6. *Nanosaurus agilis* Marsh, 1877. (A) Holotype block YPM VP 1913 as received by O.C. Marsh in 1877 and described and photographed by Huene and Lull (1908, plate 13) with (B) an interpretation of the elements present (Huene and Lull, 1908, figure 1). (C) The specimen as described by Galton (1978) after damaged bone was removed leaving impressions of the exterior surface of the bones. (D) Interpretative drawing composite based on Galton (1978, figure 3) from latex peels of the bone impressions. (E) Juvenile neornithischian represented by bone impressions (DMNH 21716) in matrix similar to the holotype *N. agilis*. Although some of the bones are similar to those of *N. agilis* (indicating that the holotype is a neornithischian), there remains the possibility that DMNH 21716 is a juvenile *Dryosaurus*. Scales in cm.

mature individuals. In *Fruitadens* the dentary tapers, but more abruptly, and the posterior teeth are closely packed. In both *Camptosaurus* and *Dryosaurus*, the dentary does not taper, but rather the alveolar margin is almost parallel to the ventral margin. Furthermore, the crowns taper towards the roots and the posterior teeth are closely packed to form a continuous wear surface. Finally, the coronoid process is laterally offset so that

the posterior-most teeth are medial to the process; this leaves room for a fleshy cheek as previously suggested by Galton (1973).

Despite the poor quality of the holotype of *Nanosaurus agilis*, the dentary is adequate to show that it is very similar to those referred to *Drinker nisti* and *Othnielosaurus consors* as discussed above. We therefore conclude that *Nanosaurus agilis* Marsh, 1877, is the se-

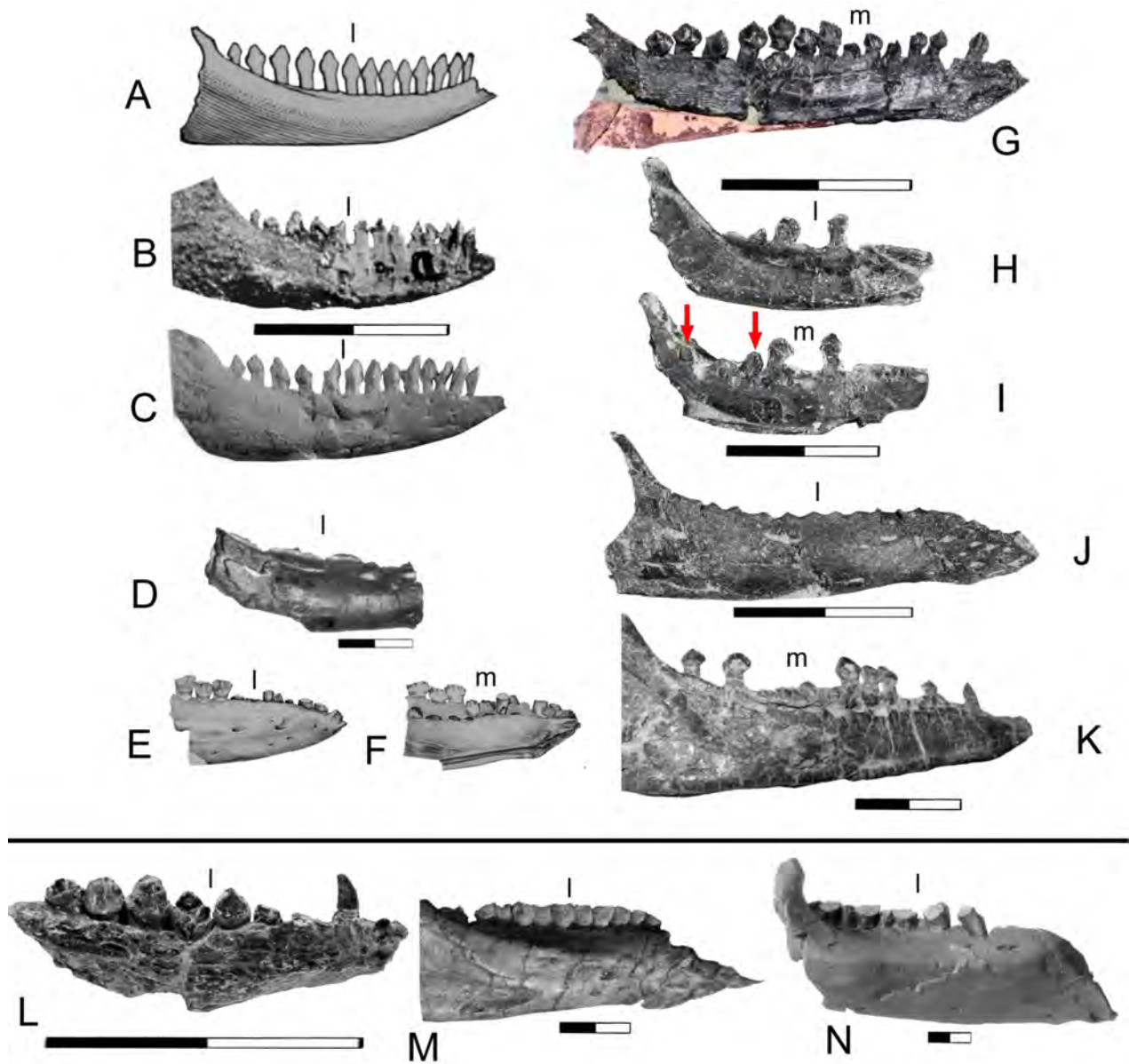


Figure 7. Caption is on the following page.

nior synonym under the Principle of Priority (ICZN, 1999, Art. 23.1), and that *Drinker nisti* Bakker and others (1990) and *Othnielosaurus consors* (Galton, 2007) are both junior subjective synonyms (ICZN Article 61.3). We are aware that this proposal will be controversial and contentious, but we believe the evidence speaks for itself. We now discuss some of the important specimens.

*Nanosaurus agilis* is the most common bipedal ornithischian in the Morrison Formation, thus statistically, it is no surprise that this was the first taxon dis-

covered. It is represented by several nearly complete skeletons (figure 8), including the holotype of *Laosaurus consors* (a.k.a. *Othnielosaurus consors* of Galton, 2007). That specimen was collected from Como Bluff, Wyoming, and named by Marsh (1894b); the specimen was later made the type of *Othnielosaurus* by Galton (2007). Galton and Jensen (1973) described a headless skeleton from near Willow Springs, Utah, as *Nanosaurus? rex* (figures 8B to 8D) and Lovelace (2006) very briefly reported on another headless skeleton collected

Figure 7 (figure is on the previous page). *Nanosaurus agilis* Marsh, 1877. Dentaries (A to K) compared to non-*Nanosaurus* dentaries (L to N); scaled to common dentary depth for comparison. (A) Illustration of the dentary (YPM VP 1913) given by Marsh (1896, figure 42, reversed). (B) Dentary as photographed by Huene and Lull (1908, plate 13, reversed) before the bone was removed. (C) Latex peel after the bone was removed. (D) Type (YPM VP 1882) of "*Laosaurus consors*" and type of "*Othnielosaurus*" Galton, 2006 (as *O. consors*) (reversed). Although not visible in this view, the posterior alveoli are widely spaced, indicating widely spaced teeth as in YPM VP 1913. (E) and (F) (reversed) Dentary referred to "*Drinker nisti*" (no scale). Note the teeth extend to near the dentary tip as in the holotype *N. agilis*, the roots are exposed, and the lower margin is curved. (G) Dentary (MWC 5822) originally described as "*Othnielia rex*" by Pierce (2006). Note the unique widely spaced posterior teeth, procumbent anterior teeth that extend almost to the dentary tip, roots exposed, and coronoid process arising from the posterior end of the tooth row. These characters are shared with the holotype of *N. agilis*. This specimen is the key linking the holotype with specimens previously referred to "*Othnielia*," "*Othnielosaurus*," and "*Drinker*." Red section digitally restored from the counterpart slab. Images courtesy of Julia McHugh, Museums of Western Colorado. (H) lateral view (reversed), (I) medial view of dentary from the Marsh-Felch Quarry (USNM V 5829). The posterior teeth (arrows, see figure 10O) and alveoli (between the arrows) are widely spaced, some of the teeth have tricuspid denticles whereas others do not as noted by Scheetz (1999, p. 100, figure 37; key specimen showing that "*Othnielia*" and "*Drinker*" teeth occur in the same jaw), the roots are exposed and coronoid process rises from the posterior end of the tooth row. Note the curved ventral margin, a juvenile character. (J) Dentary of "Minimax" (SMA 0006 reversed). The alveoli extend to the prementary facet. (K) Lower jaw of "Barbara" (SMA 0010), with exposed roots and widely spaced posterior teeth (photo from H.J. Siber, Athal Saurier Museum). (L) Dentary (LACM 128258) of *Fruitadens* showing closely packed posterior teeth, roots that are not exposed, a canine, and a small precanine. (M) Lower jaw (CM 3392) of *Dryosaurus* with closely packed teeth of uniform height through wear; coronoid process offset laterally. (N) Lower jaw of *Camptosaurus* (cast from the Cleveland-Lloyd Dinosaur Quarry courtesy of Jim Madsen [deceased] Utah Division of State History) which also has closely packed teeth worn to a uniform height and a laterally offset coronoid process. Abbreviations: l, lateral side; m, medial side. Scale = 2 cm.

near Alcova Reservoir in central Wyoming (figure 8E). More recently, a remarkably complete specimen with partial skull was collected near Shell in the Bighorn Basin (figure 8F). These specimens were used to recreate the skeleton of *Nanosaurus agilis* (figure 8G).

For fragmented, but equally important material is that which was used to establish *Drinker nisti* by Bakker and others, 1990. The material includes parts of five juveniles from an alleged 30 found together in an oval mass of mudstone 1 m across that was interrupted as a communal burrow (Bakker, 1996). The holotype is a partial juvenile skeleton, including parts of the upper and lower jaws, centra from all sections of the vertebral column, and partial fore- and hindlimbs. Seven additional specimens, CPS 107, 108, 109, 197, 198, USNM V 5808, YPM VP 9524, were referred to the taxon. The holotype catalog number, CPS 106, was said to belong to the Colorado Palaeontographical Society housed at the University of Colorado Museum, Boulder, Colorado. Such a society nor its collection was ever recognized by the museum (P. Robinson, University of Colorado, personal communication, 2017) nor was the material

curated there. Subsequently, it was said to be at the Tate Geological Museum, Casper College, Wyoming, as Tate 4001 (Bakker, 1996, p. 41), but is not curated there either (J.P. Cavigelli, Tate Museum, personal communication, 2017). The current location of the material is unknown. Owing to the difficulty to access the original publication describing "*Drinker*," we present modified versions of the original illustrations and supplement them with additional illustrations provided to us.

The postcranial material of *Nanosaurus* is not very good but the impressions do fit the better skeletal material of "*Othnielosaurus*" (figure 9). Several characters are shared by "*Othnielosaurus*" and "*Drinker*" specimens: (1) The multi-cuspid marginal denticles on the cheek teeth, once thought to be unique to the type material of "*Drinker*," are now known to occur in the posterior teeth of juvenile "*Othnielosaurus*" (see discussion by Galton, 1983) (figure 10). (2) Some of the cheek teeth have a variably developed cingulum, often denticulate, along the posterior(?) edge that curves onto the lingual(?) face; this unusual character is otherwise only known in some Late Cretaceous ornithischians, such as *Pachycephalo-*

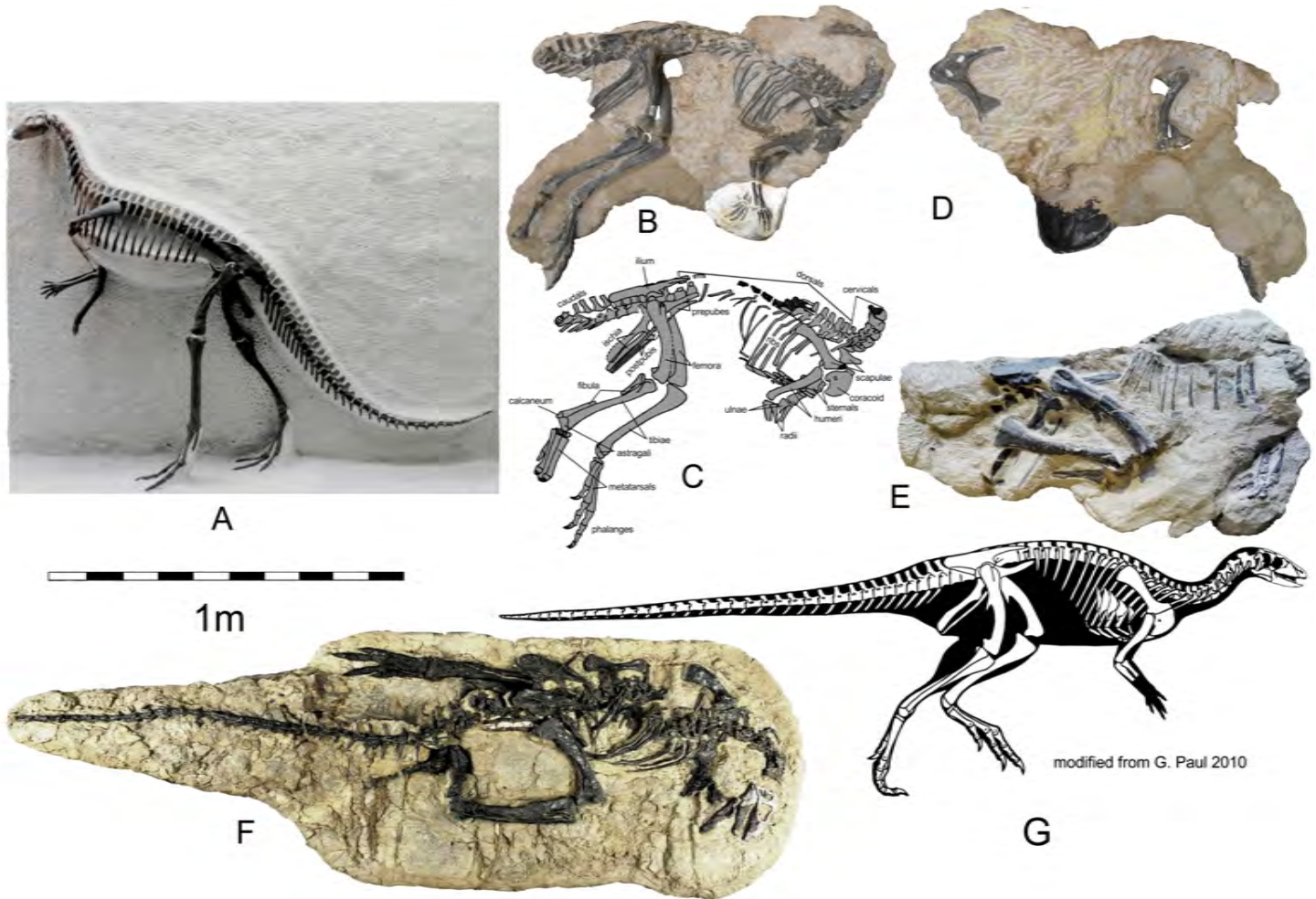


Figure 8. *Nanosaurus agilis* Marsh, 1877. (A) Mounted skeleton at the Peabody Museum of Natural History, YPM VP 1882, the holotype of “*Laosaurus consors*” Marsh, 1894b, type species of “*Othnielosaurus*” Galton, 2007 as “*O. consors*” (Marsh, 1894b). A great deal of plaster of Paris obscures details of some of the bones. (B) Headless juvenile specimen (BYU 163) from near Willow Springs, Emery County, Utah, (C) with interpretative sketch. This specimen was well illustrated and described by Galton and Jensen (1973). (D) Opposite side of (BYU 163) showing *Allosaurus* lacrymal and lateral side of left femur in window. (E) Another headless partial skeleton (UW 24823) preserved three-dimensionally from near Alcova, Wyoming. This specimen is a little larger than BYU 163. (F) “Barbara” (SMA 0010), the most complete and articulated specimen that was excavated at the Howe Ranch, Wyoming (photo from H.J. Siber, Athal Saurier Museum). (G) Composite skeletal reconstruction courtesy Greg Paul (independent paleoartist).

*saurus* (figure 10; Brown and Schlaikjer, 1943, plate 40, figure 1). (3) The tooth row of the dentary extends to posterior end of the tomial edge of predentary (figure 7). This can be inferred for the holotype of *Nanosaurus* because of how far forwards the teeth extend. (4) Jugal with ornamentation, which is an unusual feature among ornithopods (figure 11). (5) The ilium has an antitrochanter dorsal and adjacent to ischial peduncle (figure 15). (6) The brevis shelf of the ilium is narrow compared

to length of postacetabular process (figure 15). (7) The pubis has a slightly compressed, tapering, rod-like anterior process (figure 15). (8) The ascending ramus of the astragalus is a short, vertical spur either located near the middle of the front edge (YPM 1882) or offset towards the calcaneum (BYU 613) (see figure 17). (9) Metatarsal I is over 50% the length of metatarsal III and bears two unreduced phalanges (figure 18).

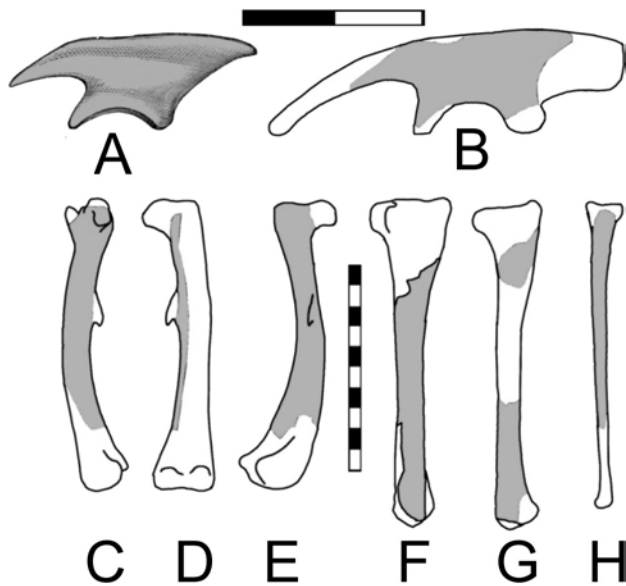


Figure 9. *Nanosaurus agilis* Marsh, 1877, holotype YPM VP 1913, (A) left ilium as illustrated by Marsh (1896, figure 43). (B) Alternative interpretation of the ilium based on the observation that the rock is irregularly split and therefore the ilium is probably not split perfectly on the horizontal plane. A best fit is with the outline of the ilium of BYU 163 (gray area ilium as interpreted by Galton, 1978, figure 4A, from a latex peel). New interpretations of Galton's (1978, figure 5) latex peels: (C) right femur in medial and (D) posterior views, (E) left femur in medial view, (F) right tibia in lateral, (G) left tibia in medial, and (H) left fibula in lateral views. The fourth trochanter appears to have been located in the proximal half of the femur (see figures 16A to 16I).

**Cerapoda**  
**Ornithopoda**  
**Iguanodontia**  
**Dryomorpha**  
**Ankylopollexia**

*Camptosaurus* Marsh, 1885  
Figures 4 and 19 to 26

The genus was originally named *Camptonotus* by Marsh (1879) but later (1885) renamed *Camptosaurus* because *Camptonotus* was preoccupied by an insect. *Camptosaurus* is the second most common neornithischian in the Morrison Formation. It was probably facultatively quadrupedal and robustly built with a massive carpus and manus, a femur longer than the tibia, and digit I reduced in size (figure 19). Specimens range

from a hatchling or embryo 24 cm long (Chure and others, 1994), to a very large adult 6.75 m long (Erickson, 1988). Currently two species, *Camptosaurus dispar* and *Camptosaurus aphanoecetes*, are recognized.

*Camptosaurus dispar* (Marsh, 1879)

Figures 4, 19A to 19D, 19F to 19H, 20, 21A to 21O, 21Q, 21R, 22A, 22B, 22D, 22F to 22J, 23A to 23F, and 23I

- Camptonodus dispar* Marsh, 1879
- Camptosaurus dispar* Marsh 1885
- Camptosaurus medius* Marsh, 1894b
- Camptosaurus nanus* Marsh, 1894b
- Camptosaurus browni* Gilmore, 1909
- Camptosaurus dispar* Galton and Powell, 1980
- Camptosaurus dispar* McDonald, 2011

Osteologically this is the best-known neornithischian from the Morrison Formation represented by entire skeletons; in contrast, the skull is imperfectly known in *Nanosaurus*. Originally it was described for material from the Quarry 13 bone bed by Marsh and later in a monograph by Gilmore (1909). Marsh (1894b, p. 85) used size as a criterion for separating the species *C. nanus* (smallest), *C. medius*, *C. dispar*, and *C. amplus* (largest). Marsh assumed an evolutionary size gradient through the Morrison Formation, with the smallest species at the bottom and the largest species at the top. This interpretation is interesting in that it shows that the evolutionary idea of species increasing in size through time was already established in paleontology. However, perhaps most damning for Marsh was forcing the facts to fit a preconceived idea, given that it was from reports of the collectors where the specimens came from. Author Lakes, who collected the material of *C. amplus*, wrote to Marsh (letter August 31, 1879) that "the interest attached to it was greater owing to its being in the very lowest horizon we have so far discovered bones" and that the site was "roughly 56 [feet] above *Sauranodon*," i.e., *Baptanodon* beds a.k.a. Sundance Formation. Marsh also knew that the material of *C. dispar*, *C. medius*, and *C. nanus* all came from Quarry 13. *C. amplus* has since been shown to be based on a pes of a large individual of the theropod dinosaur *Allosaurus* (Galton and others, 2015).

Galton and Powell (1980) correctly synonymized *Camptosaurus nanus* and *C. medius* with the first named

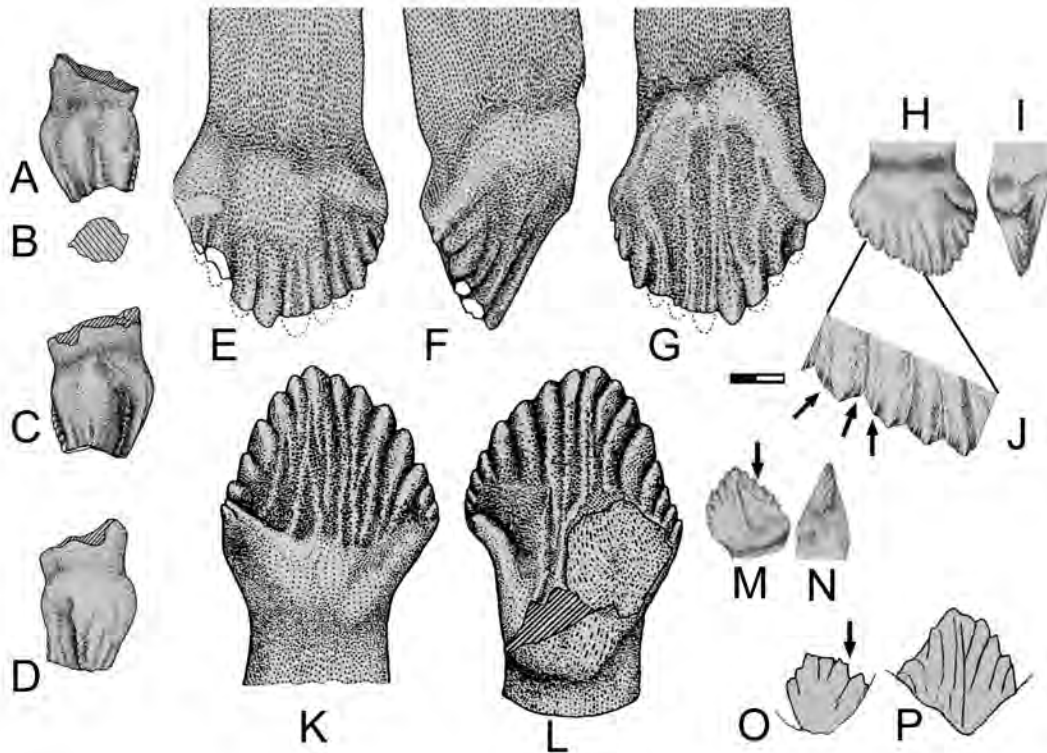


Figure 10. *Nanosaurus agilis* Marsh, 1877. Premaxillary (YPM VP 9522) tooth in (A) anterior; (B) cross section at broken surface, (C) posterior, and (D) marginal views. Maxillary tooth (YPM VP 1882) in (E) lingual, (F) marginal, and (G) labial views. Juvenile maxillary tooth with multi-cuspid cusps in (H) lingual, (I) marginal view, (J) enlarged crown margin showing multi-cuspid (arrows) (adapted from Bakker and others, 1990). Dentary tooth (YPM VP 1882) in (K) labial and (L) lingual views. Juvenile dentary tooth in (M) labial (multi-cuspid at arrow) and (N) marginal views; USNM V 5829 (O) posterior tooth with multi-cuspid crown (arrow), and (P) mid-dentary tooth without multicuspid crown; see figure 7I, arrows, for size of teeth. The presence of multi-cuspid crowns was originally used to separate “*Drinker*” from “*Othnielosaurus*,” but this specimen shows both crown types occur in the same specimen. Scale for A to I and K to N = 2 mm.

taxon, *C. dispar*. *C. dispar* is a robustly built ornithopod that may have been a part-time quadruped. Several new specimens, including those with disarticulated skulls, are expected to shed new light on this species. It differs from *C. aphanoecetes* and the English *C. prestwichii* in having a large intramaxillary fossa on the medial side of the maxilla; this fossa is the opening into the maxillary sinus. It differs from *C. aphanoecetes* in having proportionally short cervical centra compared to their height, generally straighter scapular blade, deep ilium, and gently curved preacetabular process, and a ventrally curved ischial shaft. It also differs in having a generally more robust skeleton, but this is partially ontogenetic as seen by comparing the material of the juvenile “*C. nanus*” with the larger specimens of *C. dispar* (figure 19). Whether this character will hold once a more mature individual of *C. aphanoecetes* is found remains to be seen.

*Camptosaurus aphanoecetes* Carpenter and Wilson, 2008  
Figures 11F, 11J, 13R, 14B, 14E, 14I, 15F, 15G, 15V to 15X,  
15CC, 15DD, 15GG, 15KK, 15LL, 16G to 16I, 16L, 16O,  
16U to 16Z, 16BB to 16EE, 16GG to 16II, 16PP, and 16OO

*Camptosaurus medius* Gilmore, 1925

*Uteodon aphanoecetes* McDonald, 2011 (in part)

*Camptosaurus aphanoecetes* Carpenter and Lamanna, 2015

This species is based on an articulated postcranial skeleton (CM 11337) from Dinosaur National Monument. It was originally referred to *C. medius* Marsh, 1894b by Gilmore (1925), who thought it was a valid taxon that was “lighter and more delicately constructed” than *C. dispar* (Gilmore, 1909). It differs from *C. dispar* in the proportionally long, low cervical centra, scapular blade more curved, shallow ilium with a

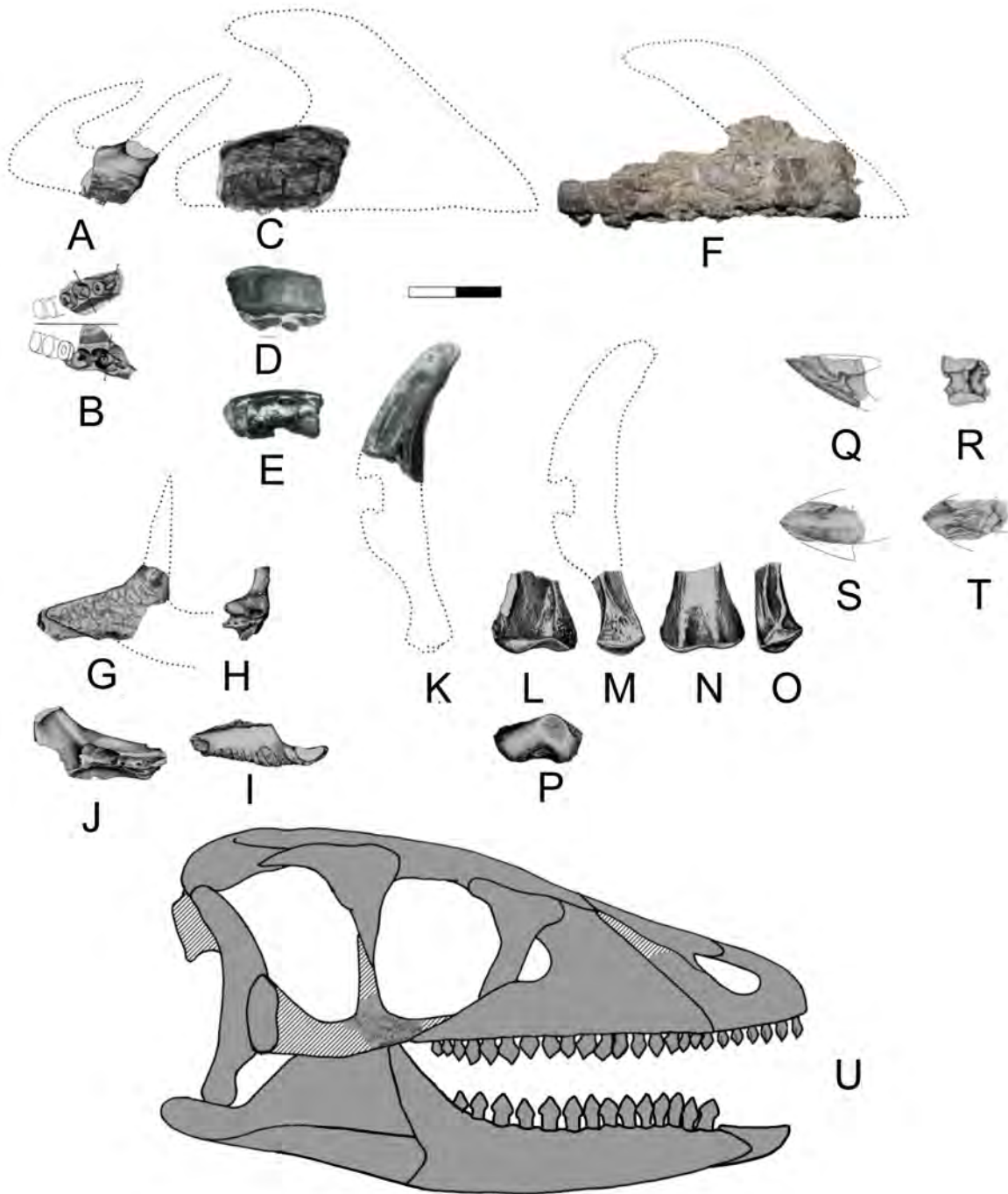


Figure 11. *Nanosaurus agilis* Marsh, 1877. Left premaxilla in (A) lateral, B occlusal views (courtesy R.T. Bakker, Houston Museum of Natural History). Maxilla fragment (YPM VP 1822) in (C) labial, (D) lingual and (E) occlusal views. (F) Partial right maxilla (SMA 0010) in lateral view. Left jugal in (G) lateral, (H) anterior, (I) dorsal, and (J) medial views. External surface is mildly textured (courtesy R.T. Bakker, Houston Museum of Natural History). (K) The dorsal or proximal end of quadrate (YPM VP 1822). The gently curved, tapered proximal end is unlike the abrupt posterior angle and squared end of *Camptosaurus* (figure 20G and 20K) and *Dryosaurus* (figures 28I, 28J, 28Q, and 28BB). Distal end of quadrate in (L) anterior, (M) lateral, (N) posterior, (O) medial, and (P) distal views (courtesy R.T. Bakker, Houston Museum of Natural History). Prementary in (Q) lateral, (R) posterior, (S) ventral, and (T) dorsal views (courtesy R.T. Bakker, Houston Museum of Natural History). Scale in cm. (U) reconstructed skull of *Nanosaurus agilis*.



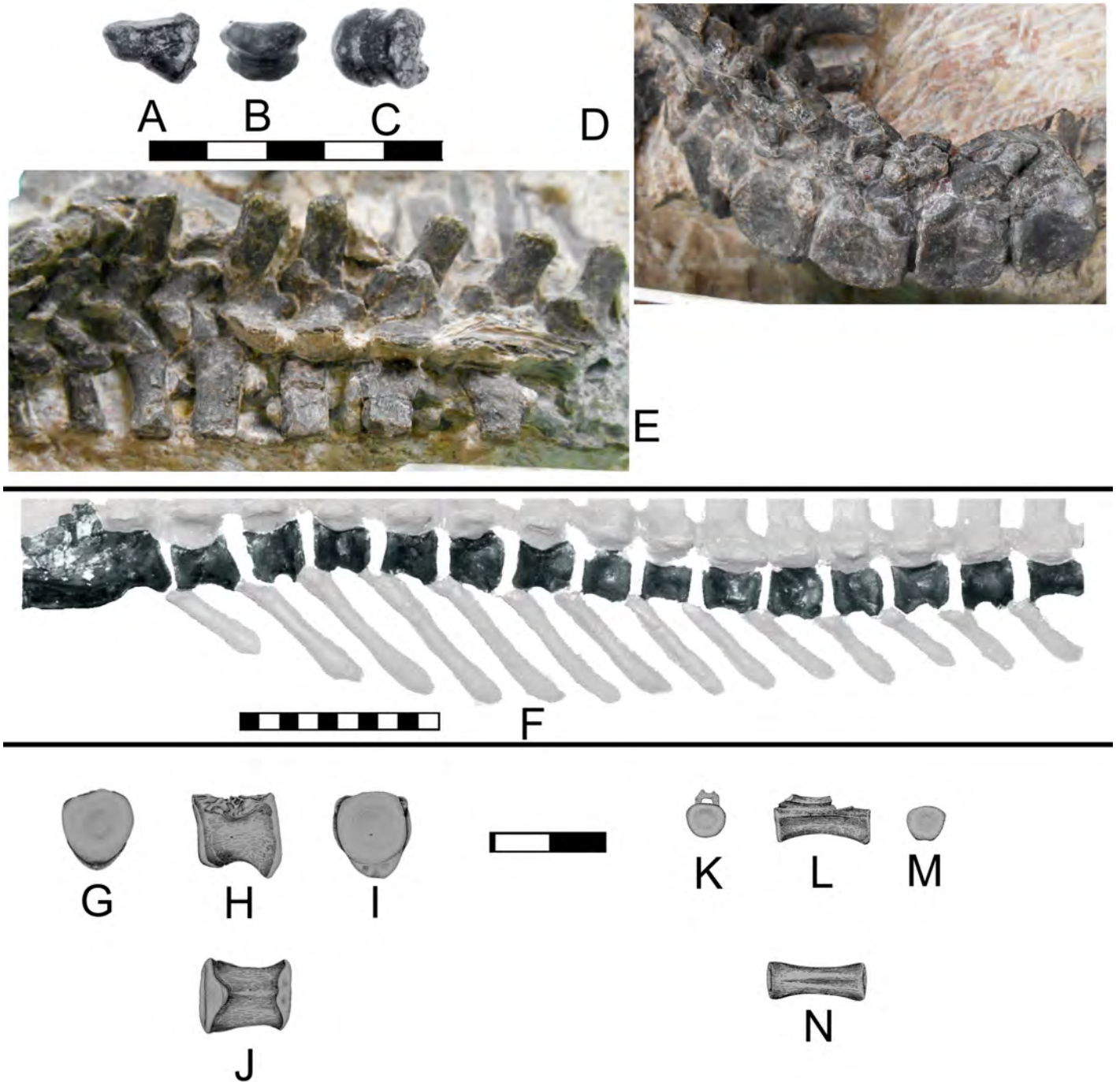


Figure 12. *Nanosaurus agilis* Marsh, 1877. Low, wide odontoid (YPM VP 1882) seen in (A) lateral, (B) dorsal, and (C) ventral views. (D) Cervical vertebrae (BYU 163) in right lateral view. (E) Dorsal vertebrae (BYU 163) in dorsal view (anterior to left). (F) Caudal centra (YPM VP 1882) in left lateral view. Caudals drawn for Marsh: proximal centrum in (G) anterior, (H) lateral, (I) posterior, (J) ventral; distal vertebra in (K) anterior, (L) lateral, (M) posterior, (N) ventral views. Scales in cm.

sharply bent preacetabular process, and a straight ischium shaft. Despite its obvious similarities with *C. dispar* (as acknowledged by Gilmore, 1925), the skeleton was re-described as the type of *Camptosaurus aphanoeectes*

Carpenter and Wilson, 2008, and subsequently made the type species of *Uteodon* McDonald, 2011. However, as shown by Carpenter and Lamanna (2015), *Uteodon* is a chimera of the postcranial skeleton of *C. aphanoeectes*

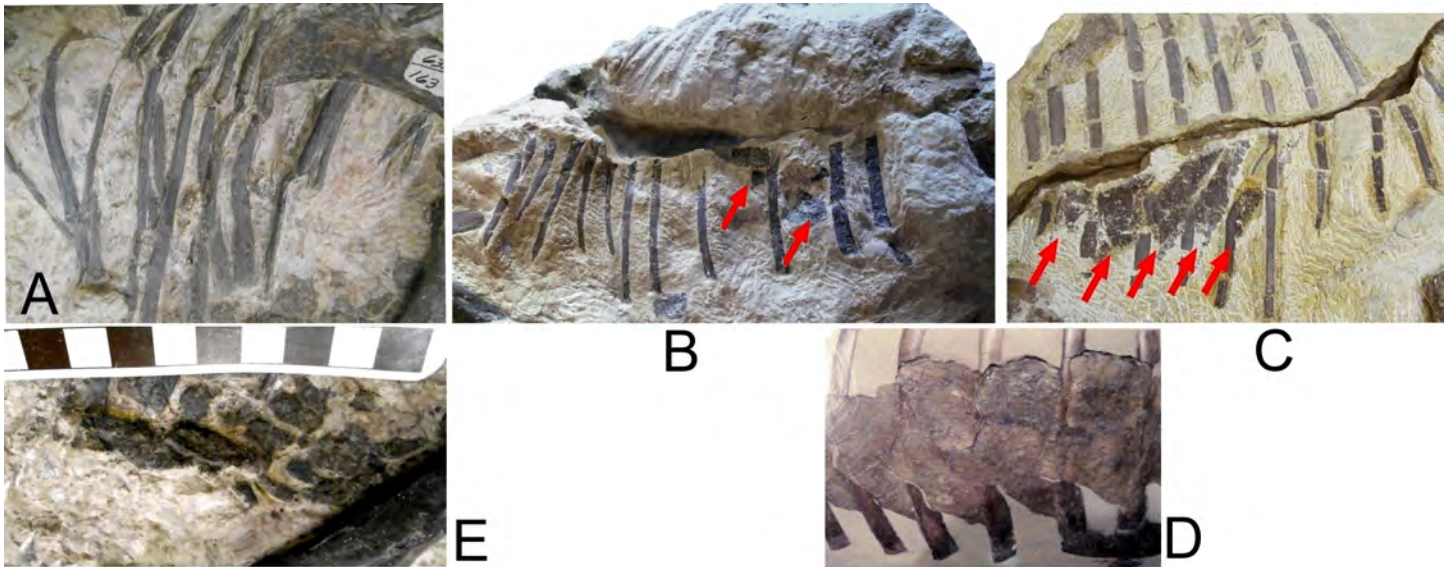


Figure 13. *Nanosaurus agilis* Marsh, 1877. (A) Ribs of BYU 163. Ossified intercostal plates (red arrows) in UW 24823, (B) two on right side, (C) five on left. These are not seen in either BYU 163 or SMA 0010. Each rhomboid plate originates on the distal surface of an anterior rib (Lovelace, 2006) and extends posteriorly to overlap the following rib obliquely in a ventral direction; “in most ornithischians, the plates extend obliquely in a dorsal direction as seen in (D) *Thescelosaurus* (NCSM 15728). Intercostal plates are known in other ornithischians where their sporadic presence may be at least partially controlled ontogenetically (Butler & Galton, 2008; Boyd and others, 2011). (E) BYU 163, ossified costal cartilage which connect to ossified sternal plates. These are not ossified in UW 24823 and SMA 0010. Scale for (E) in cm.”

and a braincase of *Dryosaurus*. The only proposed autapomorphy, the occipital condyle projecting farther ventrally than the basal tubera, was based on a damaged braincase (CM 87688) of *Dryosaurus* (see next section).

## Dryosauridae

*Dryosaurus* Marsh, 1894b

Figures 4 and 27 to 31

*Dryosaurus* Marsh, 1894b was erected by Marsh for *Laosaurus altus* Marsh, 1878 after it was concluded that its form was intermediate between that of *Camptosaurus* and *Laosaurus consors*. The intermediate state was seen in the pubis: “The prepubis, or anterior branch of this bone, which was very large and broad in *Camptosaurus*, still long and spatulate in *Dryosaurus*, is here [*Laosaurus consors*] reduced to a pointed process not much larger than in some birds.” Of course, we now know that the anterior process of “*Laosaurus consors*” (= *Nanosaurus*) was incomplete and interpreted backwards by Marsh (figures 15N and 15O).

Two species are recognized from the Morrison Formation, as well as a probable third species, *D. lettowvorbecki* (Pompeckj, 1920), from the Upper Jurassic of Tanzania, although that still remains a subject of debate (see Galton, 1977, 1980, 1981, 1983 and Hübner, 2011 versus Carpenter and Lamanna, 2015). Hübner (2011) argued that the differences in the postcrania of *Dryosaurus* and *Dysalotosaurus* are greater than those between many accepted hadrosaur genera and interpreted this as evidence to support the generic separation of the two dryosaurids. However, Carpenter and Lamanna (2015) noted that similar morphological conservatism has not been demonstrated for non-hadrosaurid iguanodontians and there is no prior reason to assume that it existed. The large differences noted among iguanodontids would argue against morphological conservatism. Furthermore, Carpenter and Lamanna (2015) noted that the strong emphasis placed on differences in the quadrates by Hübner (2011) to separate *Dysalotosaurus* from *Dryosaurus* is based on plaster reconstruction of a damaged quadrate on a skull (CM 3392) referred

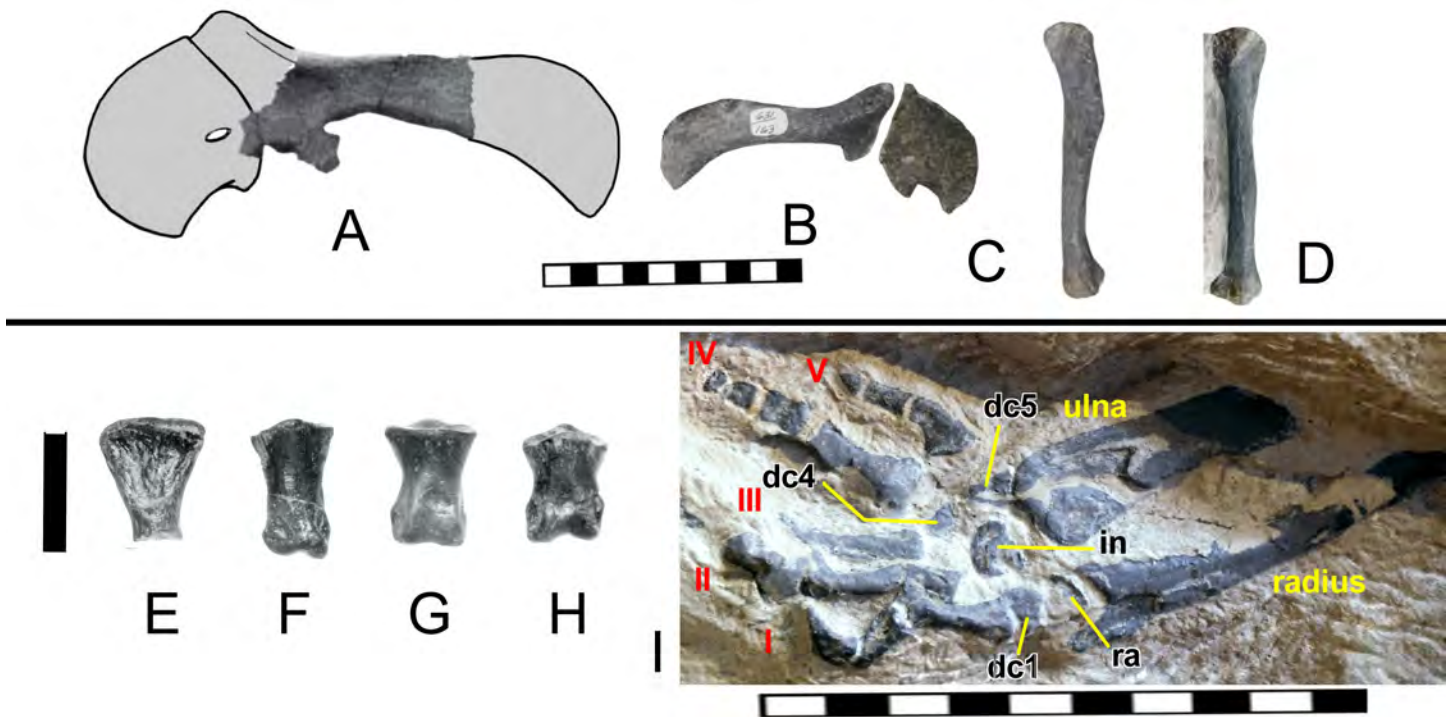


Figure 14. *Nanosaurus agilis* Marsh, 1877. Forelimb includes (A) a partial scapula and fragment of coracoid (YPM VP 1882) and (B) scapula and coracoid (BYU 163). The coracoid is proportionally large compared to the scapula. Right humerus (BYU 163) in (C) lateral view showing short, proximally placed deltopectoral crest, and (D) posterior view showing large humeral head. The left humerus of YPM VP 1882 is supposed to include real bone, but it is so extensively restored in plaster of Paris that its actual shape cannot be determined. (E) Proximal end of a metacarpal (YPM VP 1882) and (F), (G), and (H) several phalanges (YPM VP 1882). (I) Articulated left manus (UW 24823) in palmar view shows a digit count of 2-3?-?-3-2. Digits IV and V may not have had terminal unguals. The wrist bones are widely separated and suggests a considerable amount of cartilage, possibly due to the immaturity of the individual. No trace of dc2 and dc3 is seen, although these may still be buried in the matrix. Abbreviations: I to V – digit I to digit V; dc1, dc4, and dc5 – distal carpal; in – intermedium; ra – radiale. Scales in cm.

below to a new species of *Dryosaurus*. Scheetz (1999) and Boyd (2015) treated *Dysalotosaurus* and *Dryosaurus* separately in their phylogenetic analyses. It is questionable as to whether the dryosaurid *Eousdryosaurus nanohallucis* Escaso and others, 2014, from Portugal is a distinct genus given that some of the supposed autapomorphies used in the diagnosis are either age-related, such as the entheses (the “small, horn-like anterior process”), which are common in older individuals of many dinosaurs, or are characters, such in the hind limb, that Escaso and others (2014) acknowledge as occur in *Dryosaurus*.

*Dryosaurus altus* (Marsh, 1878)

Figures 4, 28A to 28P, 28BB to 28EE; 29A to 29H, 29K to 29R, 30A to 30C, 30E to 30FF, 31A, and 31K to 31TT

*Laosaurus altus* Marsh, 1878

*Dryosaurus altus* Marsh, 1894b

*Dryosaurus altus* Galton, 1981

*Dryosaurus altus* Galton, 1983

*Dryosaurus altus* Norman, 2004

The anatomy of *Dryosaurus altus* was described in detail by Galton (1981, 1983, 1989), although this included material we assign to a new species below. We separate the material by species in the figures. Histolog-

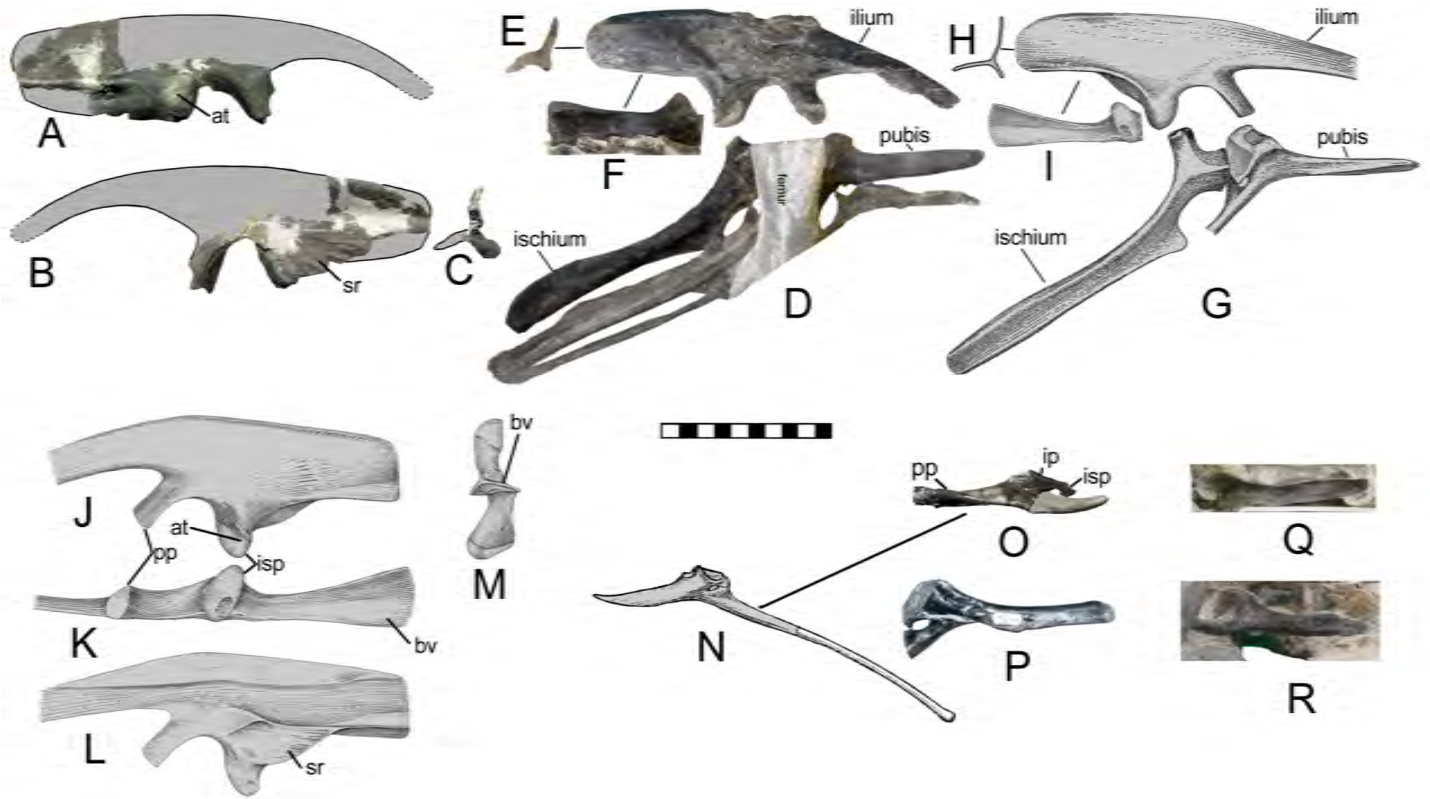


Figure 15. *Nanosaurus agilis* Marsh, 1877. Partial right ilium (YPM VP 1882) with a deep, narrow acetabulum in (A) lateral, (B) medial, and (C) posterior views. The acetabulum is proportionally wider and shallower in *Camptosaurus* (e.g., figures 25C, 25I, and 25J) and *Dryosaurus* (figures 31A, and 32G). On the lateral side of the ischial peduncle is an expansion (i.e., swelling or boss) whose position and form is analogous to the avian antitrochanter. The location of this structure is not the same as the structure that has erroneously been called the antitrochanter in hadrosaurs (see discussion in Gilpin and others, 2007). A similar antitrochanter is also present in *Camptosaurus* (figure 16D) and *Dryosaurus* (figure 20G). On the medial side of the ilium, scarring shows that a sacral rib (sr) braced the ischial peduncle (figure 15B). The brevis shelf on the postacetabular process forms a shallow fossa as seen in posterior view (C). (D) Complete right pelvis (BYU 163) in lateral view. The posterior end of the postacetabular process is rounded, and the dorsal border gently curved. (E) Posterior view showing the brevis shelf with a shallow fossa. (F) Ventral view of the brevis shelf. (G) Composite pelvis of “*Drinker nisti*” (courtesy of R.T. Bakker, Houston Museum of Natural History). The ilium shares the distally rounded postacetabular process and gently curved dorsal border. (H) Posterior view showing brevis shelf. (I) Ventral view of brevis shelf. Left ilium referred to “*Drinker nisti*” (courtesy of R.T. Bakker, Houston Museum of Natural History) in (J) lateral, (K) ventral, (L) medial (reversed), and (M) posterior views. Note the large sacral rib scar as in YPM VP 1882. Pubis (N) reconstruction presented by Marsh (1894b, p. 7, figure 1). The pubis is actually incomplete and restored in reverse. (O) Pubis (medial view) correctly oriented showing that the postpubic shaft is actually the prepubic or anterior process; the distal end is incomplete. (P) Pubis with complete prepubic process (YPM 7324). The prepubic process (BYU 163) in right lateral (Q) and left medial (R) views. Although the prepubic process in *Nanosaurus* appears to be a rod-like structure in lateral view, it is actually twisted as can be seen in (O) and dorso-ventrally compressed. Abbreviations: at – antitrochanter; bv – brevis shelf; ip – facet for the pubic peduncle of the ilium; isp – ischial peduncle; pp – prepubic process; sr – sacral rib facet.

ical changes for a growth series of femora of *Dryosaurus altus* were given by Horner and others (2009, figures 4 to 6). However, their large sub-adult femur (CM 1949) is associated with a *Camptosaurus*-like ilium leading us

question their conclusions regarding growth rate in this taxon. We believe that this specimen represents a new, unnamed ornithopod (see below).

*Dryosaurus altus* is characterized by cheek teeth having

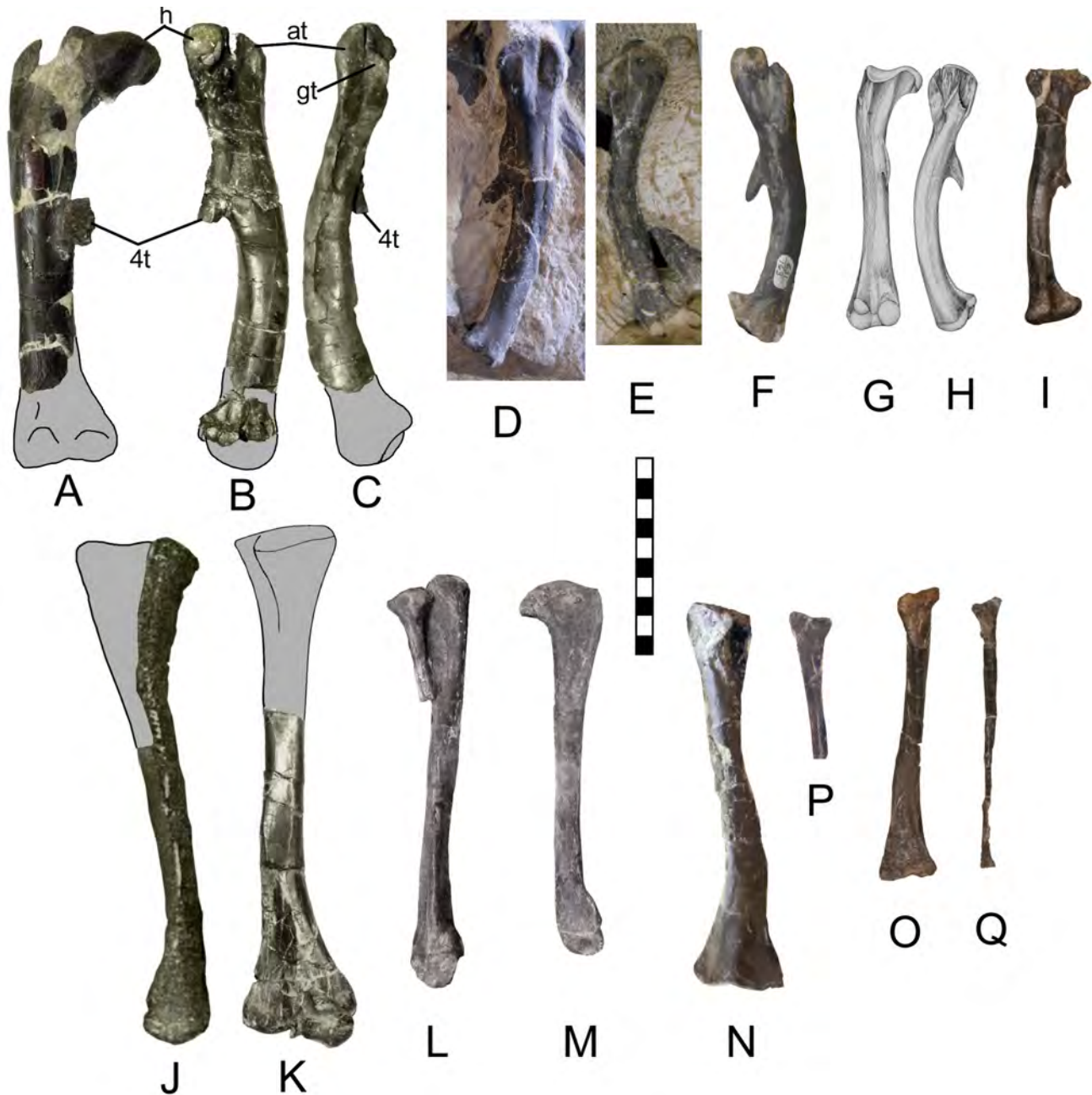


Figure 16. *Nanosaurus agilis* Marsh, 1877. YPM VP 1882, right femur in (A) posterior, and left femur in (B) medial, and (C) lateral views; crushing has pushed the fourth trochanter posteriorly in (A). The femoral shaft is straight, not bowed in posterior view, but anteriorly bowed in side view. The angle between the neck of the head and the shaft is around 135°; there is also a slight constriction under the femoral head. The anterior trochanter is arcuate and as tall as the greater trochanter. The fourth trochanter is damaged but enough is present to show that it was pendant and located entirely on the proximal half of the shaft. (D) Right femur (UW 24823) in lateral view. Femora (BYU 163) (E) left and right (F) in lateral views. Left femur of “*Drinker nisti*” (courtesy of R.T. Bakker, Houston Museum of Natural History) in (G) posterior and (H) lateral views. (I) Smallest complete femur (SMA 0006) with crushed head. Right tibia (YPM VP 1882) with astragalus in (J) medial and (K) anterior views. Right tibia with astragalus and calcaneum, and proximal end of fibula (BYU 163) in (L) lateral view and left with astragalus in (M) medial view. Right tibia (UW 24823) in (N) posterior view and proximal end of right fibula in (O) medial view. Right tibia (SMA 0006) in (O) anterior view and left(?) fibula in (P) medial view. (Q) Fibula in lateral view. Abbreviations: 4t – fourth trochanter; at – anterior trochanter; gt – greater trochanter; h – femoral head. Scale in cm.

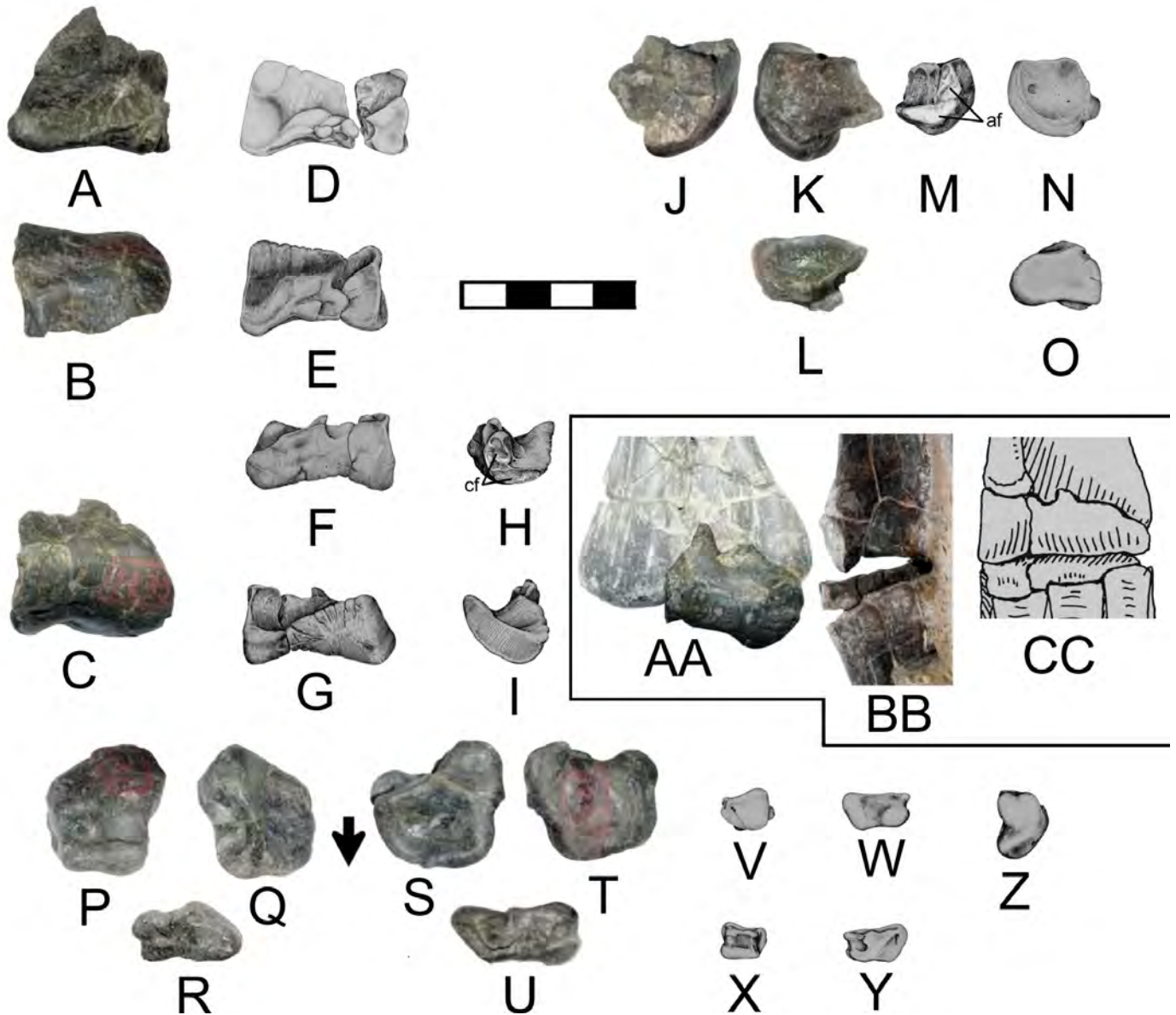


Figure 17. *Nanosaurus agilis* Marsh, 1877. Left astragalus (YPM VP 1882) in (A) dorsal, (B) ventral, and (C) anterior views. Left astragalus and calcaneum (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (D) dorsal, (E) articulated oblique anterior, (F) articulated anterior, (G) articulated posterior, (H) astragalus in lateral showing facet (cf) for calcaneum, and (I) astragalus in medial view. Left calcaneum (YPM VP 1882) in (J) medial, (K) lateral, and (L) proximal views. Left calcaneum (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (M) medial showing astragular facet (af), (N) lateral, and (O) proximal view. Lateral(?) distal tarsal (YPM VP 1882) in (P) proximal, (Q) ventral, and (R) anterior views; and medial(?) distal tarsal in (S) proximal, (T) ventral, and (U) anterior views; arrow is anterior. The medial(?) tarsal has a slight overlap with the lateral(?) tarsal (the question mark is that the medial and lateral designations may be switched). Distal medial(?) tarsal (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (V) dorsal?, (W) posterior?, (X) lateral?, (Y) anterior, and (Z) dorsal views. Right astragalus articulated with tibia (YPM VP 1882) in (AA) anterior view. Right astragalus and calcaneum (BYU 163) in (BB) anterior view. Right astragalus and calcaneum, with distal tarsals (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (CC) anterior view. The ascending process is either a pair of short spike-like structures (AA) and (CC), which may have had a cartilage wedge, or an oblique triangle (BB). Note that filling of the gap between the double process (AA, CC) would result in an oblique triangle (BB). Scale in cm.

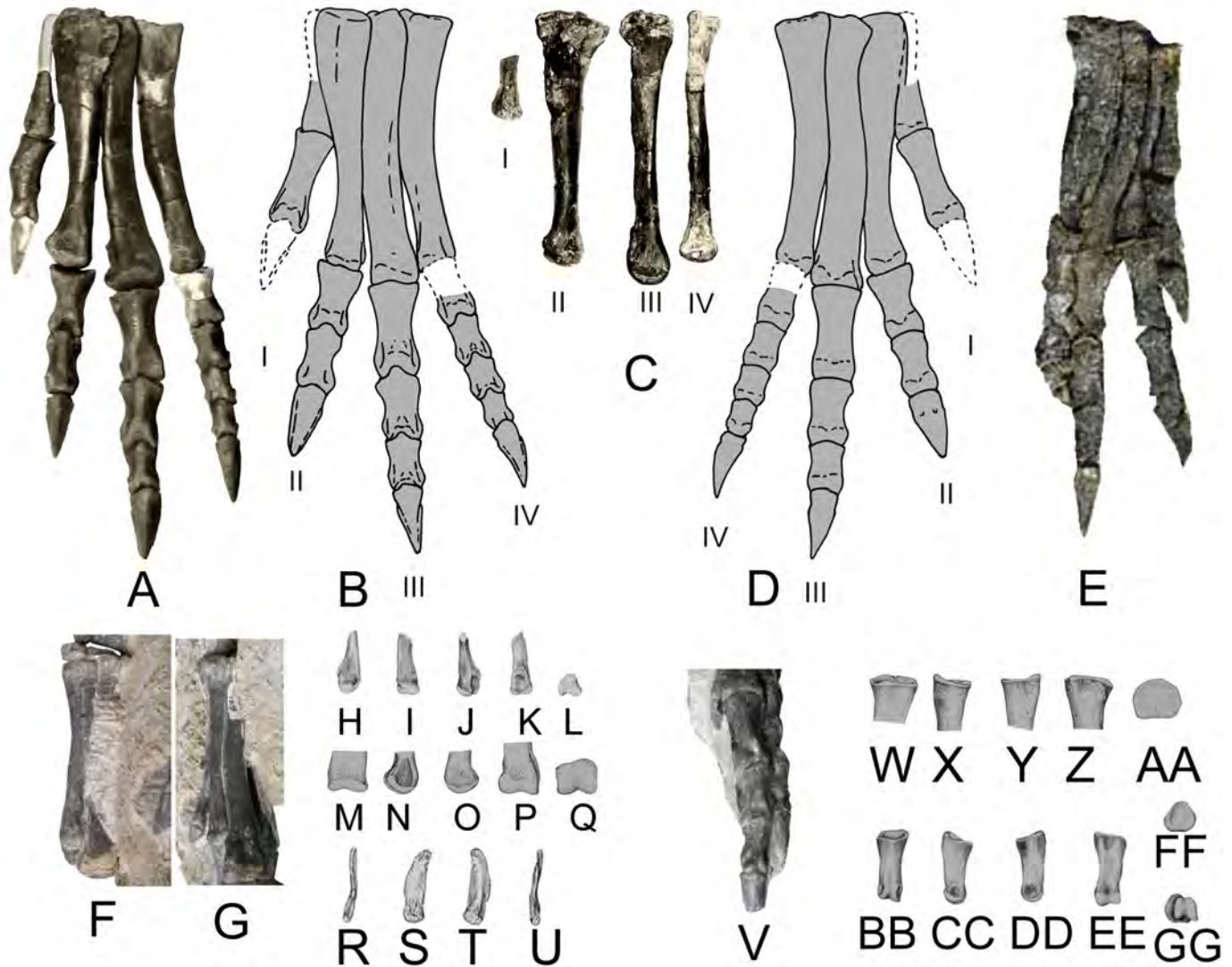


Figure 18. *Nanosaurus agilis* Marsh (1877). Nearly complete, gracile left pes (YPM VP 1822) in (A) anterior view, (B) sketch of anterior side, (C), metatarsals in medial view, and (D) sketch of posterior side. Although the first digit (I) is present, it is short and there were only three functional digits (II to IV); Boyd (2015) considers this foot the derived state in ornithischians. (E) Articulated left pes (SMA 0010) in posterior view. Right metatarsals (BYU 163) in (F) anterior view, and left metatarsals in (G) anterior view. Metatarsal I (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (H) anterior, (I) medial, (J) lateral, (K) posterior, and (L) distal views; distal end of metatarsal III in (M) anterior, (N) lateral, (O) medial, (P) posterior, and (Q) distal views; metatarsal V in (R) anterior, (S) lateral, (T) medial, and (U) posterior views. Articulated left pes phalanges (BYU 163) in (V) anterior view. Proximal end of phalanx I-1 (“*Drinker nisti*” courtesy of R.T. Bakker, Houston Museum of Natural History) in (W) anterior, (X) lateral, (Y) medial, (Z) posterior, and (AA) proximal views; phalanx II?/IV?-1 in (BB) anterior, (CC) lateral, (DD) medial, (EE) posterior, (FF) proximal, and (GG) distal views. Scales in cm.

a narrow midline-ridge and two to three fine longitudinal ridges on the enameled surface; a horizontal maxillary ramus of jugal below orbit slender as in *D. lettowvorbecki* (or *Dysalotosaurus lettowvorbecki*). Basal tuberae are a posteroventral sheet or wedge and there are no midline sulcus, as in

*D. lettowvorbecki*. Anterior cervical vertebrae are short and tall as in *D. lettowvorbecki*. Ilium long and low compared to most ornithopods, but less than *D. elderae*. The preacetabular process are gently curved, postacetabular process proportionally short and deep as compared to *D. elderae*.

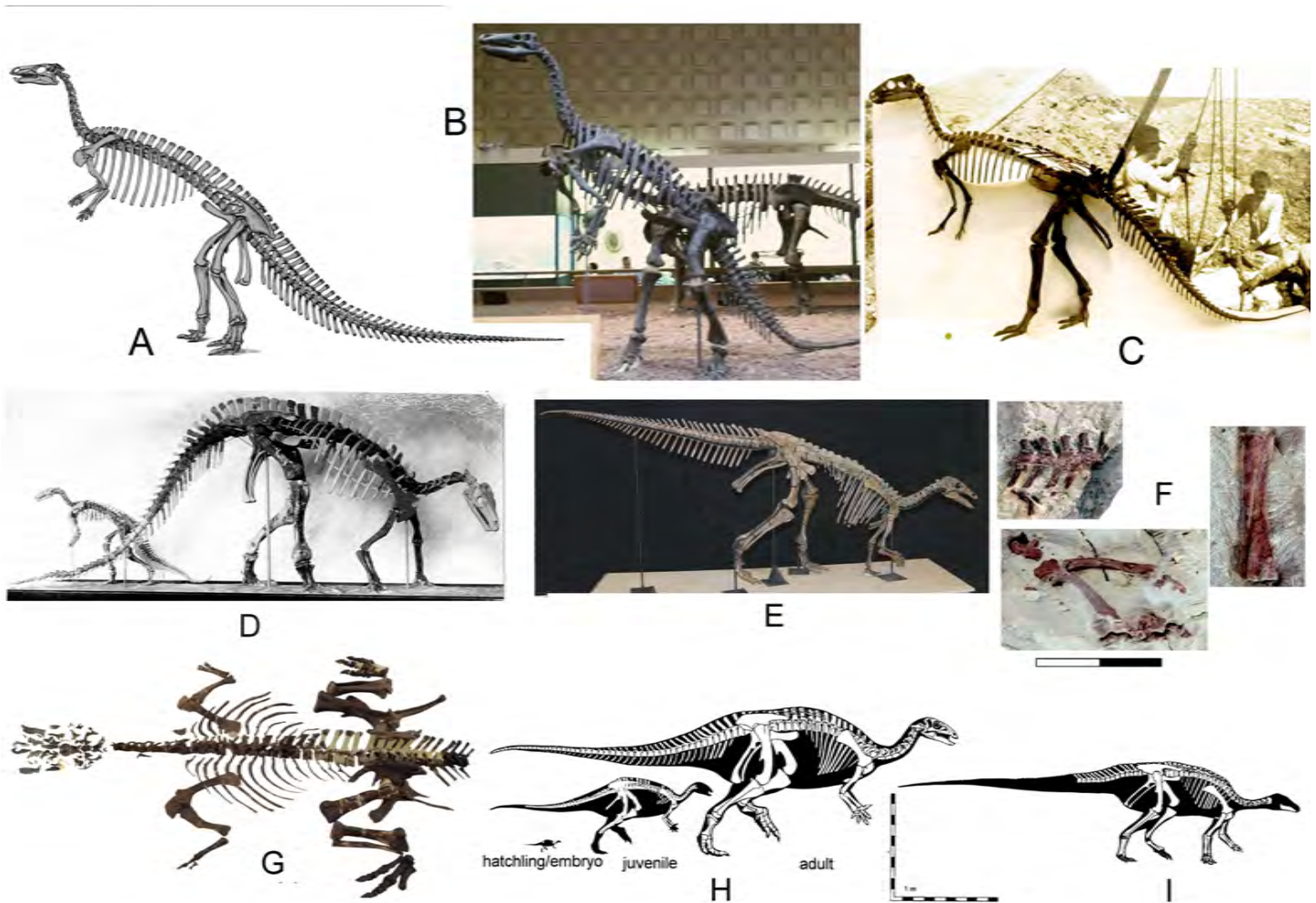


Figure 19. *Camptosaurus* Marsh, 1885. (A) Skeletal reconstruction of *C. dispar* (Marsh, 1879) presented by Marsh (1894a). (B) Skeletal mount of *C. dispar* (YPM VP 1880, holotype of *C. medius* Marsh, 1894b) at the Peabody Museum of Natural History made in 1937 by R.S. Lull pays homage to Marsh's restoration (A). Lull did reduce the number of presacral vertebrae following Gilmore (1912). (C) Skeletal mount of a young *C. dispar* (AMNH FARB 6120) from Bone Cabin Quarry, Wyoming. (D) The first mounted skeletons of *Camptosaurus dispar* were made by or under the direction of C.W. Gilmore of a juvenile and adult *C. dispar* from YPM Como Bluff Quarry 13 material. In making these mounts Gilmore (1912) was able to demonstrate that the presacral vertebral column did not have as many vertebrae as Marsh thought. In addition, Gilmore determined that all dorsal vertebrae bore ribs and therefore a mammalian lumbar region was not present (compare with B). (E) *Camptosaurus aphanoecetes* (CM 11337, holotype) as currently mounted. The specimen was originally described as *C. medius* by Gilmore (1925), then made the type of *Camptosaurus aphanoecetes* by Carpenter and Wilson (2008). It was subsequently made the type species of *Uteodon* by McDonald (2011) as *U. aphanoecetes*, but that taxon was shown by Carpenter and Lamanna (2015) to be a chimera of *Dryosaurus* and *Camptosaurus*. (F) The smallest known specimen of *Camptosaurus* is a hatchling (?) or late stage embryo described by Chure and others (1994). It was identified as *Camptosaurus* primarily on its coracoid shape. (G) Skeleton of a subadult *Camptosaurus dispar* excavated from Bone Cabin Quarry by the Western Paleontological Laboratories as it was displayed at *The Gigantic Dinosaur Expo 2006*, Makuhari Messe Convention Center in Chiba City, Japan. (H) Size comparison of taxa referred to *C. dispar* (courtesy of Greg Paul, independent paleoartist). (I) Size comparison of *C. aphanoecetes* to *C. dispar* (same scale as H). Scales in cm.



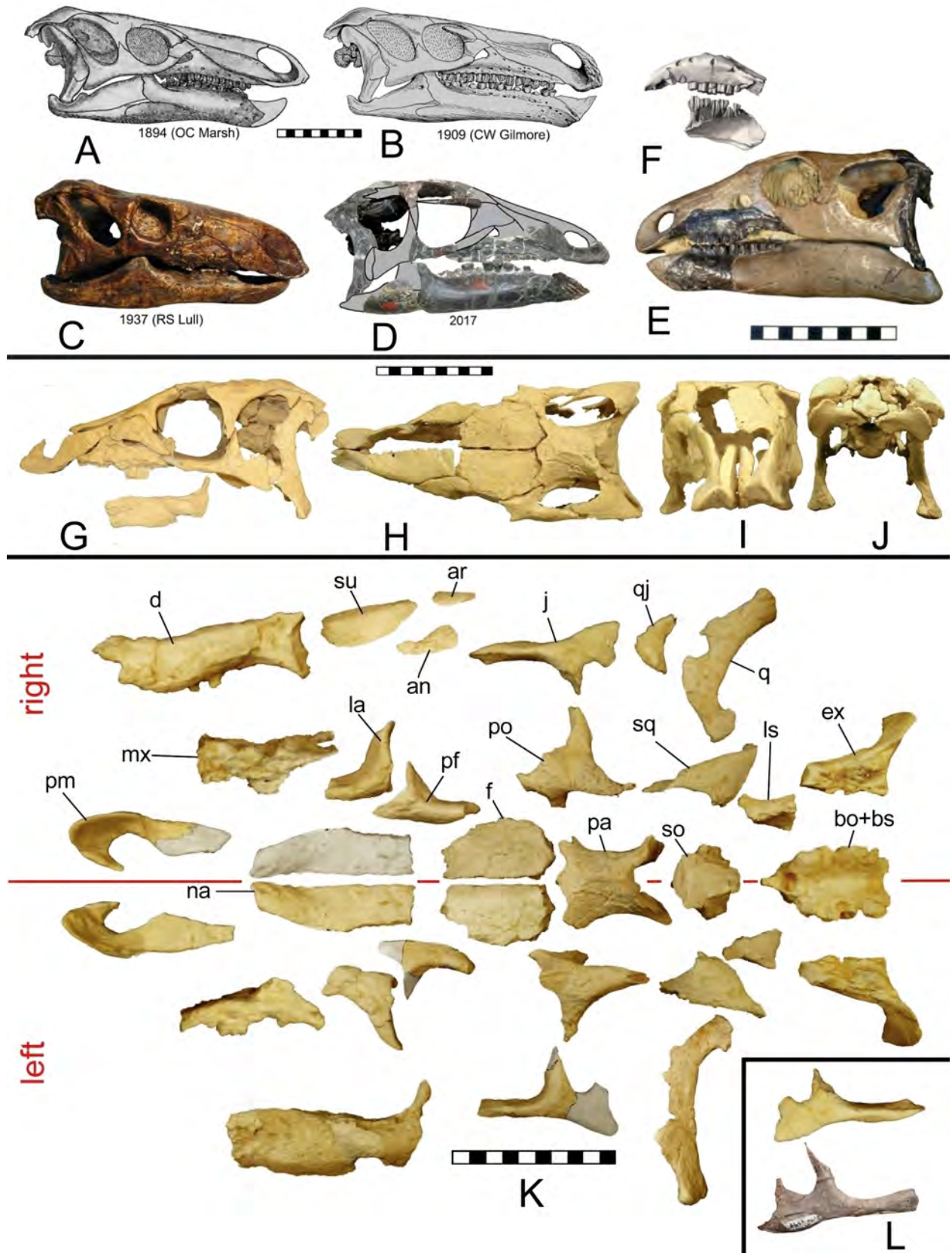


Figure 20. Caption is on the following page.

Figure 20 (figure is on the previous page). *Camptosaurus* Marsh, 1885. Comparison of the various reconstructions of the skull of *C. dispar* based on material from YPM Quarry 13, Como Bluff, Wyoming. (A) The earliest version was by O.C. Marsh (1894a; skeleton). (B) C.W. Gilmore reconstructed the skull in 1909, but the deep snout was based upon a skull now known to be from the Early Cretaceous (YPM VP 1887, *Theiophytalia kerri*, Brill and Carpenter, 2007). (C) R.S. Lull reconstructed the skull using plaster of Paris and the bones of YPM VP 1880 for the mounted skeleton at the Peabody Museum in 1937. Note the deep snout as influenced by B. (D) A recent digital reconstruction is based on YPM VP 1880, and YPM-PU 14553 prementary. Note that we conclude that the snout was low, as originally reconstructed by Marsh. See also discussion in Brill and Carpenter (2007). (E) Right maxilla and dentary AMNH FARB 6120 in medial view used to create the skull (E) for the mount in figure 19C. The most complete single skull (DMNH 50131, Bone Cabin Quarry) assembled from casts of isolated bones; in (G) left lateral, (H) dorsal, (I) anterior, and (J) posterior views. (K) Cast of disarticulated skull bones (DMNH 50131) also seen with skeleton in figures 19G and 19L, comparison of the jugal of *C. dispar* (top) with that of *C. aphanoecetes* (DINO 7144, bottom). Note the more curved ventral margin and deeper anterior (orbital) process. Abbreviations: an – angular; ar – articular; bo+bs – basioccipital + basisphenoid; d – dentary; ex – exoccipital; f – frontal; j – jugal; la – lacrymal; ls – laterosphenoid; mx – maxillary; na – nasal; pa – parietal; pf – prefrontal; pm – premaxillary; po – postorbital; q – quadrate; qj – quadratojugal; so – supraoccipital; sq – squamosal; su – surangular. Scales in cm.

### *Dryosaurus elderae* n.sp.

Figures 4, 27, 28Q to 28AA, 28FE, 29I, 29J, 30D,  
and 31B to 31J

*Dryosaurus altus* Gilmore 1925

*Dryosaurus altus* Galton, 1977

*Dryosaurus altus* Galton 1981

*Dryosaurus altus* Galton, 1983

*Dryosaurus altus* Galton, 1989

*Dryosaurus altus* Carpenter, 1994

*Dryosaurus altus* Galton, 2007

*Uteodon aphanoecetes* McDonald, 2011 (in part)

*Dryosaurus* cf. *C. altus* Carpenter and Lamanna, 2015

### Etymology

Latin genitive ending for Ann Schaffer Elder (1958–2009), in recognition of her considerable assistance to Carpenter in his studies at the Carnegie Quarry in Dinosaur National Monument, Utah (Carpenter, 2013).

### Holotype

CM 3392, a partial, articulated skeleton: skull and lower jaw, first six cervical vertebrae, thirteen dorsal vertebrae with proximal portions of ribs, sacrum, pelvis, right scapula, coracoid, and humerus, proximal third of right femur, proximal end of the right tibia, one complete metatarsal and distal portions of two others, articulated left hind foot (Gilmore, 1925). Bones also described by Galton (1981, 1983, 1989) and by Carpenter and Lamanna (2015).

### Holotype Locality

Douglass map coordinates A:E15, Carnegie Quarry, Dinosaur National Monument, Uintah County, Utah.

### Holotype Stratigraphic Position

Middle of the Brushy Basin Member, Morrison Formation.

### Paratype material

CM 11340, partial juvenile articulated skeleton with skull (Carpenter, 1994); CM 87688 braincase (used to establish *Uteodon aphanoecetes* by McDonald, 2011); DINO 4619 left ilium; DINO 1031 right scapula. All from the Carnegie Quarry, Dinosaur National Monument.

### Diagnosis

Teeth with broad midline ridge and up to three fine longitudinal ridges on the enameled surface; horizontal maxillary ramus of jugal below orbit deep, compared with slender ramus in *D. altus* and *D. lettowvorbecki* (or *Dysalotosaurus lettowvorbecki*); basal tuberae are massive projections separated by a midline sulcus, versus posteroventral sheet or wedge and no sulcus in *D. altus* and *D. lettowvorbecki*; anterior cervical vertebrae low compared to length, comparably shorter and taller in *D. altus* and *D. lettowvorbecki*; ilium long and low, especially the postacetabular

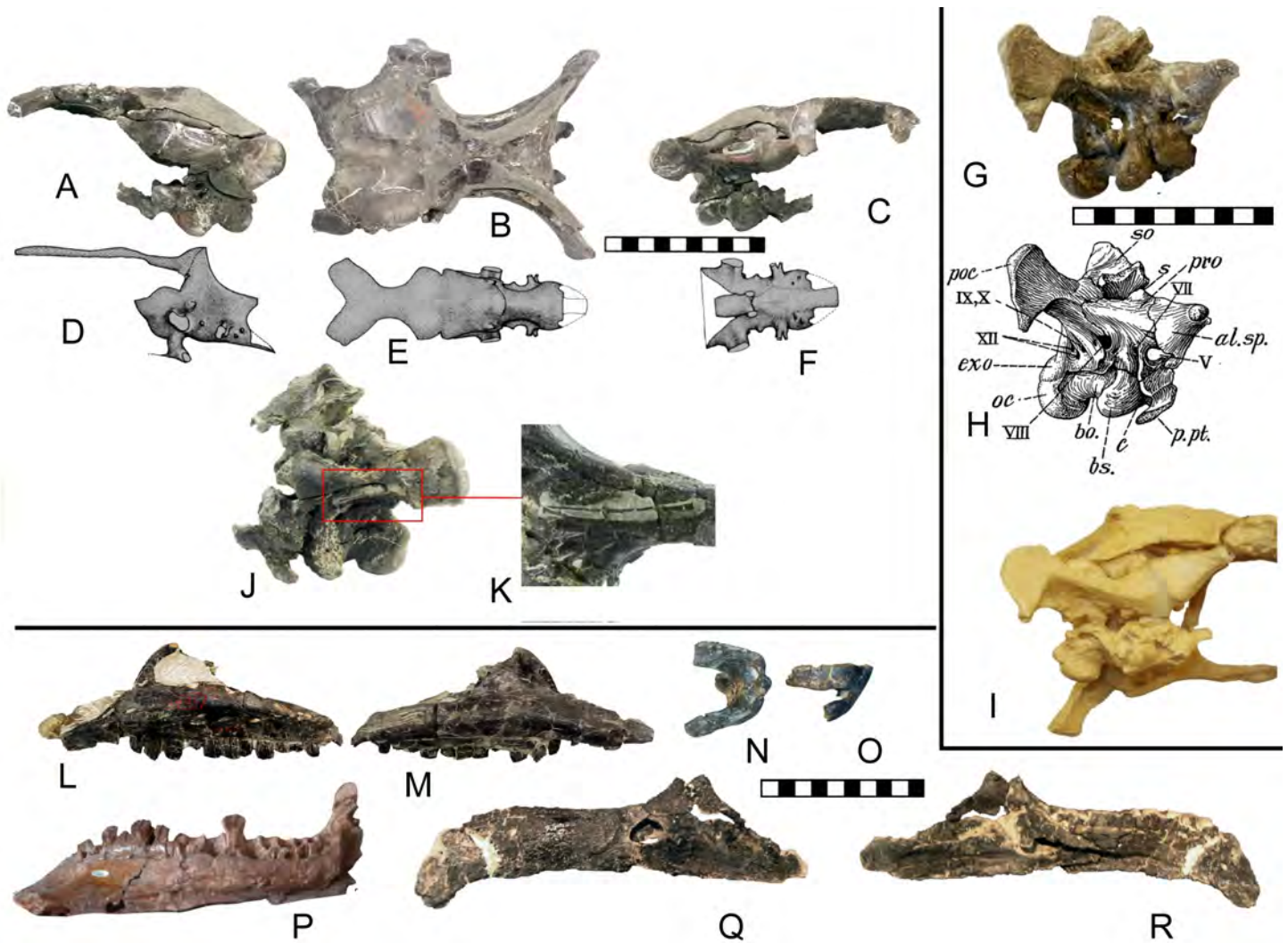


Figure 21. *Camptosaurus* Marsh, 1885. Brainscase of *C. dispar* (YPM VP 1880) in (A) left lateral, (B) dorsal, and (C) right lateral views. Drawings of endocast made from YPM VP 1880 in (D) left lateral, (E) dorsal, and (F) ventral views. Brainscase (USNM V 5473, Quarry 13) in (G) right lateral view and (H) interpretive drawing by Gilmore (1909, figure 5). (I) Brainscase assembled from casts (DMNH 50131) shown in figure 20K. Brainscase (YPM VP 1856A) showing stapes (J) and (K) in close-up. (J to K not to scale). Left maxilla (YPM VP 1886) in (L) lateral and (M) medial views. Predentary (YPM-PU 14553, Cleveland-Lloyd Dinosaur Quarry) in (N) dorsal and (O) right lateral view. This predentary was used in the digital reconstruction figure 20D. *C. aphanoecetes* (DINO 0556, Dinosaur National Monument) right dentary in (P) medial view. The most complete known mandible of *C. dispar* in (Q) left lateral and (R) medial view, from Bone Cabin Quarry, Western Paleontology Lab. Scales in cm.

process, more similar to *D. lettowvorbecki* than *D. altus*.

Earl Douglass wrote in his notebook about the specimen: "No. 26. ~~Laosaurus~~ [sic] Dryosaurus About opposite (south of (A:E15). Skull neck and considerable part of skeleton. In top of gray compact- clayey sandstone near and perhaps partly in red stratum above the harder sandstones in which the most of the bones of the

C[arnegie] M[useum] Dinosaur Quarry were found. No other good specimens were found in this level. At about 12 ft. higher level than No.1[*Apatosaurus lousae* type]. Found in excavating cut- south of principal bone layer. The bones were in heavy compact, greenish rock which had been cracked into irregular blocks by blasts for excavating cut at each end of the specimen. Found by

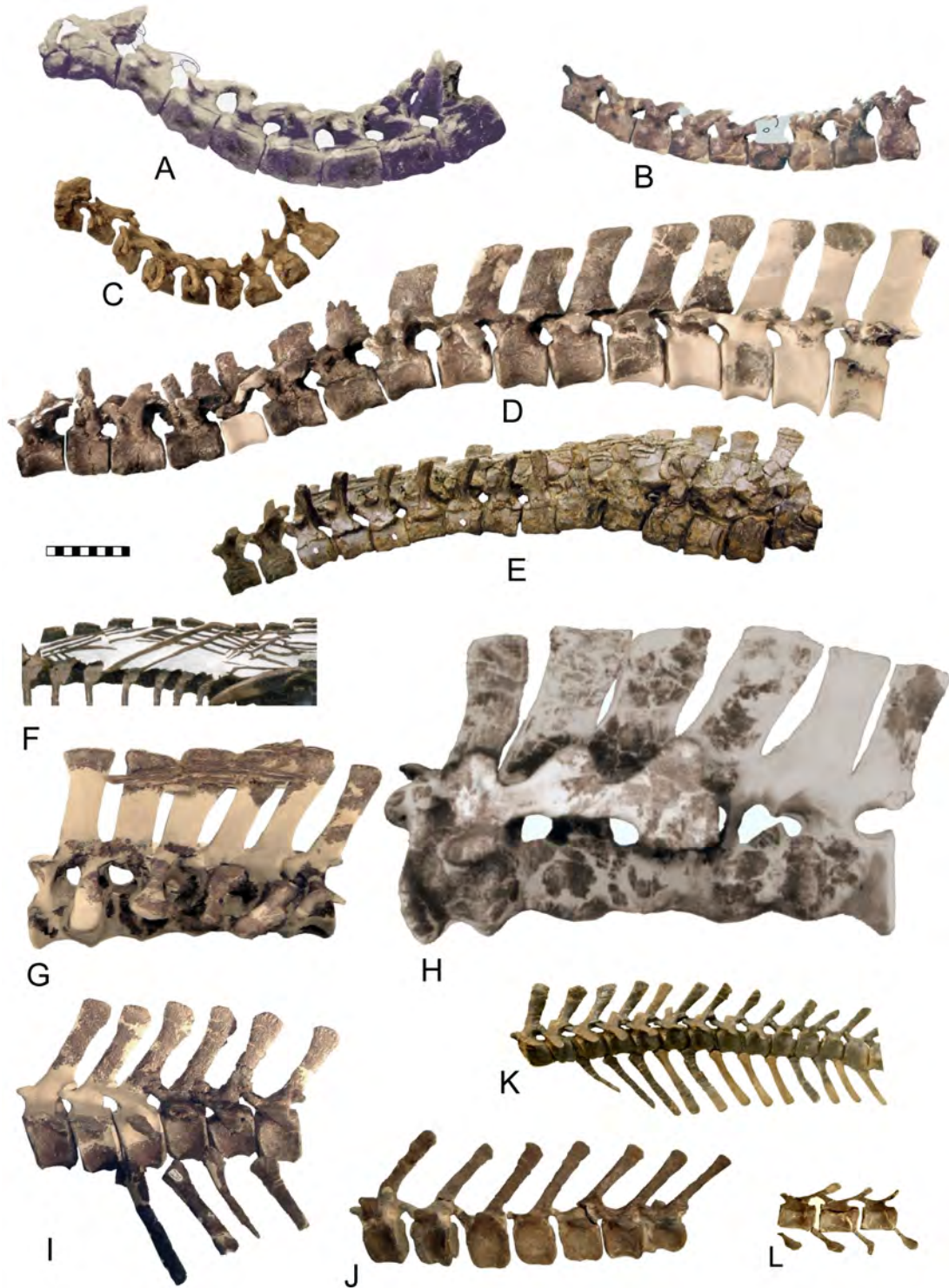


Figure 22. *Camptosaurus* Marsh, 1885. Vertebrae in left lateral view. Cervical vertebrae of (A) *C. dispar* (USNM V 5473), (B) *C. dispar* juvenile (USNM V 2210), and (C) *C. aphanoecetes* (CM 11337). Dorsal vertebrae of (D) *C. dispar* (same specimen as figure 19G) and (E) *C. aphanoecetes* with ossified tendons (CM 11337). (F) *C. dispar* (AMNH FARB 6120) posterior dorsals with ossified tendons. Sacra of (G) *C. dispar* (same specimen as figure 19G) and (H) *C. cf. dispar* (SMM P84.15.5). Anterior caudal vertebrae of (I) *C. dispar* (same specimen as figure 19G) and (J) *C. aphanoecetes* (CM 11337). (K) Mid-caudal and (L) distal caudal vertebrae of *C. dispar* (NAMAL; Bone Cabin Quarry, Wyoming). Scale in cm.

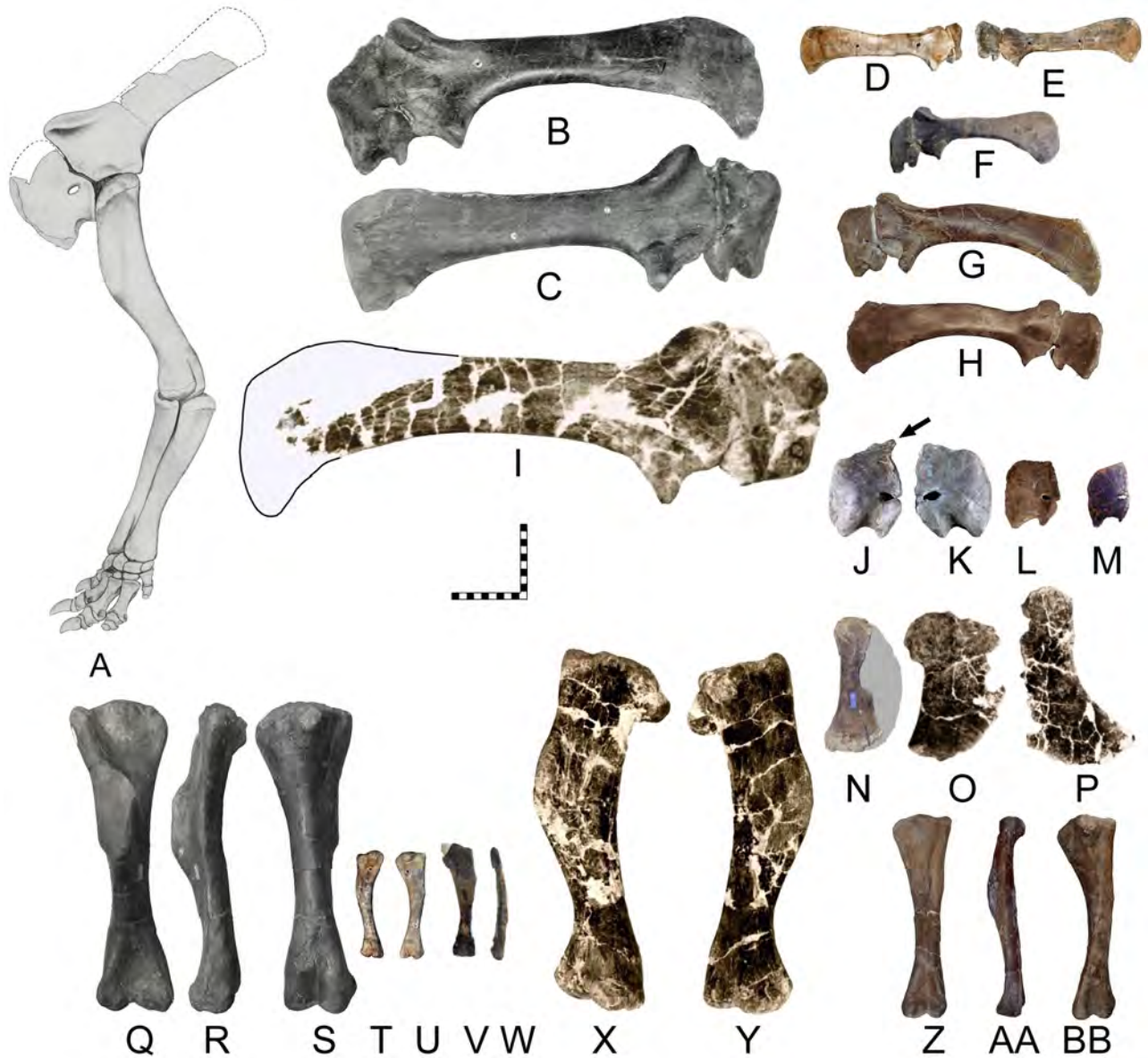


Figure 23. *Camptosaurus* Marsh, 1885. (A) Drawing of the left forelimb and girdle in lateral view of *C. dispar* made under the direction of O.C. Marsh, based primarily on YPM VP 1877 (Quarry 13); not to scale with other bones. A later version increased the length of the scapular blade based on specimens received subsequently (e.g., Marsh, 1894b, plate 5, figure 2). Scapula-coracoids of *C. dispar* (USNM V 4282, Quarry 13), (B) left, (C) right in lateral views; right scapula-coracoid of *C. dispar* juvenile (USNM V 2210, Quarry 13) in (D) lateral, and (E) medial views. (F) Left scapula and coracoid (AMNH FARB 6120) in lateral view. Left scapula-coracoid of *C. aphanoecetes* (CM 11337) in (G) lateral and (H) medial views. Scapula-coracoid of a very large *C. cf. dispar* (SMM P84.15.5) in (I) right lateral view. Coracoids showing the characteristic square shape of *Camptosaurus*: *C. dispar* (USNM V 4282) (J) left with pathological spur (arrow) and (K) right normal, in lateral views; (L) *C. aphanoecetes* (CM 11337) left in lateral view, and *C. dispar* (AMNH FARB 6120) (M) in lateral view. Sternal plates of *C. dispar* (USNM V 5473, Quarry 13) (N) previously described by Dodson and Madsen (1981), and *C. cf. dispar* (SMM P84.15.5) (O) pathological left and (P) partial right that preserves length. Right humerus of *C. dispar* (USNM V 4282, Quarry 13), in (Q) anterior, (R) medial and (S) posterior views; juvenile right humerus (USNM V 2210) in (T) anterior and (U) posterior views; another juvenile left humerus (AMNH FARB 6120) in (V) anterior and (W) lateral (crushed) views; large individual *C. cf. dispar* (SMM P84.15.5) right humerus in (X) anterior and (Y) posterior views. *C. aphanoecetes* (CM 11337) left humerus in (Z) anterior, (AA) lateral, and (BB) posterior views.

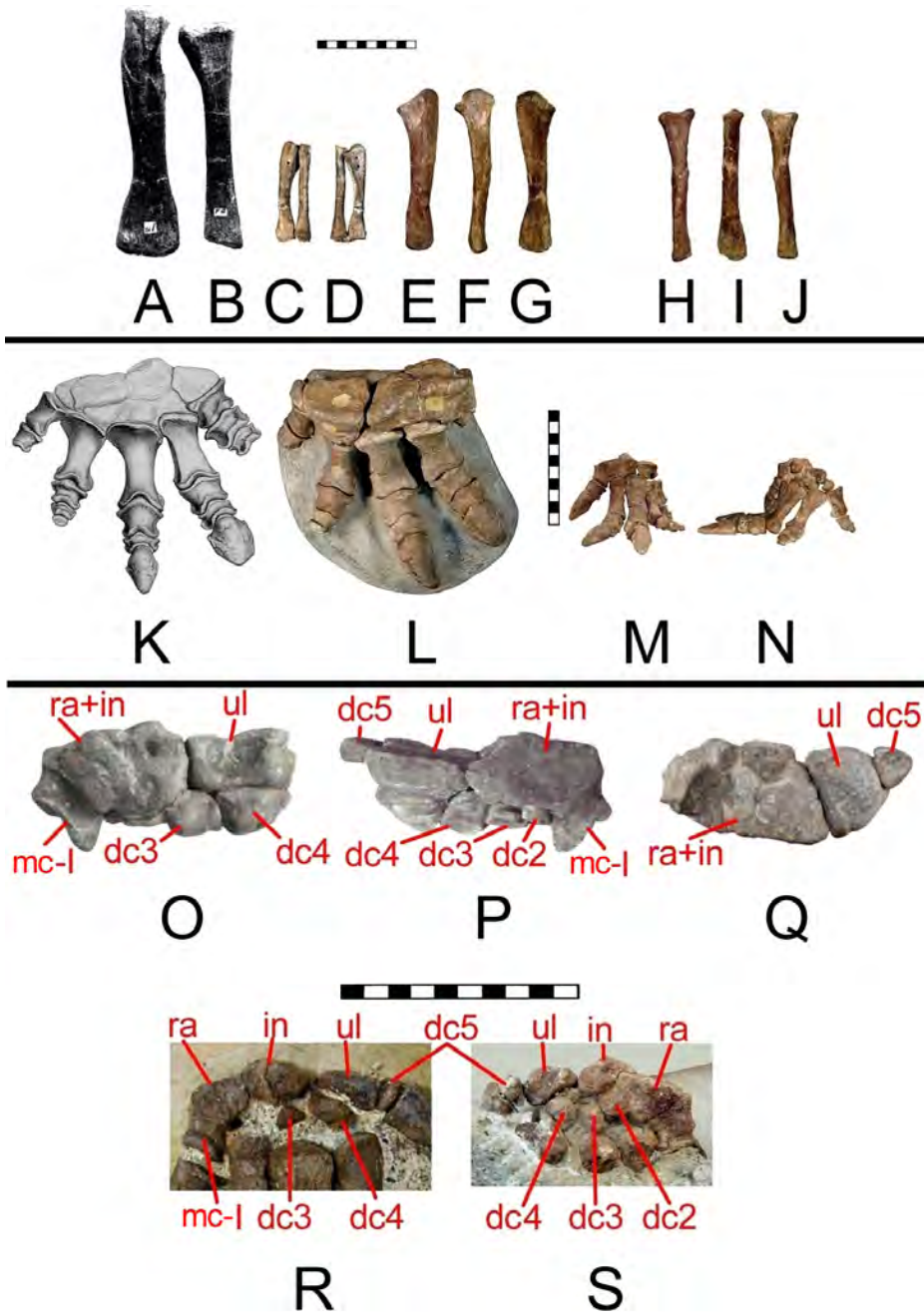


Figure 24. *Camptosaurus* Marsh, 1885. *C. dispar* (USNM V 4282) right (A) ulna and (B) radius in anterior view. Juvenile (USNM V 2210) right ulna and radius in (C) lateral and (D) medial views. *C. aphanoecetes* (CM 11337) left ulna in (E) lateral, (F) anterior, and (G) medial views, and left radius in (H) lateral, (I) anterior, and (J) medial views. (K) Unpublished drawing of *C. dispar* right manus (YPM VP 1877) made under the direction of O.C. Marsh compared with (L) an actual specimen (USNM V 4277). Left manus of *C. aphanoecetes* (CM 11337) in (M) anterior and (N) lateral views. Details of the carpals of *C. dispar* (USNM V 4282) in (O) anterior, (P) posterior, and (Q) dorsal (proximal) views. Details of the carpals of *C. aphanoecetes* (CM 11337) before preparation in (R) anterior and (S) posterior views. Abbreviations: dc2 to dc5 – distal carpals 2 to 5; in – intermedium; mc-1 – metacarpal; ra – radiale; ul – ulnare. Scales in cm.

Joe Ainge and Clarence Neilsen. March 7, 1910. The greater portion of the skeleton was taken up in a heavy block (about 5400 lbs. with crate). The removal of the block broke through the cervicals or near them. A long time afterward, I think the next year, I set a man to do a little further excavating here. I soon found he had reached the skull. When I went to take it out a small portion of a jaw was not in place. The dirt all around was carefully looked over and the dump searched repeatedly but no trace of jaw with two of three teeth was found” (figures 27C to 27F). The holotype specimen went

on display around 1940 as a slab or panel mount and was remounted freestanding in 2006 (figures 27A and 27B).

The species is known from the holotype subadult skeleton with skull and a partial juvenile skeleton with skull (figure 27AA). These skulls show that ontogenetic changes most prominently affect the orbital and posterior portions, and other, less extreme changes in the position of the fenestra between the premaxilla and maxilla, and size and position of the antorbital fenestra due to elongation of the facial region (Carpenter, 1994).



Figure 25. *Camptosaurus* Marsh, 1885. (A) Drawing of the right pelvis of *C. dispar* made under direction of O.C. Marsh based on YPM VP 1878. (B) Actual specimen as illustrated by Gilmore (1909, plate 16). (C) Left ilium of *C. dispar* (USNM V 5473, Quarry 13) in lateral view. Sacrum and ilia of *C. dispar* (USNM V 2210, Quarry 13) in (D) dorsal and (E) right lateral views. (F) Pelvis of *C. dispar* (AMNH FARB 6120) in left lateral view; missing parts restored. Sacrum and ilia of *C. aphanoecetes* (CM 11337) in (G) dorsal and (H) right lateral views. (I) Left ilium of *C. aphanoecetes* (DINO 4225) in (left) lateral view; note the abrupt curve characteristic of the species. Pelvis of a large individual *C. cf. dispar* (SMM P84.15.5) in (J) left lateral view. Pubes of *C. dispar*: (K) left (YPM VP 1878), (L) juvenile right (USNM V 2210), and (M) *C. aphanoecetes* (CM 11337) right in lateral view. Ischia of *C. dispar*: (N) left (USNM V 5473), (O) left (USNM V 4697), (P) left (USNM V 5818), (Q) right juvenile (USNM V 2210), and (R) *C. aphanoecetes* (CM 11337) right in lateral view. The ischium of *C. dispar* curves with maturity (compare Q and O); the condition in *C. aphanoecetes* is uncertain because no very large (old) individuals are known.

### Unnamed Dryomorpha?

Figure 32

*Dryosaurus altus* Shepherd and others, 1977

*Dryosaurus altus* Galton, 1981

Among the material studied by us, is a specimen from the Elk Mountain region of north-central Wy-

oming that consists of three dorsals and four sacral vertebrae articulated to 28 caudal vertebrae, right ilium, femur, tibia, fibula, and metatarsals (CM 1949). It was referred to *Dryosaurus altus* without explanation by Shepherd and others (1977) and by Galton (1981). However, our reanalysis makes us question the original referrals and suggests the possibility of a previously un-

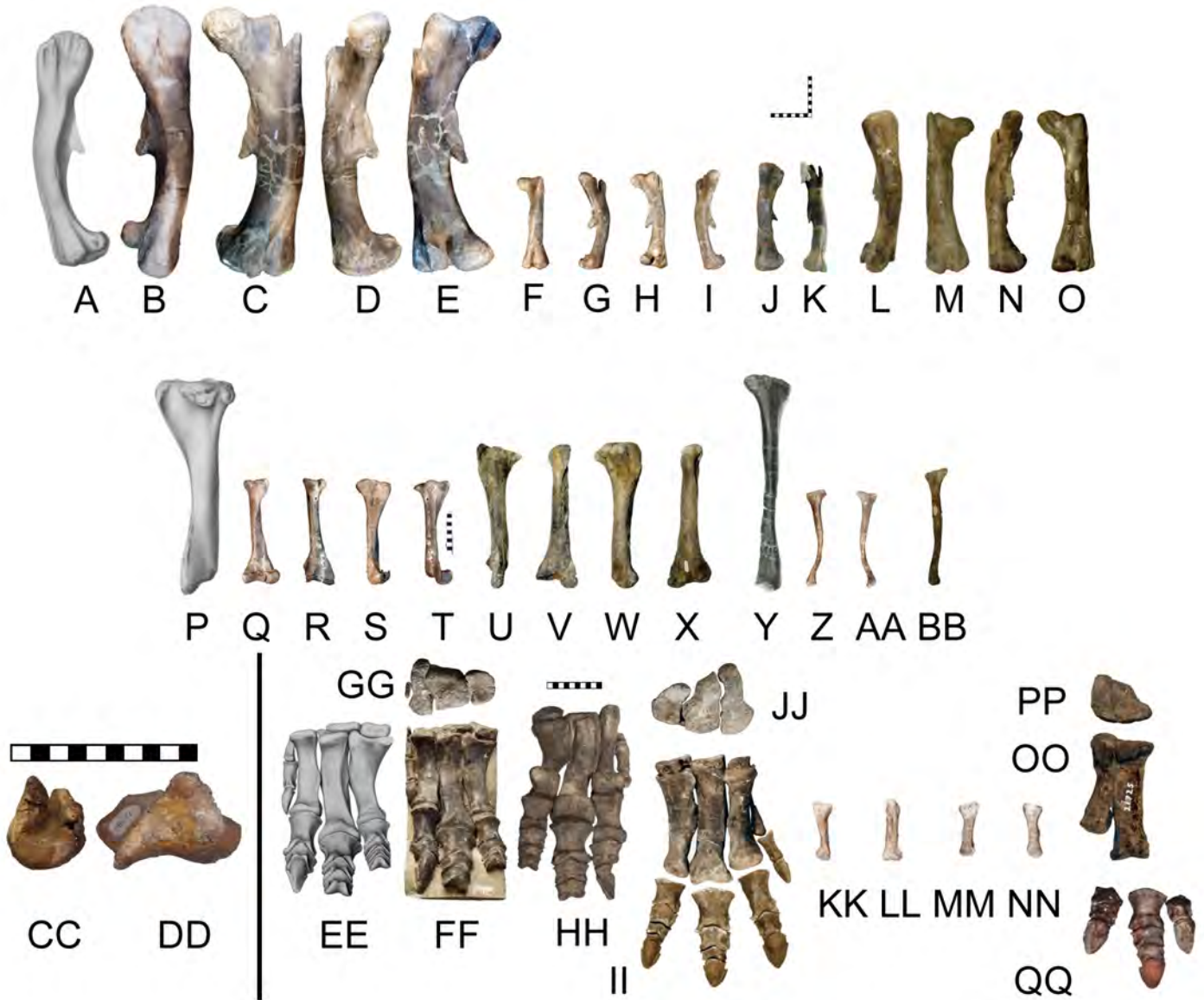


Figure 26. *Camptosaurus* Marsh, 1885. Hind limb material (A) drawing of *C. dispar* left femur (YPM VP 1877) lateral view made under the direction of Marsh and right femur (USNM V 5818, Quarry 13) in (B) lateral, (C) anterior, (D) medial, and (E) posterior views. Juvenile (USNM V 2210) left femur in (F) anterior, (G) medial; right femur (H) posterior and (I) medial views. Right femur (AMNH FARB 6120) in (J) lateral and (K) anterior views. Right femur of *C. aphanoecetes* (CM 15780) in (L) lateral, (M) anterior, (N) medial, and (O) posterior views. Left tibia (YPM VP 1887) drawing in (P) lateral view of *C. dispar* made under the direction of Marsh. Juvenile (USNM V 2210) tibia in (Q) anterior, (R) posterior (S) medial, and (T) lateral views. (U to X) Left tibia of *C. aphanoecetes* (CM 15780) in (U) lateral, (V) anterior, (W) medial, and (X) posterior views. (Y) Left fibula of *C. dispar* (YPM V 1877) in lateral view, juvenile (USNM V 2210) fibula in (Z) lateral and (AA) medial views. Right fibula of *C. aphanoecetes* (CM 11337) in lateral view (BB). Left astragalus of *C. aphanoecetes* (CM 11337) in (CC) lateral and (DD) anterior views. Pes: (EE) drawing of *C. dispar* left pes made under the direction of Marsh and original (YPM 1877) in (FF) anterior, (GG) proximal showing two distal tarsals, and (HH) posterior views. Right pes of *C. dispar* (USNM V 4277) in (II) anterior and (JJ) proximal views. Metatarsal III of *C. dispar* (USNM V 2210) in (KK) lateral, (LL) anterior, (MM) medial, and (NN) posterior views. Left metatarsals III and IV of *C. aphanoecetes* (CM 21725) in (OO) anterior and (PP) proximal views. (QQ) Right phalanges of *Camptosaurus* sp. (MWC 2) previously described as *Iguanodon* (Averett, 1991). Scales in cm.



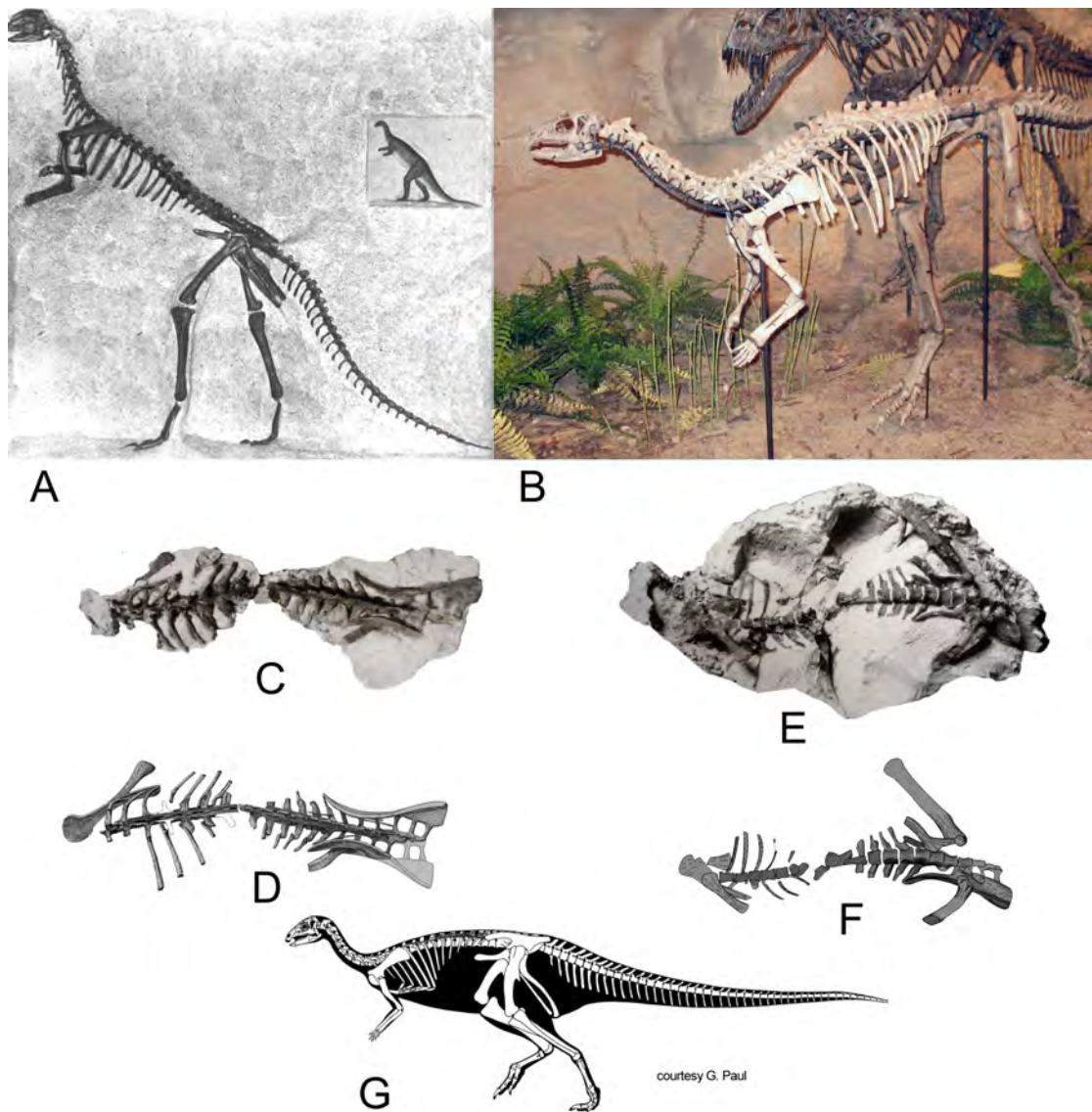


Figure 27. *Dryosaurus* Marsh, 1878. *Dryosaurus elderae* holotype (CM 3392) skeleton (A) as originally mounted and (B) current mount. Skeleton (CM 3392) during preparation in (C) dorsal view and interpretive drawing (D) as presented by Gilmore (1925). (E) Ventral side and (F) interpretative drawing. The skull and anterior cervicals were recovered in a separate, third block the following year. (G) Skeletal reconstruction by Greg Paul (independent paleoartist).

recognized large-sized ornithopod in the northern part of the Morrison depositional basin. Horner and others (2009) utilized the femur as that of *Dryosaurus altus* in their long bone histological study of “hypsilophodontids.” This led them to erroneous conclusions regarding growth in *Dryosaurus*.

The specimen is unusual in the combination of a *Camptosaurus dispar*-like ilium (figure 32C to 32D) with a tibia longer than the femur (figures 32F and 32G vs. 32H). Despite the apparent incompatibility of the

ilium with the femur and tibia (*Camptosaurus* tibia is shorter than the femur), all of the material was found associated and the caudals articulated. The material was found with *Diplodocus* hind limb material (CM 2098 and 2099). The locality data associated with the specimens is “Elk Mountains near Brown’s Ranch,” Johnson County, Wyoming. There is an Elk Mountain in Johnson County, but no “Elk Mountains” The Elk Mountain Anticline is northwest of Kaycee, Wyoming, and has exposures of the Morrison Formation along a hogback

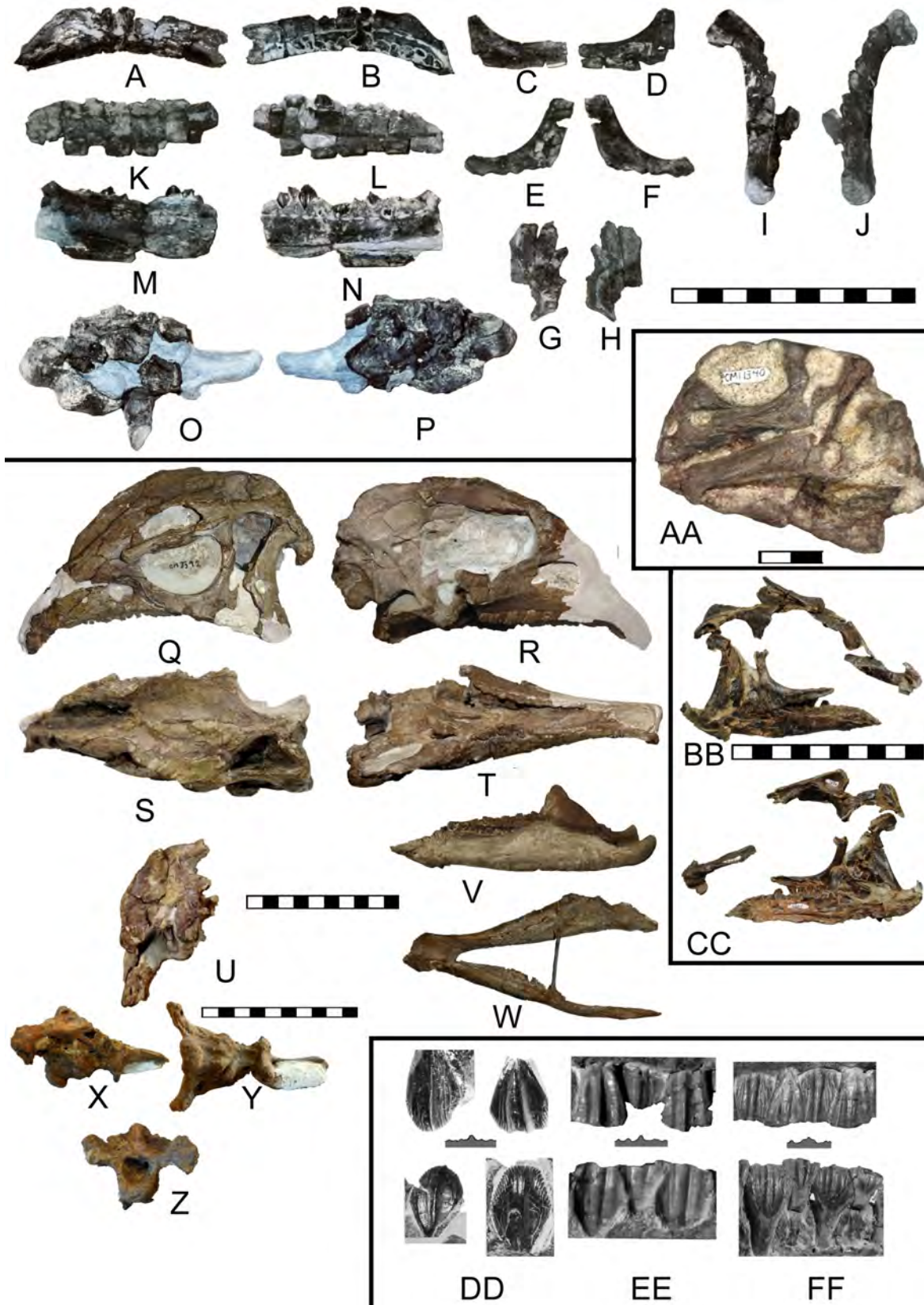


Figure 28. Caption is on the following page.

Figure 28 (figure is on the previous page). *Dryosaurus* Marsh, 1894b. The holotype, YPM 1876, of *Laosaurus altus* Marsh (1878) as *Dryosaurus altus* (Marsh, 1878), consists of a partial skeleton from Quarry 5 at Como Bluff, Wyoming. Cranial parts include left maxilla in (A) dorsal and (B) ventral views, right jugal in (C) lateral and (D) medial views, left jugal in (E) lateral and (F) medial views, right frontal in (G) dorsal and (H) ventral views, right quadrate in (I) lateral and (J) medial views, left dentary in (K) lateral and (L) medial view, right dentary in (M) lateral and (N) medial views, and braincase with plaster restoration of a generic parasphenoid in (O) right lateral and (P) left lateral views. *Dryosaurus elderae* holotype skull (CM 3392) in (Q) left lateral, (R) right lateral with the postorbital, squamosal, quadrate, and quadratojugal removed to expose the lateral wall of the braincase, (S) dorsal, (T) ventral, and (U) posterior views. Mandible in (V) left lateral and (W) dorsal views. Note the depressed nasals forming a trough as previously noted by Brill and Carpenter (2007) in other ornithopods. *D. elderae* braincase (CM 87688) in (X) right lateral, (Y) ventral, and (Z) posterior views. This braincase was used to establish *Uteodon aphanoecetes* by McDonald (2011). (AA) Juvenile skull of *D. elderae* (CM 11340) in left lateral view. Partial juvenile skull of *Dryosaurus altus* (DMNH 9001) in (BB) right lateral (external) and (CC) medial (internal) views. Note the slenderness of the suborbital ramus as compared with the juvenile (AA) and older *D. elderae* (Q). This same slenderness is seen in C to F, the holotype, YPM V 1876. Comparison of *Dryosaurus* teeth: top row are maxillary in labial view, bottom row are dentary in lingual view, and cross section of the maxillary crown (silhouettes) showing primary and secondary ridges: (DD) *D. altus* (YPM V 1876), (EE) *D. lettowvorbecki* (modified from Galton, 1983), and (FF) *D. elderae*. Scales in cm. (DD) to (FF) not to scale.

about 2.4 km east. A 1913 landowner map of Johnson County (University of Wyoming Digital Collections) does show a Brock Ranch east of Elk Mountain and would be adjacent to the Morrison Formation. If these assumptions are correct, then CM 1949 and associated *Diplodocus* most likely come from somewhere between Pass Creek on the south and Alkali Draw on the north.

## CONCLUSIONS

We presented the first photodocumentation of the bipedal ornithischians from the 6 million year interval of the Morrison Formation. Six species and four genera are recognized and make about 15% of the dinosaur specimens found (data in Foster, 2003). The stratigraphic and geographic distribution patterns of these taxa do not show clear trends. For example, the two most common ornithopods, *Nanosaurus agilis* and *Camptosaurus dispar*, are stratigraphically long ranging and geographically wide spread. In contrast, three taxa are only known from two localities: *Fruitadens haagarorum* is only known from the Fruita Paleontological Area, Colorado, and *Camptosaurus aphanoecetes* and *Dryosaurus elderae* are only known from the Carnegie Quarry, Utah. *Dryosaurus altus* is not very common, but is wide spread; its stratigraphic range is uncertain.

## ACKNOWLEDGMENTS

We thank John Foster, Kelli Trujillo, Cary Woodruff, and Octávio Mateus for inviting us to participate in this Morrison symposium collection of papers. Over the years, we have been greatly helped by numerous individuals at various institutions: Brigham Young University Museum of Paleontology (Provo, Utah): Jim Jensen, Wade Miller, and Ken Stadtman. Carnegie Museum of Natural History (Pittsburgh, Pennsylvania): David Berman, Mary Dawson, Amy Henrici, Matt Lamanna, and Yvonne Wilson. Denver Museum of Nature and Science (Denver, Colorado): Logan Ivy. Dinosaur National Monument (Jensen, Utah; Dinosaur, Colorado): Dan Chure and Ann Elder. National Museum of Natural History (Washington, D.C.): Mike Brett-Surman, Nick Hotton, and Robert Purdy. Yale Peabody Museum of Natural History (New Haven, Connecticut): Dan Brinkman, the late John Ostrom and Mary Ann Turner. Saurier Museum (Aathal, Switzerland): Hans Jacob Siber. Science Museum of Minnesota (Saint Paul, Minnesota): Bruce Erickson. Natural History Museum of Utah (Salt Lake City, Utah): Jim Madsen, Mike Getty, and Randy Irmis. Western Paleontological Laboratory (Lehi, Utah): Cliff Miles. Wyoming Dinosaur Center (Thermopolis, Wyoming): William Wahl and Burkhard Pohl. We thank Greg Paul (Baltimore, Maryland) for the use of his skeletal reconstructions, for which he re-

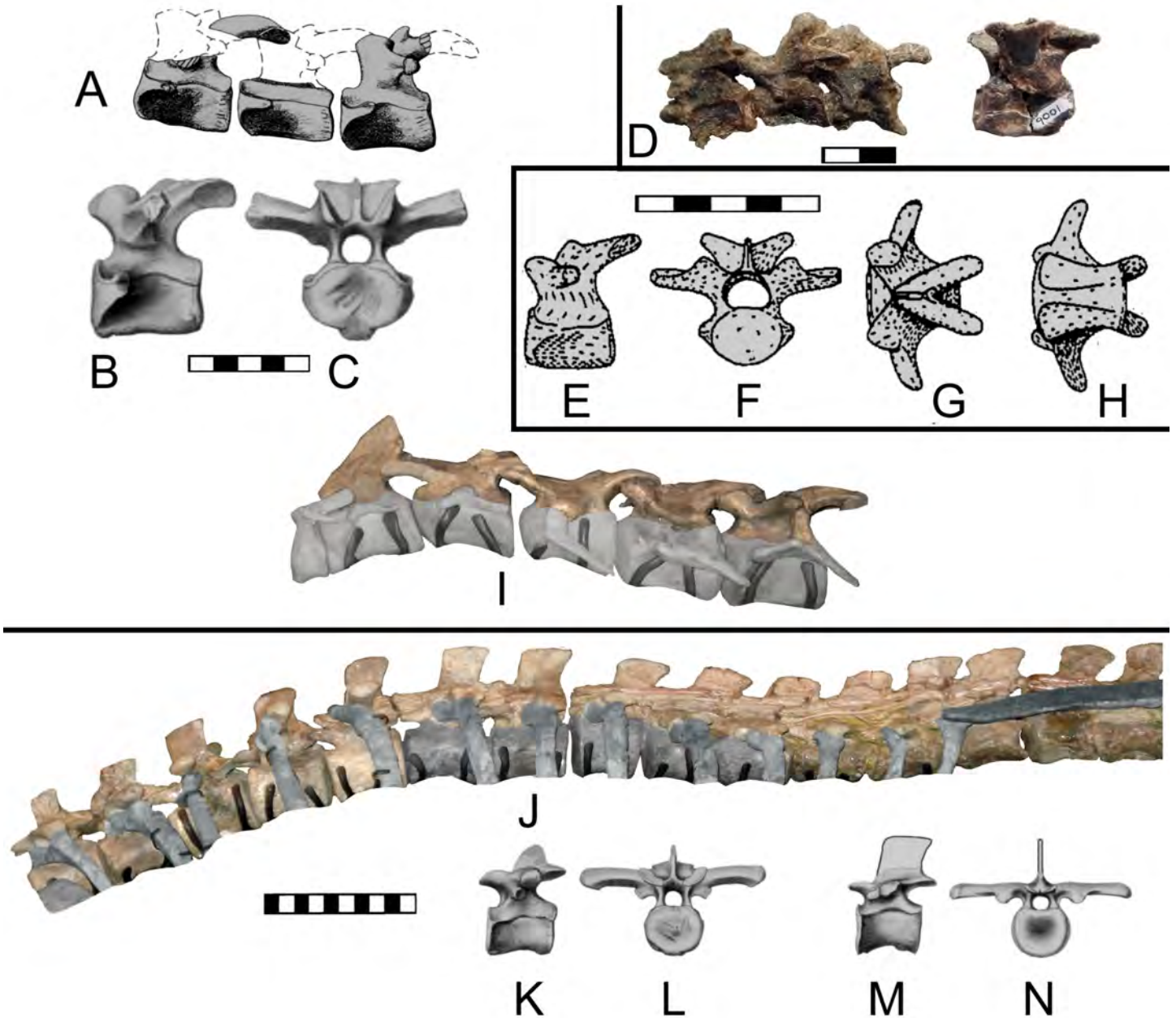


Figure 29. *Dryosaurus* Marsh, 1894b. *D. altus* cervicals: (A) (YPM V 1876, holotype) cervicals 4 to 6. Drawings made under the direction of O.C. Marsh of *D. altus* (YPM 1876, holotype) vertebrae: cervical 9 in (B) left lateral and (C) anterior views. (D) *D. altus* (DMNH 1006) cervicals 2 to 5 and 9? *D. altus* (AMNH FARB 834) cervical 9 in (E) lateral, (F) anterior, (G) dorsal, and (H) ventral views (modified from Shepherd and others, 1977). *D. elderae* cervicals 2 to 6 (I), missing centra grayed out. The low, long neural arches of *D. elderae* indicate that the cervicals were lower and had proportionally longer centra as compared to *D. altus*; this is noticeable in comparing cervical 6 in both specimens. In addition, the short neural spines disappear at cervical 5 in *D. elderae*, but are still well developed in cervical 6 in *D. altus*. *D. elderae* dorsals 3 to 15 in left lateral view (missing centra grayed out). *D. altus* (YPM VP 1876) anterior dorsal in (K) left lateral, (L) anterior views; posterior dorsal in (M) left lateral and (N) anterior views. As with the cervicals, the dorsal neural arches are proportionally longer relative to height in *D. elderae* than in *D. altus*. Proportionally, the vertebrae of *D. letterovvobecki* are more similar to those of *D. altus*, rather than to those of *D. elderae*. Scales in cm.

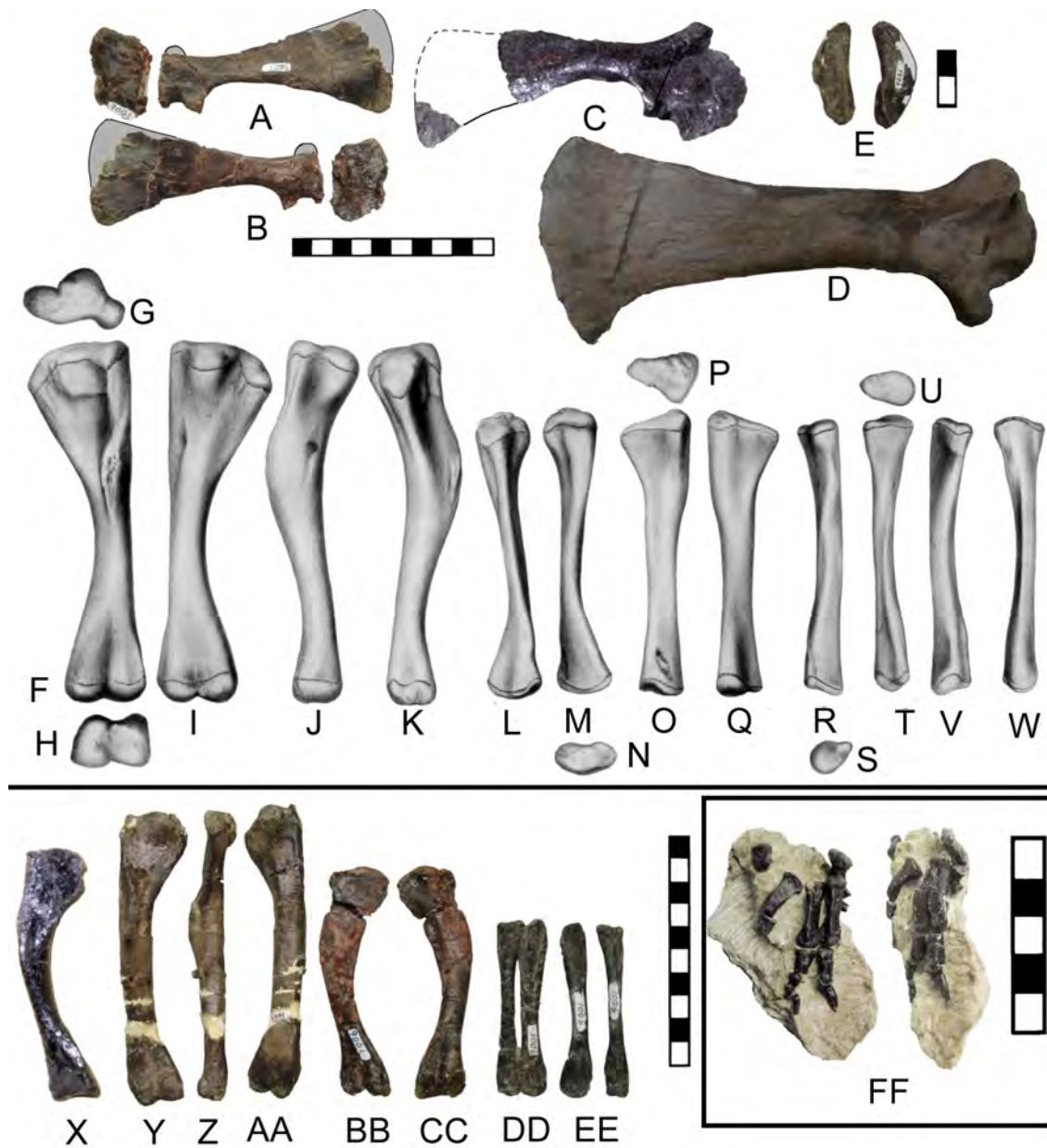


Figure 30. *Dryosaurus* Marsh, 1894b, shoulder and forelimbs. *D. dispar* left scapula and coracoid (DMNH 1006) in (A) lateral and (B) medial views; right scapula and coracoid (AMNH FARB 834) in (C) lateral view. *D. elderae* right scapula (DINO 1031) in (D) lateral view. The scapular neck is deeper in *D. elderae* than *D. altus*, but it is not known if this changes ontogenetically. The scapula of *Dryosaurus* has a supraglenoid fossa just above the glenoid similar to that seen in *Camptosaurus*. Such a fossa is not seen in other Morrison bipedal ornithischians. *D. dispar* sternal plates (E) (juvenile, DMNH 1006). Drawings made under the direction of O.C. Marsh of YPM VP 1876: left humerus in (F) anterior, (G) proximal, (H) distal, (I) posterior, (J) lateral, and (K) medial views; left ulna in (L) anterior, (M) posterior, (N) distal, (O) lateral, (P) proximal, (Q) medial views; left radius in (R) anterior, (S) distal, (T) posterior, (U) proximal, (V) lateral, and (W) medial views. *D. dispar* right humerus (AMNH FARB 834) in anterior view (X). Large juvenile (DMNH 1006a) right humerus in (Y) anterior, (Z) medial, and (AA) posterior views. (BB) to (FF): *D. dispar* small juvenile (DMNH 1006b) right humerus in (BB) anterior and (CC) posterior views, (DD) left ulna and radius in lateral view, (EE) right ulna and radius in lateral view, and (FF) two views of left manus. Scales in cm.

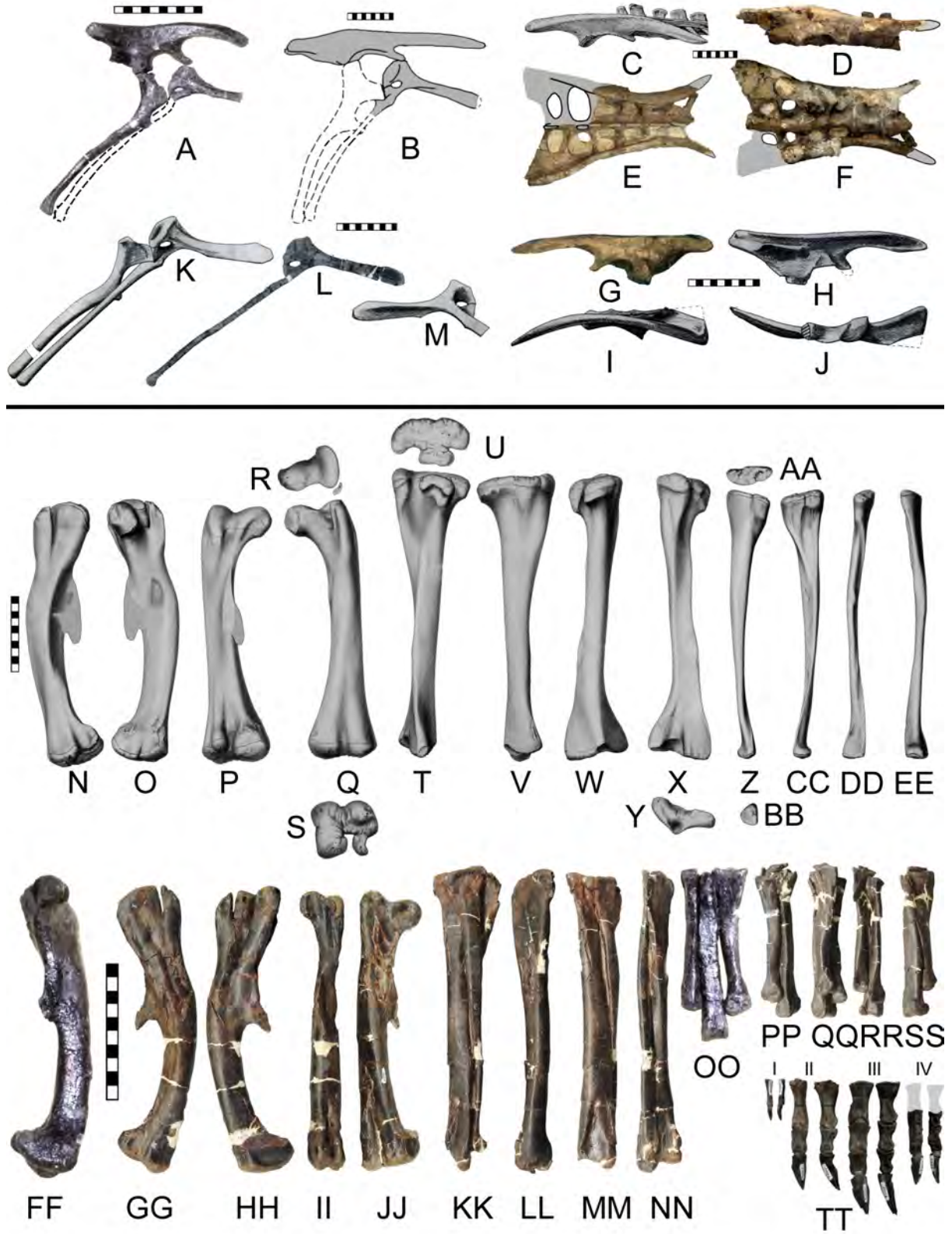


Figure 31. Caption is on the following page.

Figure 31 (figure is on the previous page). *Dryosaurus* Marsh, 1894a, pelvis and hindlimbs. (A) *D. altus* (AMNH FARB 834) pelvis in right lateral view compared with (B) *D. elderae* (sketch based on CM 3392 as mounted) in right lateral view. Sacrum and ilia of *D. elderae* (CM 3392, holotype) (C) as presented by Gilmore (1925) who drew attention to the low profile; (D) actual right lateral view; (E) dorsal, and (F) ventral views. Referred left ilium of *D. elderae* (DINO 4619) in (G) lateral, (H) medial, (I) dorsal, and (J) ventral view. The ilium of *D. elderae* is characterized by its long, low profile as compared to *D. altus*, especially the postacetabular process, which is proportionally lower and longer. (K) Drawings of pubis and ischium of *D. altus* (YPM VP 1876) in right lateral view prepared for O.C. Marsh. Compare pubis with actual specimen, (L) in lateral view view; (M) drawing of right pubis of *D. altus* (YPM VP 1876) in medial view prepared for O.C. Marsh. *D. altus* drawings made under the direction of O.C. Marsh of YPM VP 1876: left femur in (N) lateral, (O) medial, (P) posterior, (Q) anterior, (R) proximal (note anterior trochanter well separated from greater trochanter), and (S) distal views; left tibia in (T) lateral, (U) proximal, (V) medial, (W) posterior, (X) anterior, and (Y) distal views; left fibula in (Z) lateral, (AA) proximal, (BB) distal, (CC) medial, (DD) posterior, and (EE) anterior views. *D. altus* left femur (AMNH FARB 834) in (FF) medial view; (GG) to (NN): DMNH 1006 large juvenile, right femur in (GG) lateral, (HH) medial, (II) posterior, and (JJ) anterior views; right tibia and fibula in (KK) lateral, (LL) medial, (MM) posterior, and (NN) anterior views; metatarsals (AMNH FARB 834) in (OO) anterior view; (PP) to (TT): DMNH 1006, distal tarsal and metatarsals II to V in (PP) right lateral, (QQ) medial, (RR) posterior (note very small metatarsal V), (SS) anterior views, (TT) phalanges of digits I to IV in anterior and lateral views. Scales in cm.

tains the copyright, R.T. Bakker (Houston Museum of Natural History, Texas) for figures of “*Drinker nisti*.” Thanks to Matt Lamanna for bringing Horner and others (2009) to our attention.

A variety of colleagues have generously provided us with photographs of specimens: Mike Brett-Surman (National Museum of Natural History, Washington, D.C.); Dan Brinkman (Peabody Museum of Natural History, New Haven, Connecticut); Dan Chure, (Dinosaur National Monument Jensen, Utah; Matt Lamanna (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania), Andrew McAfee (Carnegie Museum of Natural History, Pittsburgh, Pennsylvania); Julia McHugh (Museums of Western Colorado, Fruita, Colorado), Dale Russell (North Carolina Museum of Natural Sciences, Raleigh, NC), and Hans-Jacob Siber (Saurier Museum, Aathal, Switzerland). Finally, thanks to John Foster and James Kirkland for review comments, and Doug Sprinkel for his patient editing. This publication in part is the sixth in a series on Dinosaur National Monument by the senior author.

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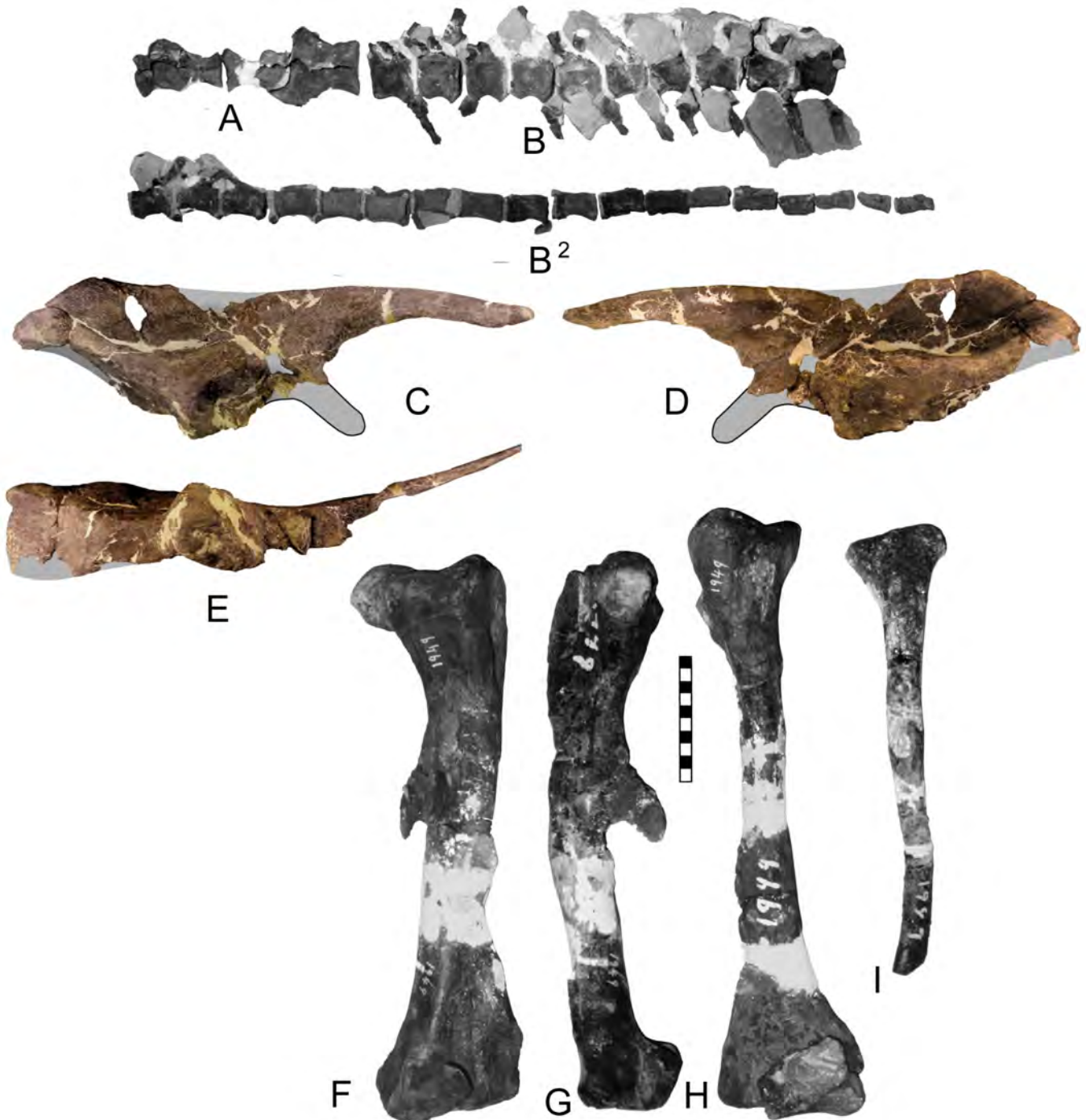


Figure 32. Large, unnamed ornithopod, CM 1949. (A) Four sacral centra; (B and B<sup>2</sup>) articulated first 28 caudal vertebrae. Right ilium (44 cm long) in (C) lateral, (D) medial, and (E) ventral views. Note the overall similarities with the ilium of *Camptosaurus* (figures 25A to 25I), especially the postacetabular portion, including the dorsal projection (variable in *Camptosaurus*; see Carpenter and Wilson, 2008). The brevis shelf is also moderately wide as in *Camptosaurus* as well. If only this ilium were known, we would have referred it to *Camptosaurus* cf. *dispar*. It is the associated hind limb that causes hesitancy because the tibia is longer than the femur, which is the reverse for *Camptosaurus*, and the fourth trochanter is more proximally placed than in *Camptosaurus* (figures 26B to 26E). Right femur (46 cm long) in (F) anterior and (G) medial views. (H) Right tibia (49 cm long) and astragalus in anterior view. (I) Right fibula in lateral view. Photographs of ilium courtesy of M. Lamanna and A. McAfee (Carnegie Museum of Natural History).



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