

THE BRAINCASE ASSIGNED TO THE ORNITHOPOD DINOSAUR
UTEODON McDONALD, 2011, REASSIGNED TO *DRYOSAURUS* MARSH, 1894:
 IMPLICATIONS FOR IGUANODONTIAN MORPHOLOGY AND TAXONOMY

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ABSTRACT

The braincase from the Upper Jurassic (lower Tithonian) Morrison Formation of the Carnegie Quarry at Dinosaur National Monument (Utah), which was assigned to the ankylopollexian iguanodontian ornithopod dinosaur *Uteodon aphanoeetes* (Carpenter and Wilson, 2008) is actually that of the dryosaurid iguanodontian *Dryosaurus* cf. *D. altus* (Marsh, 1878). The purported braincase autapomorphy of *U. aphanoeetes*, occipital condyle projects farther ventrally than basal tubera, is an artifact of damage to the latter structures in this specimen. The newly identified braincase of *Dryosaurus* Marsh, 1894, reveals features that are not easily observed in other specimens of this taxon, such as well-developed fossae on the anterior surfaces of the paroccipital processes and a spike-shaped parasphenoid that lacks the dorsal process seen in *Dysalotosaurus* Virchow, 1919. The distinction of this latter dryosaurid genus from *Dryosaurus* is here regarded as tentative.

The removal of the braincase in question from the hypodigm of *U. aphanoeetes* substantially reduces the morphological difference between this taxon and another ankylopollexian species, *Camptosaurus dispar* (Marsh, 1879). Furthermore, some of the postcranial characters used to support the proposed sister-taxon relationship of *U. aphanoeetes* and *Cummnoria prestwichii* (Hulke, 1880) are based on hypothetical reconstructions of selected skeletal elements of the latter, or are more widespread within Ornithopoda. The ilium of *Cummnoria prestwichii* cannot currently be distinguished from that of *Camptosaurus dispar* based on known material. Indeed, the only presently recognized autapomorphy of *Cummnoria prestwichii* is the small size of the opening into the maxillary sinus on the dorsomedial side of the maxilla (i.e., the intramaxillary fossa); in *Camptosaurus dispar*, by contrast, this opening is large and occupies most of the dorsomedial surface of the bone. This single feature is not considered sufficient to warrant the continued separation of the genera *Camptosaurus* Marsh, 1885, and *Cummnoria* Seeley, 1888. Similarly, the anatomical differences between *U. aphanoeetes* and *Camptosaurus dispar* are regarded as meriting distinction at the species rather than the genus level. Consequently, the genera *Cummnoria* Seeley, 1888, and *Uteodon* McDonald, 2011, are here regarded as junior subjective synonyms of *Camptosaurus* Marsh, 1885 (***Cummnoria* as revised synonymy, and *Uteodon* as new synonymy**). The species *Cummnoria prestwichii* and *Uteodon aphanoeetes* are returned to the genus *Camptosaurus*, as ***Camptosaurus prestwichii*, revised combination, and *Camptosaurus aphanoeetes*, revised combination**, respectively.

KEY WORDS: Ankylopollexia, *Camptosaurus*, *Cummnoria*, Dryosauridae, *Dysalotosaurus*, Dinosaur National Monument, Morrison Formation, Upper Jurassic

INTRODUCTION

Dinosaur National Monument straddles the Utah–Colorado border. The Carnegie Quarry, at the western end of the monument, is famous for its well-preserved skeletal material of a diverse Late Jurassic dinosaur fauna (e.g., McIntosh 1977; Gregson and Chure 2000; Carpenter 2013). Found by Earl Douglass of the Carnegie Museum in the summer of 1909, the site was worked by the museum until December 31, 1922 (as noted in Douglass' unpublished Record Book 1909–1923), although the last shipment of fossils to Pittsburgh was not made until June 13, 1923 (unpublished letter from Douglass to Carnegie Museum Director Douglas Stewart, June 13, 1923). The Smithsonian Institution worked the east end of the quarry in the summer of 1923, removing two partial skeletons that had been left exposed. The Smithsonian was followed by the University of Utah beginning on November 26, 1923 (Douglass, Record Book 1909–1923).

Among the specimens excavated by Douglass and his team in the eastern half of the quarry was a nearly complete postcranial skeleton of an iguanodontian ornithopod (CM 11337; Fig. 1). Gilmore (1925) briefly described the specimen and referred it to *Camptosaurus medius* Marsh, 1894. The skeleton was fully described and designated as the holotype of a new species, *Camptosaurus aphanoeetes* Carpenter and Wilson, 2008, by Carpenter and Wilson (2008), who also referred all specimens of *Camptosaurus* Marsh, 1885, from Dinosaur National Monument to this species. More recently, McDonald (2011) referred all of this iguanodontian material to a new genus, *Uteodon* McDonald, 2011, as *U. aphanoeetes* (Carpenter and Wilson, 2008), based in part on a single autapomorphy from a referred braincase in which the occipital condyle was said to project farther ventrally than the basal tubera.

This braincase was catalogued with a nearly complete

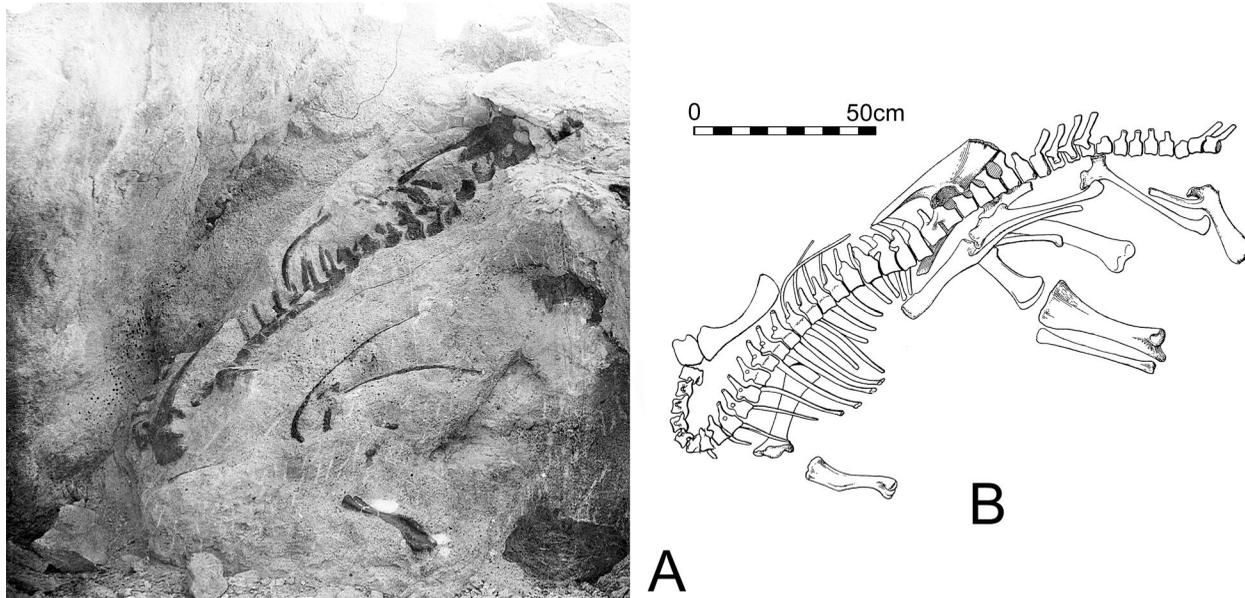


Fig. 1.—**A**, Holotypic skeleton of *Camptosaurus aphanoeetes* (CM 11337) as originally discovered in the east end of the Carnegie Quarry, Dinosaur National Monument, Utah. **B**, drawing of same specimen as presented by Gilmore (1925: pl. 8 lower). In comparing A with B, note that the scapulocoracoid was actually found overlying the cervical series, the humerus was rotated 180 degrees and positioned farther away from the rest of the skeleton, and that several loose dorsal ribs were also found. These changes should be noted on the revised quarry map published by Carpenter (2013). A, courtesy of the Leo Thorne Photograph Collection, Uintah County Regional History Center.

right hind limb, CM 15780 (Fig. 2). This hind limb was named as part of the paratype series of *Camptosaurus aphanoeetes* by Carpenter and Wilson (2008). It was assigned field number 315 by Douglass (McIntosh 1981) and was found wedged on the upstream side of a posterior cervical vertebra of field number 310, a partial skeleton of the large diplodocid sauropod *Barosaurus lentus* Marsh, 1890 (Fig. 3A). Now catalogued as CM 11984, this specimen of *Barosaurus* Marsh, 1890, consists of a sequence of 13 articulated cervical vertebrae that were oriented at an obtuse angle to seven articulated dorsal vertebrae and several presacral ribs. Carnegie Quarry excavation records (Appendix 1) show that field number 315 was collected with a posterior cervical (field number 310/12) of this *Barosaurus*: “Block 310/F. Cervical, and two small Limb Bones. (C^a:e42). Cervical 310/12. Also No. 215 [sic]. Two small limb bones. Box 373A.” (“215” should clearly be “315” here, because field number 215 is a turtle shell.) Preparation of this block eventually revealed more of number 315 than just the two limb bones that Douglass could see in the field: the specimen was found to consist of the femur, tibia, fibula, astragalus, and metatarsal IV of the right leg (Fig. 2).

Another block, field number 310/N, was collected from the downstream side of the *Barosaurus* neck (Fig. 3B), and contained a mixture of bones: “Block 310/N. Toe Bones etc. (A^b:e44). Toe Bones probably belonging with 310 Portions of Neck and Skull of No. 325. Box 395” (Appendix 1). Number 325 (CM 11969) is a large individual of *Camarasaurus* cf. *C. lentus* (Marsh, 1889) (McIntosh 1981).

Also recovered were an ulna of a juvenile *Camarasaurus* sp. (CM 42275), an ornithopod braincase (Fig. 4), and five ornithopod cervical vertebrae (Fig. 5). The ornithopod braincase and cervicals from Block 310/N were catalogued with CM 15780, presumably under the assumption that they pertained to the same individual as the hind limb from Block 310/F. This association was implicitly accepted by McDonald (2011), who referred to the braincase as part of CM 15780 (e.g., McDonald 2011: fig. 7b) in the paratype series of *Uteodon aphanoeetes*, and cited a morphology that he observed in this element as the sole autapomorphy of this taxon. However, the Carnegie Quarry block that contained the braincase and cervicals (310/N) was found 2.75 m from the block that included the hind limb (310/F), with the articulated *Barosaurus* vertebrae between them (Fig. 3). Thus, the ornithopod braincase and cervicals cannot be assumed to be part of CM 15780, and have accordingly been given their own catalog number, CM 87688. In addition, as shown below, this latter specimen pertains to the dryosaurid *Dryosaurus* cf. *D. altus* (Marsh, 1878), and as such it has significant implications for iguanodontian taxonomy and the status of *Uteodon*. The specimen is also important in that it reveals information about the braincase of *Dryosaurus* Marsh, 1894, that is not readily available from previously described cranial material of this taxon (Galton 1983, 1989).

Institutional abbreviations.—**CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **DINO**, Dinosaur National Monument, Vernal, Utah, U.S.A.;

DMNH, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **GPIT**, Institut und Museum für Geologie und Paläontologie, University of Tübingen, Tübingen, Germany; **MB**, Museum für Naturkunde, Berlin, Germany; **OXFUM**, Oxford University Museum of Natural History, Oxford, United Kingdom; **USNM**, United States National Museum (now National Museum of Natural History), Washington, District of Columbia, U.S.A.; **YPM**, Yale Peabody Museum, New Haven, Connecticut, U.S.A.

Material examined.—*Camptosaurus dispar*: DMNH 50131, subadult skull (cast) associated with a nearly complete skeleton from Bone Cabin Quarry West, Wyoming; USNM 5473, braincase and ilium from Quarry 13 of Como Bluff, Wyoming; USNM 2210, USNM 5959, USNM 7631, and YPM 1880, ilia from Quarry 13 of Como Bluff, Wyoming; USNM 5818, ilium and ischium from Quarry 13 of Como Bluff, Wyoming; USNM 4282, ischium from Quarry 13 of Como Bluff, Wyoming; *Camptosaurus aphanoecetes*: CM 11337, skeleton, DINO 4225, ilium, CM 79050, ischium, and CM 15780, hind limb, all from Carnegie Quarry at Dinosaur National Monument, Utah; *Dryosaurus altus*: YPM 1876, quadrate from Quarry 5 of Como Bluff, Wyoming; *Dryosaurus* cf. *D. altus*: CM 3392, skull and CM 87688, braincase, both from Carnegie Quarry at Dinosaur National Monument, Utah. All of the above specimens are from the Morrison Formation. *Camptosaurus prestwichii* (Hulke, 1880): OXFUM J.3303, partial skeleton from the Kimmeridge Clay of Cumnor, England. *Dysalotosaurus lettowvorbecki* Virchow, 1919: MB.R.1320, MB.R.1326, GPIT /RE /3608, quadrates from the Middle Saurian Bed of Quarry Ig NW of Tendaguru Hill, near Kindope, Tanzania.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
 Ornithischia Seeley, 1887
 Ornithopoda Marsh, 1881
 Iguanodontia Dollo, 1888
 Dryomorpha Sereno, 1986
 Dryosauridae Milner and Norman, 1984

Dryosaurus Marsh, 1894

Dryosaurus cf. *D. altus* (Marsh, 1878)

Laosaurus altus Marsh, 1878. Original combination.

Dryosaurus altus (Marsh, 1878). Marsh, 1894.

Uteodon aphanoecetes: McDonald, 2011 (**misidentification** in part: braincase of CM 87688).

Referred specimen.—CM 87688, a braincase and five semi-articulated cervical vertebrae.

Locality and horizon.—Carnegie Quarry at Dinosaur National Monument, Uintah County, Utah, U.S.A. Brushy Basin Member of the Morrison Formation (Upper Jurassic: lower Tithonian).



Fig. 2.—Right hind limb of *Camptosaurus aphanoecetes* (Carnegie Quarry field number 315/CM 15780). **A**, femur in anterior view (greater trochanter to lateral condyle length = 39.1 cm); **B**, fibula in lateral view (midline length = 30.7 cm); **C**, tibia in anterior view (midline length = 35.0 cm); **D**, astragalus in anterior view; **E**, metatarsal IV in medial view (midline length = 11.0 cm). Scale = 10 cm.

DESCRIPTION

The braincase of CM 87688 consists of the supraoccipital, the braincase floor (basioccipital, basisphenoid, parasphenoid), and most of the paired bones of the braincase walls (both exoccipitals, opisthotics, and prootics; Fig. 4). Missing are the skull roof bones, including the parietals, orbitosphenoids, and laterosphenoids. The braincase is small, about 8.2 cm in length (measured in a straight line from the anterior end of the parasphenoid to the posterior end of the occipital condyle) and 4.7 cm tall (from the basal tubera to the apex of the supraoccipital), and has an occipital condyle that is 2.4 cm wide. Although the distal ends of both paroccipital processes are damaged, enough of them remain to estimate that the paroccipital process-to-paroccipital process width was 6.5 cm. The braincase matches in size the portion that can be seen in the *Dryosaurus* cf. *D. altus* skull CM 3392 (Fig. 6). In the following, comparisons are also made with *Camptosaurus* (Figs. 7–8) to demonstrate that CM 87688 does not represent a juvenile individual of that taxon.

Basioccipital.—The basioccipital is well ossified to the basisphenoid, although a faint trace of the suture between

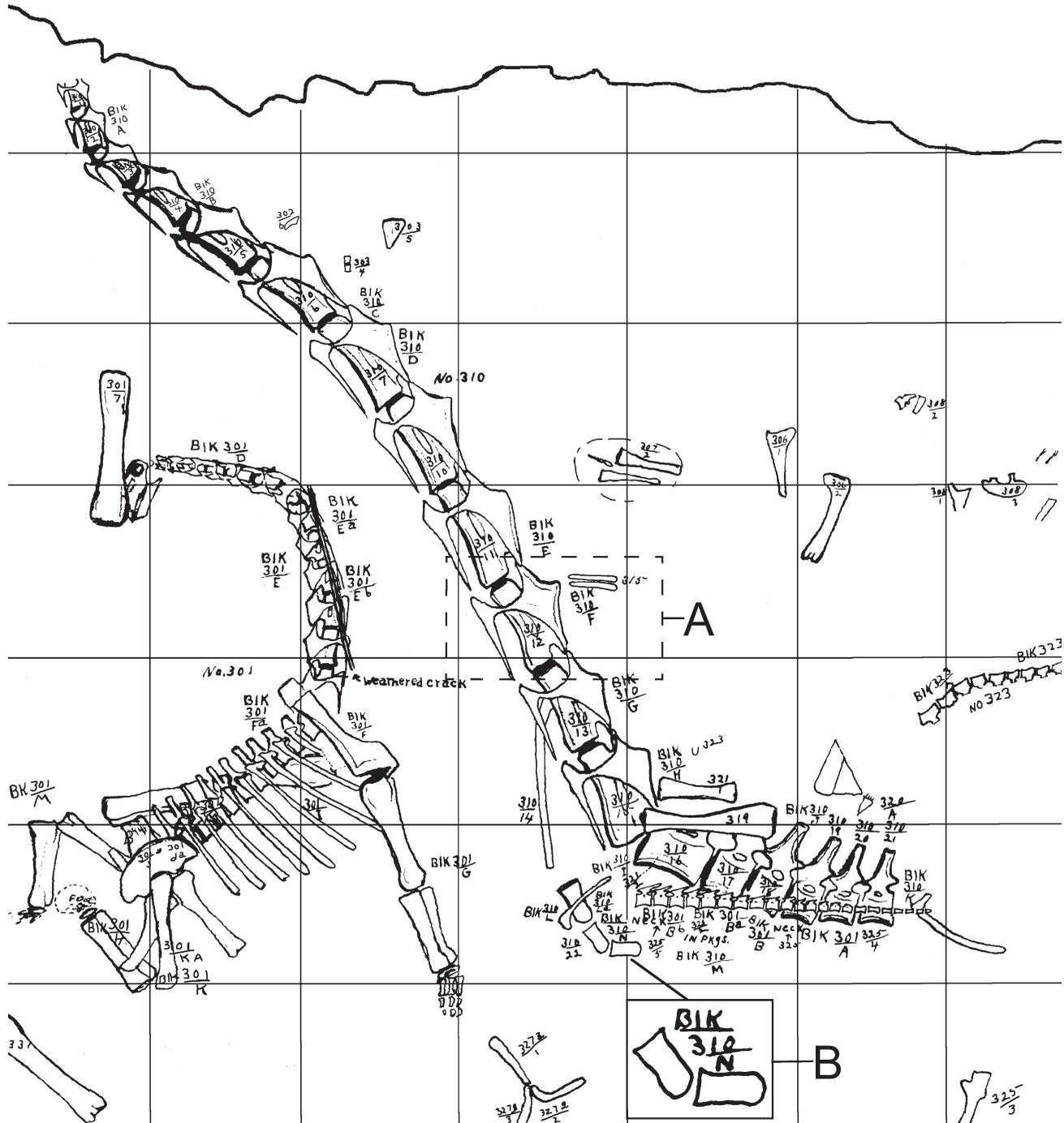


Fig. 3.—Portion of Carnegie Quarry map showing location of specimens 315 (*Camptosaurus aphanoeetes* hind limb CM 15780, collected as part of block 310/F) (A) and 310/N (block including *Dryosaurus* cf. *D. alus* braincase and cervicals CM 87688) (B). Numbers correspond to Carnegie Quarry field and block numbers; grid squares are four feet by four feet.

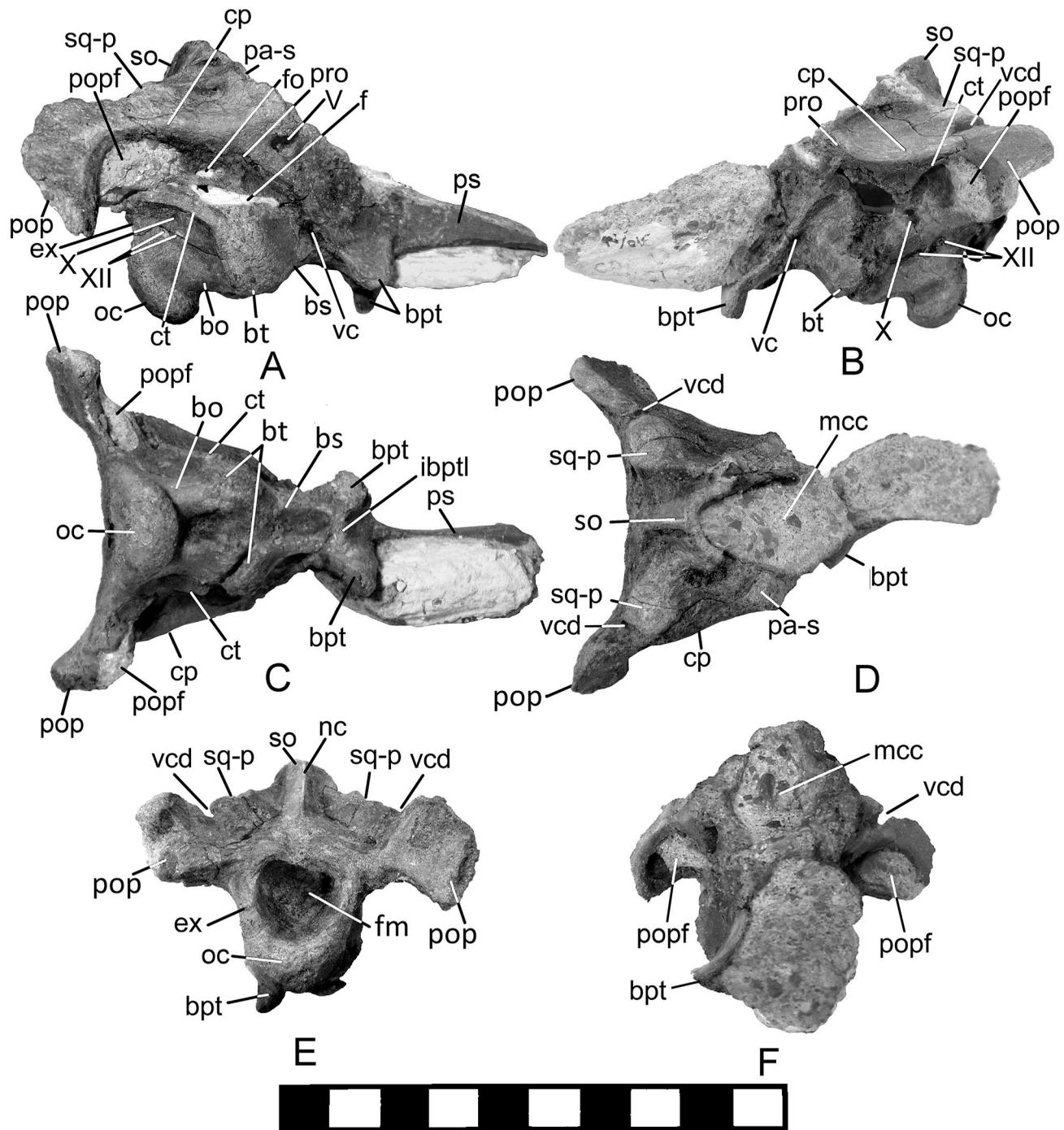


Fig. 4.—Braincase of *Dryosaurus* cf. *D. altus* (CM 87688), formerly assigned to *Uteodon aphanocetes* (CM 15780). **A**, right lateral view; **B**, left lateral view; **C**, ventral view; **D**, dorsal view; **E**, posterior view; **F**, anterior view. Abbreviations: **bo**, basioccipital; **bpt**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tuber; **cp**, crista prootica; **ct**, crista tuberalis; **ex**, exoccipital; **f**, plaster-filled fracture; **fm**, foramen magnum; **fo**, fenestra ovalis; **ibptl**, interbasipterygoid process lamina; **mcc**, matrix-filled cranial cavity; **nc**, nuchal crest; **oc**, occipital condyle; **pa-s**, surface for parietal; **pop**, paroccipital process; **popf**, paroccipital process fossa; **pro**, prootic; **ps**, parasphenoid; **so**, supraoccipital; **sq-p**, pedicle for squamosal; **vc**, vidian canal; **vcd**, sulcus for vena capitis dorsalis; **V**, **X**, **XII**, cranial nerve foramina. Scale = 10 cm.

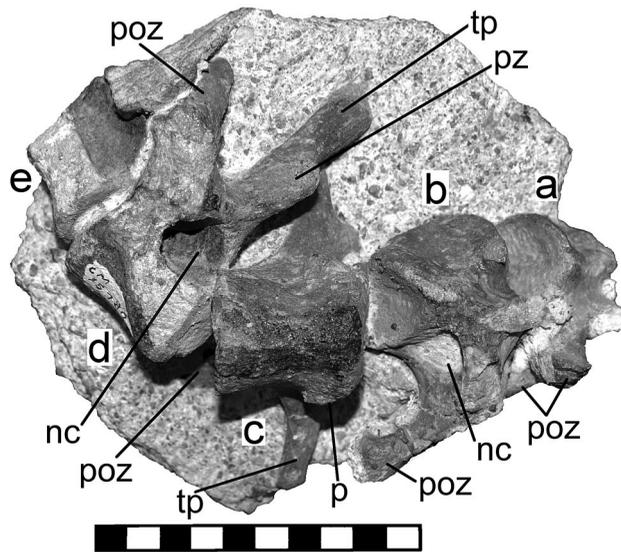


Fig. 5.—Anterior to middle cervical vertebrae (CM 87688) associated with the braincase of *Dryosaurus* cf. *D. altus*, anterior towards right. Anteriormost two vertebrae in sequence (a, b) exposed in left posterolateral view, third vertebra (c) exposed in ventral view, and posteriormost two vertebrae (d, e) exposed in right anterolateral view. Anteroposterior lengths (cm) of centra along midline from most anterior to most posterior vertebra: 3.9, 3.7, 3.7, ~3.6, >3.3. Abbreviations: **nc**, neural canal; **p**, parapophysis; **poz**, postzygapophysis; **pz**, prezygapophysis; **tp**, transverse process. Scale = 10 cm.

these elements is visible on the ventral side, showing a tapering wedge extending anteriorly between the basal tubera (Fig. 4C). In addition, the left basal tuber is split at approximately the area where the basioccipital and basisphenoid have a suture in DMNH 50131, an undescribed specimen of *Camptosaurus dispar* (Fig. 7D). However, the split in CM 87688 is also where the specimen had been previously broken in half and repaired with plaster of Paris. Traces of the sutures between the basioccipital and the exoccipitals remain as well (Fig. 4E). These show that small portions of the occipital condyle are formed by the exoccipitals, as in *Camptosaurus* (Fig. 7E) and most other ornithomorphs. In posterior view, the occipital condyle is crescentic because its dorsal margin (i.e., the ventral rim of the foramen magnum) is deeply and widely notched (Fig. 4E). The condyle is less crescentic in *Camptosaurus* (Figs. 7E, 8E). In addition, the floor of the *Dryosaurus* braincase is angled posteroventrally relative to the occipital condyle–parasphenoid axis. This suggests that the head was habitually carried at an angle relative to the anterior part of the neck. In contrast, the braincase floor is parallel with the same axis in *Camptosaurus*, suggesting that the head was carried more parallel to the anterior part of the neck. These differences may correlate with the apparent locomotor distinctions between bipedal *Dryosaurus* and mostly quadrupedal *Camptosaurus* (Carpenter and Wilson 2008). In lateral view, the ventral margin of the occipital condyle of CM 87688 (Figs. 4A–B) and CM 3392 (Fig. 6B)

is well developed and ventrally projecting, thus forming a short but distinct condylar neck. A similar situation occurs in *Camptosaurus* (Figs. 7A–B, 8A–B). Furthermore, the articular surface of the condyle continues ventrally as a broad triangular surface in *Camptosaurus* but not in *Dryosaurus* (compare Figs. 7D and 4C). This suggests that *Camptosaurus* could have moved its head ventrally to a greater degree than could *Dryosaurus* because a more extensive articular surface was available for the atlas. Also on the ventral side of the basioccipital are a pair of low, laterally compressed ridges that extend posteriorly from each basal tuber towards the occipital condyle, enclosing a distinct fossa. In *Camptosaurus*, these bounding ridges do not extend towards the occipital condyle, but rather terminate well anterior to it. The fossa is developed into the body of the basioccipital at the base of the basal tubera. In *Dysalotosaurus lettowvorbecki*, a small sagittal ridge is present in place of this fossa (Sobral et al. 2012).

Basisphenoid.—As noted above, the basisphenoid–basioccipital suture is mostly obliterated in CM 87688. On the ventral side, the basal tubera are damaged (Figs. 4A–C), making them appear abnormally small in size and less ventrally projected than the ventral margin of the occipital condyle. Consequently, although McDonald (2011:58) proposed this condition of the CM 87688 (then CM 15780) braincase as the sole autapomorphy of his new iguanodontian genus *Uteodon*, it is in fact an artifact due to bone loss, possibly during preparation with hammer and chisel as was common during the early 20th century (e.g., McGinnis 1983:14, bottom photo). CM 3392 shows that the undamaged basal tubera of *Dryosaurus* form a prominent, projecting flange (Fig. 6B). In *Camptosaurus*, the basal tubera are thick, tongue-shaped structures that project obliquely laterally and posteroventrally from the base of the basisphenoid (Figs. 7A–B, D, 8A–C).

Dorsolaterally, the crista tuberalis extends from the basal tuber towards the paroccipital process (Figs. 4A–B). In *Camptosaurus*, the crista tuberalis does not extend from the basal tubera, but is separated by a gap (Figs. 7A–B, 8A–B). Anteriorly, a pair of low ridges extends to the base of the basiptyergoid processes in CM 87688 and forms a shallow, anteroposteriorly elongate fossa. A small, triangular fossa is present in *Camptosaurus*. The left basiptyergoid process of CM 87688 is nearly complete (Fig. 4B), although its slightly abraded surface could indicate some bone loss; the right basiptyergoid process is broken at its base. The left basiptyergoid process shows that the processes projected ventrolaterally as in *Dysalotosaurus* Virchow, 1919. They are joined by a thin wedge of bone that thickens dorsally, towards the main body of the basisphenoid. The basiptyergoid processes are short and project almost laterally in *Camptosaurus* (although they are mostly missing in USNM 5473, despite having been figured by Gilmore [1909: fig. 4] in this specimen). The deep pit between the basiptyergoid processes of *Dysalotosaurus* (Sobral et al. 2012) is absent in CM 87688 and *Camptosaurus*.

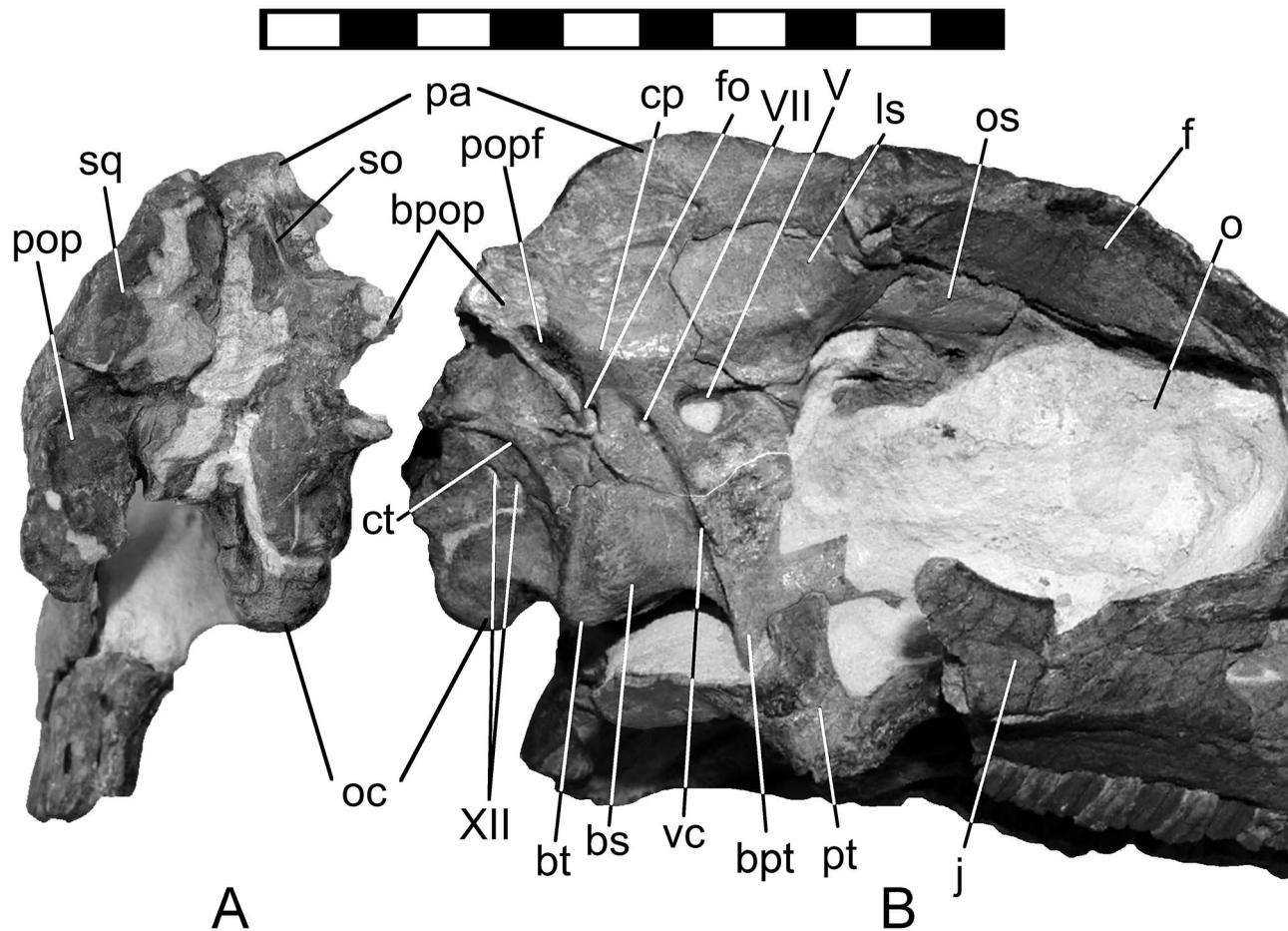


Fig. 6.—Braincase of *Dryosaurus* cf. *D. altus* (CM 3392) in posterior (A) and right lateral (B) views. Abbreviations: **bpop**, broken surface of the paroccipital process; **bpt**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tuber; **cp**, crista prootica; **ct**, crista tuberalis; **f**, frontal; **fo**, fenestra ovalis; **j**, jugal; **ls**, laterosphenoid; **o**, orbit; **oc**, occipital condyle; **os**, orbitosphenoid; **pa**, parietal; **pop**, paroccipital process; **popf**, paroccipital process fossa; **pt**, pterygoid; **so**, supraoccipital; **sq**, squamosal; **vc**, vidian canal; **V**, **VII**, **XII**, cranial nerve foramina. Scale = 10 cm.

In addition, unlike *Dysalotosaurus* (Sobral et al. 2012) and *Camptosaurus*, the vidian canal is restricted to the body of the basisphenoid, rather than being partially developed on the posterior side of the basipterygoid process.

Parasphenoid.—The parasphenoid is nearly complete, although it may lack a very small portion of one side of its apex. Embryologically, the parasphenoid is known to be a distinct bone (e.g., Hanken and Hall 1988; Hugi et al. 2010) and it is treated as such here, despite the absence of any suture with the basisphenoid. In lateral view, it is long, triangular, and dorsoventrally tapering (Fig. 4A). It is incomplete in *Camptosaurus* DMNH 50131, but what remains suggests that its dorsal and ventral margins were parallel. In CM 87688, there is no indication of the well-developed dorsal process of the parasphenoid that occurs in *Dysalotosaurus* (Janensch 1955; Hübner and Rauhut 2010).

Exoccipital.—As best observed in posterior view, the exoccipital of CM 87688 forms a small portion of the dorso-

lateral part of the occipital condyle (Fig. 4E). In CM 3392, the exoccipital is more apparent as a separate ossification in that it bulges posteriorly to overhang the basioccipital–exoccipital suture (Fig. 6); a similar condition is seen in *Camptosaurus* (DMNH 50131). Galton (1989: pl. 1, fig. 1) shows a comparable overhang in *Dysalotosaurus* (as *Dryosaurus lettowvorbecki*).

Opisthotic.—The opisthotic–basioccipital suture is visible on both sides of the braincase and can be traced to the dorsal-most part of the basal tubera. The suture is irregular, and rises abruptly just anterior to the anterior-most of the two hypoglossal nerve (cranial nerve XII) foramina. There is no sharp rise of this suture in *Dysalotosaurus* (Sobral et al. 2012: fig. 2a) or *Camptosaurus*. In CM 87688, the opisthotic forms the posterior half of the lateral wall of the braincase and the lateral edge of the foramen magnum. As in *Dysalotosaurus*, it has small contacts with the parietal and basisphenoid.

The paroccipital process has a deep, elongate excavation or fossa at its base that extends almost three-quarters

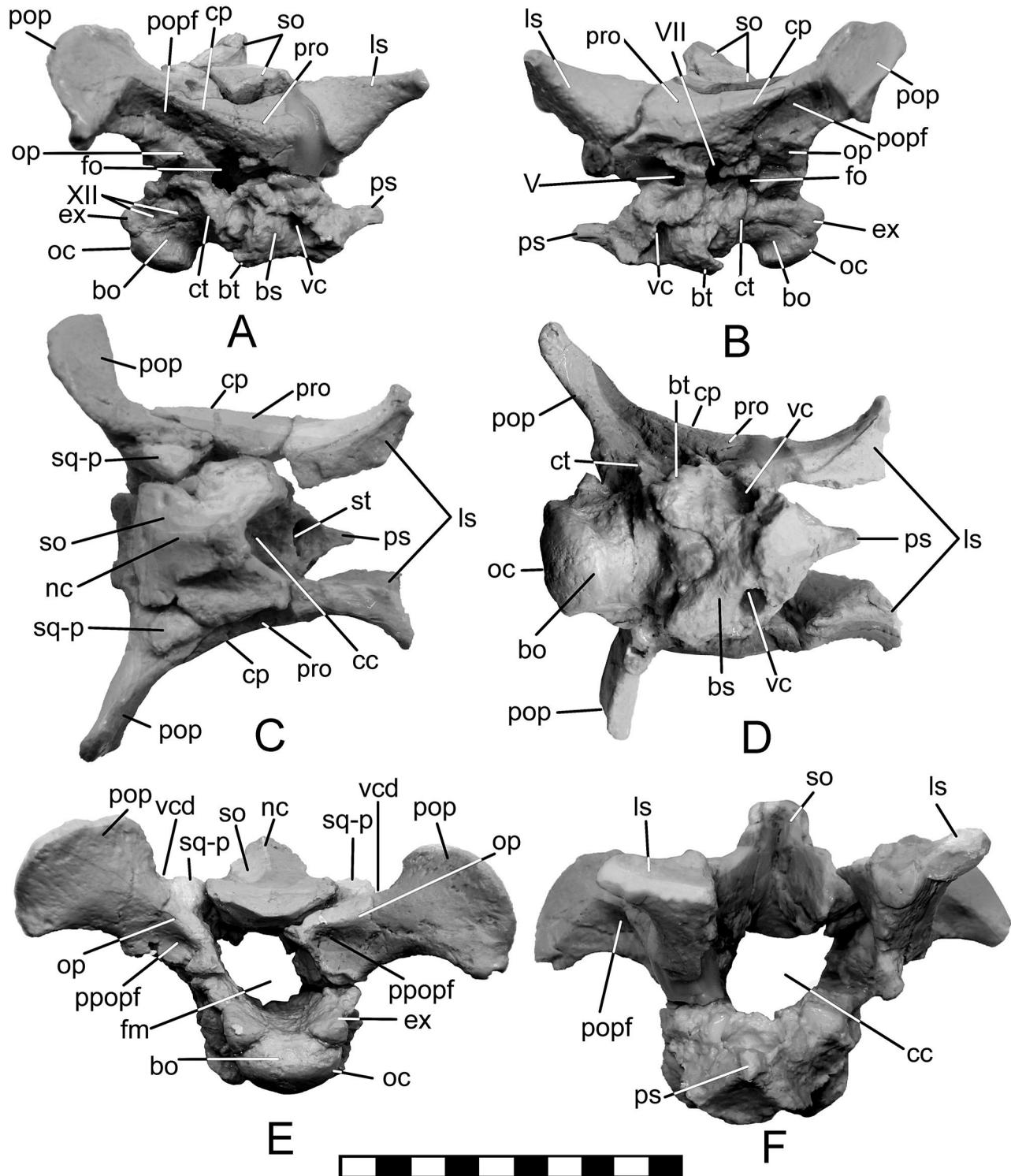


Fig. 7.—Braincase (cast) of an immature *Camptosaurus dispar* (DMNH 50131). **A**, right lateral view; **B**, left lateral view; **C**, dorsal view; **D**, ventral view; **E**, posterior view; **F**, anterior view. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **cc**, cranial cavity; **cp**, crista prootica; **ct**, crista tuberalis; **ex**, exoccipital; **fm**, foramen magnum; **fo**, fenestra ovalis; **ls**, laterosphenoid; **nc**, nuchal crest; **oc**, occipital condyle; **op**, opisthotic; **pop**, paroccipital process; **popf**, paroccipital process fossa; **ppopf**, posterior paroccipital process fossa; **pro**, prootic; **ps**, parasphenoid; **so**, supraoccipital; **sq-p**, pedicle for squamosal; **st**, sella turcica; **vc**, vidian canal; **vcd**, sulcus for vena capitis dorsalis; **V**, **VII**, **XII**, cranial nerve foramina. Scale = 10 cm.

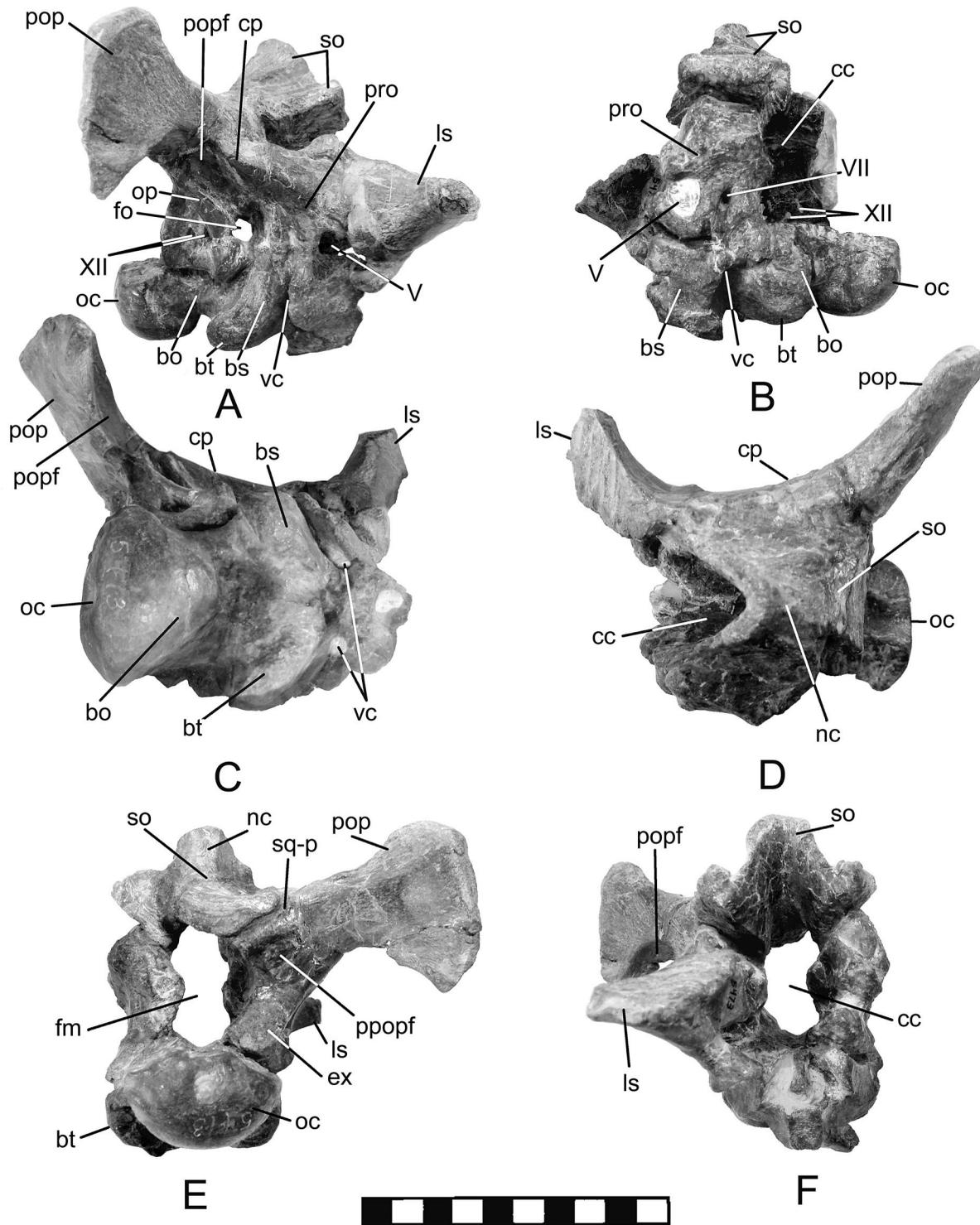


Fig. 8.—Braincase of an adult (?) *Camptosaurus dispar* (USNM 5473). **A**, right lateral view; **B**, left lateral view; **C**, ventral view; **D**, dorsal view; **E**, posterior view; **F**, anterior view. Abbreviations: **bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **cc**, cranial cavity; **cp**, crista prootica; **ex**, exoccipital; **fm**, foramen magnum; **fo**, fenestra ovalis; **ls**, laterosphenoid; **nc**, nuchal crest; **oc**, occipital condyle; **op**, opisthotic; **pop**, paroccipital process; **popf**, paroccipital process fossa; **ppopf**, posterior paroccipital process fossa; **pro**, prootic; **so**, supraoccipital; **sq-p**, pedicle for squamosal; **vc**, vidian canal; **V**, **VII**, **XII**, cranial nerve foramina. Scale = 10 cm.

of the length of the process (Figs. 4A–B, F). Although the fossa is still mostly filled with matrix, its medial and lateral ends were cleaned to reveal that the fossa is sharply and deeply developed. This fossa is very shallow and less developed in *Dysalotosaurus* (Janensch 1955: pl. 9, fig. 3b). A somewhat similar groove or fossa along the paroccipital process is present in *Camptosaurus*, although it extends from the fenestra ovalis (Figs. 7A–B, F, 8A, C); in *Dryosaurus*, this fenestra is more anteriorly placed and so does not lie within the groove. On the posterior side, the paroccipital process of *Dryosaurus* slopes anterodorsally to a swollen pedicle for the squamosal. This pedicle is also formed partially by the supraoccipital (Figs. 4D–E). A similar situation is present in the subadult *Camptosaurus dispar* (DMNH 50131; Figs. 7C, E), but there is a deep, subtriangular fossa in the adult *C. dispar* (USNM 5473; Fig. 8E).

Prootic.—The prootic is preserved ventral to the crista prootica on the right side of CM 87688 (Fig. 4A); it is damaged across the fenestra ovalis on the left side (Fig. 4B). The posterior process is a posterolaterally-tapering wedge that extends onto the anterior surface of the paroccipital process, as in *Dysalotosaurus* and *Camptosaurus*. Laterally, the crista prootica is developed on the posterior process and forms a horizontal shelf dorsal to the fenestra ovalis (Figs. 4A–B).

Supraoccipital.—The supraoccipital forms the sagittal part of the posterodorsal region of the braincase, but unlike in *Dysalotosaurus* and *Camptosaurus* (Figs. 7E, 8E), it is excluded from the dorsal margin of the foramen magnum (Fig. 4E). The bone slopes anterodorsally and has a prominent midline nuchal crest that is also present in *Camptosaurus* and *Dysalotosaurus*. Posterolaterally, the supraoccipital extends towards the paroccipital processes.

Cervical vertebrae.—A block containing five semi-articulated iguanodontian anterior to middle cervical vertebrae (assuming the centra shorten towards the middle of the cervical column before lengthening again, as is typical for ornithopods; Fig. 5) was recovered with the braincase; their size corresponds to what would be expected for the braincase, so their association with that element is probably correct despite not being in articulation. There is some damage of the exposed surfaces, at least some of which probably occurred during collecting (e.g., the loss of the right sides of the posteriormost two centra). The neurocentral sutures are nearly completely fused. The centra are longer ventrally than dorsally (i.e., along the neural canal) and are wider than tall; none have the distinctive ‘wedge shape’ of cervical vertebra 7 of *Camptosaurus aphanoeetes* (Carpenter and Wilson 2008: fig. 7a). The ventral portions of the centra are constricted (pinched) transversely and have a rounded ridge that connects their anterior and posterior articular faces. The centra are plani-concave, as is typical for *Dryosaurus* (Galton 1981) and *Dysaloto-*

saurus (Janensch 1955); cervical centra are amphiplatyan in *Camptosaurus aphanoeetes* (Carpenter and Wilson 2008). The parapophyses are developed on the anterolateral corners of the centra, near the dorsoventral midpoint, and extend from the anterior articular face posteriorly as described by Galton (1981: figs. 1a, 2e) for *Dryosaurus* and *Dysalotosaurus*. In this aspect, the CM 87688 cervicals are unlike those of *Camptosaurus aphanoeetes* and most cervicals of *Camptosaurus dispar* where the parapophyses are restricted to the anterolateral ends of the centra (Carpenter and Wilson 2008). The neural arches of the CM 87688 vertebrae are low, but their neural spines are either missing or still embedded in matrix. The steeply angled prezygapophyses are developed at the bases of the transverse processes and have a transversely elongate oval shape. The diapophysis at the distal (i.e., lateral) end of each transverse process is a rounded surface that, based on its texture, was apparently capped with cartilage in life. The postzygapophyses are posteriorly elongate and extend past the posterior ends of the centra.

Ankylopollexia Sereno, 1986

Camptosaurus Marsh, 1885

Camptosaurus Marsh, 1885. Type species: *Camptonotus dispar* Marsh, 1879.

Cummnoria Seeley, 1888. Type species: *Iguanodon prestwichii* Hulke, 1880.

Revised synonymy.

Uteodon McDonald, 2011. Type species: *Camptosaurus aphanoeetes* Carpenter and Wilson, 2008. **New synonymy.**

Camptosaurus dispar (Marsh, 1879)

Camptonotus dispar Marsh, 1879. Original combination.
Camptosaurus dispar (Marsh, 1879). Marsh 1885.

Camptosaurus prestwichii (Hulke, 1880) **Revised combination**

Iguanodon prestwichii Hulke, 1880. Original combination.
Cummnoria prestwichii (Hulke, 1880). Seeley, 1888.

Camptosaurus aphanoeetes Carpenter and Wilson, 2008. **Revised combination**

Camptosaurus aphanoeetes Carpenter and Wilson, 2008. Original combination.

Uteodon aphanoeetes (Carpenter and Wilson, 2008). McDonald, 2011 (in part).

DISCUSSION

McDonald (2011) designated specimen CM 11337, the holotype of *Camptosaurus aphanoeetes*, as the type specimen of a new genus, *Uteodon* (as *Uteodon aphanoeetes*), despite stating that the single autapomorphy of that genus



Fig. 9.—Skull of *Camptosaurus dispar* (DMNH 50131) in dorsal (A) and left lateral (B) views. The skull was reconstructed from casts of the isolated bones. Note the presence of a small antorbital fenestra. Scale = 10 cm.

was observable only in a braincase that was initially cataloged with a paratype hind limb of *C. aphanoecetes* (CM 15780). However, as shown above, the braincase does not pertain to the same ornithomimid individual as CM 15780, and is therefore not part of the hypodigm of *C. aphanoecetes*. The braincase is actually that of *Dryosaurus* cf. *D. altus*, which leaves *Uteodon* without an autapomorphy. The only other diagnosis that McDonald (2011) provided for *Uteodon* was a combination of characters that was purportedly unique to that genus and the European iguanodontian *Cumnoria prestwichii*. Therefore, after the removal of the putative autapomorphy of *Uteodon*, McDonald's (2011) diagnosis provides no basis to separate this genus

from *Cumnoria* Seeley, 1888. Furthermore, as shown below, the character combination that is supposedly unique to *Uteodon* and *Cumnoria* does not reliably distinguish these genera from *Camptosaurus*. Consequently, the genus *Uteodon* can no longer be considered valid. The partial skeleton CM 11337 and the hind limb CM 15780 (as well as specimens CM 41689, CM 79050, DINO 556, DINO 1030, DINO 1032, and DINO 4225) are herein returned to *Camptosaurus*, as *Camptosaurus aphanoecetes*, revised combination. The braincase and cervical vertebrae that were formerly cataloged as part of CM 15780 are referred to *Dryosaurus* cf. *D. altus* under a separate specimen number, CM 87688.

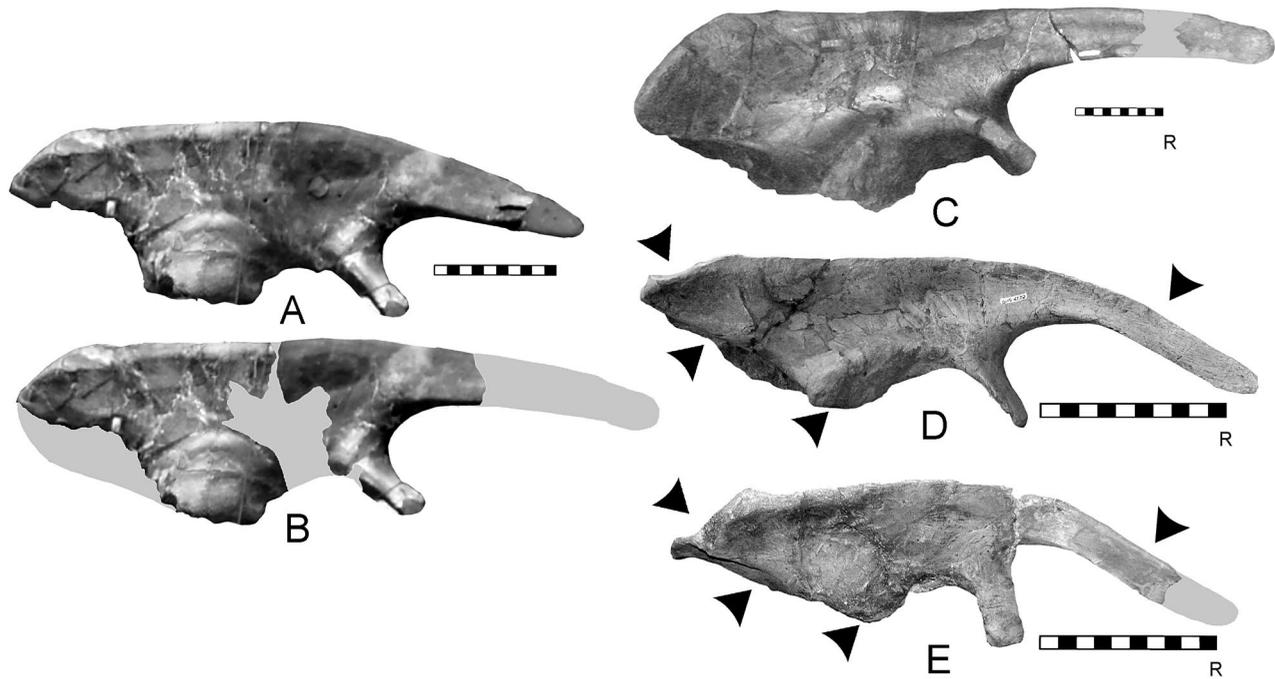


Fig. 10.—Comparison of the right ilium of *Camptosaurus prestwichii* in lateral view as currently reconstructed and mounted (A) with alternative reconstruction with missing areas shown in gray (B; based partially on Galton and Powell 1980). Ilium of *Camptosaurus dispar* (C, USNM 5473, reversed) and *Camptosaurus aphanoecetes* (D, DINO 4225, reversed; E, CM 11337, reversed) in lateral view. Darts in D and E note characters that are diagnostic for *Camptosaurus aphanoecetes* (see text). Note that the preacetabular process is anteroventrally curved in this species. Images marked with 'R' are reversed for ease of comparison. Scales = 10 cm. A, courtesy of J. Harris. D, courtesy of National Park Service.

Similarly, the reinstatement of the genus *Cumnoria*, which was first suggested by Naish and Martill (2008) and followed by McDonald (2011), is at odds with the long-standing tradition of regarding this genus as a junior synonym of *Camptosaurus* (Lydekker 1889; Gilmore 1909; Galton 1980; Galton and Powell 1980; Norman 2004). One of the characters used by Naish and Martill (2008) to separate the genera *Camptosaurus* and *Cumnoria*, the absence of a small antorbital fenestra in *Camptosaurus dispar*, is known to be erroneous (see Fig. 9). The proportionally small opening (which is only the approximate width of one maxillary tooth; Galton 1980) into the maxillary sinus on the dorsomedial side of the maxilla of *Cumnoria prestwichii* (the intramaxillary fossa of Galton and Powell 1980) is different from the much larger fenestra (~4–5 maxillary tooth widths; Galton 1980) of *Camptosaurus dispar*. In our view, however, this single distinction warrants the separation of *Cumnoria* from *Camptosaurus* at the specific rather than the generic level. Consequently and as also advocated by Galton and Powell (1980), we refer *Cumnoria prestwichii* to the genus *Camptosaurus*, and regard *Cumnoria* as a junior subjective synonym of *Camptosaurus* (revised synonymy).

In addition to the purported autapomorphy of *Uteodon*, which we have shown to be due to damage to a *Dryosau-*

rus braincase, *Uteodon* and *Cumnoria* were said to share a unique combination of characters that does not occur in *Camptosaurus*. As presented by McDonald (2011), this character combination is: 1) acromial process of scapula with convex anterior margin; 2) scapular blade with convex dorsal margin; 3) ilium with convex dorsal margin; 4) mediolateral thickening of dorsal margin of ilium; 5) postacetabular process of ilium tapers to a point with break in slope of dorsal margin; and 6) ischium with anteriorly expanded boot. We examine the alleged uniqueness of this character combination below.

The acromial processes of both scapulae of OXFUM J.3303, the holotype and only described specimen of *Cumnoria prestwichii*, are missing, as illustrated by Galton and Powell (1980: figs. 8a–b) and which can be seen as the maroon-colored restoration in McDonald (2011: fig. 3d). Thus, nothing can be said about the acromial process of this species. As for the acromial process reportedly being triangular in *Camptosaurus dispar* and more convex (i.e., rounded) in *Uteodon aphanoecetes* (sensu McDonald 2011), that is partly an artifact of the different perspectives of the photographs published by McDonald (2011: fig. 3a–c). The scapula of *Camptosaurus dispar* (McDonald 2011: fig. 3a) is shown in lateral view, whereas that of *Uteodon aphanoecetes* (sensu McDonald 2011: fig. 3b–c) is in

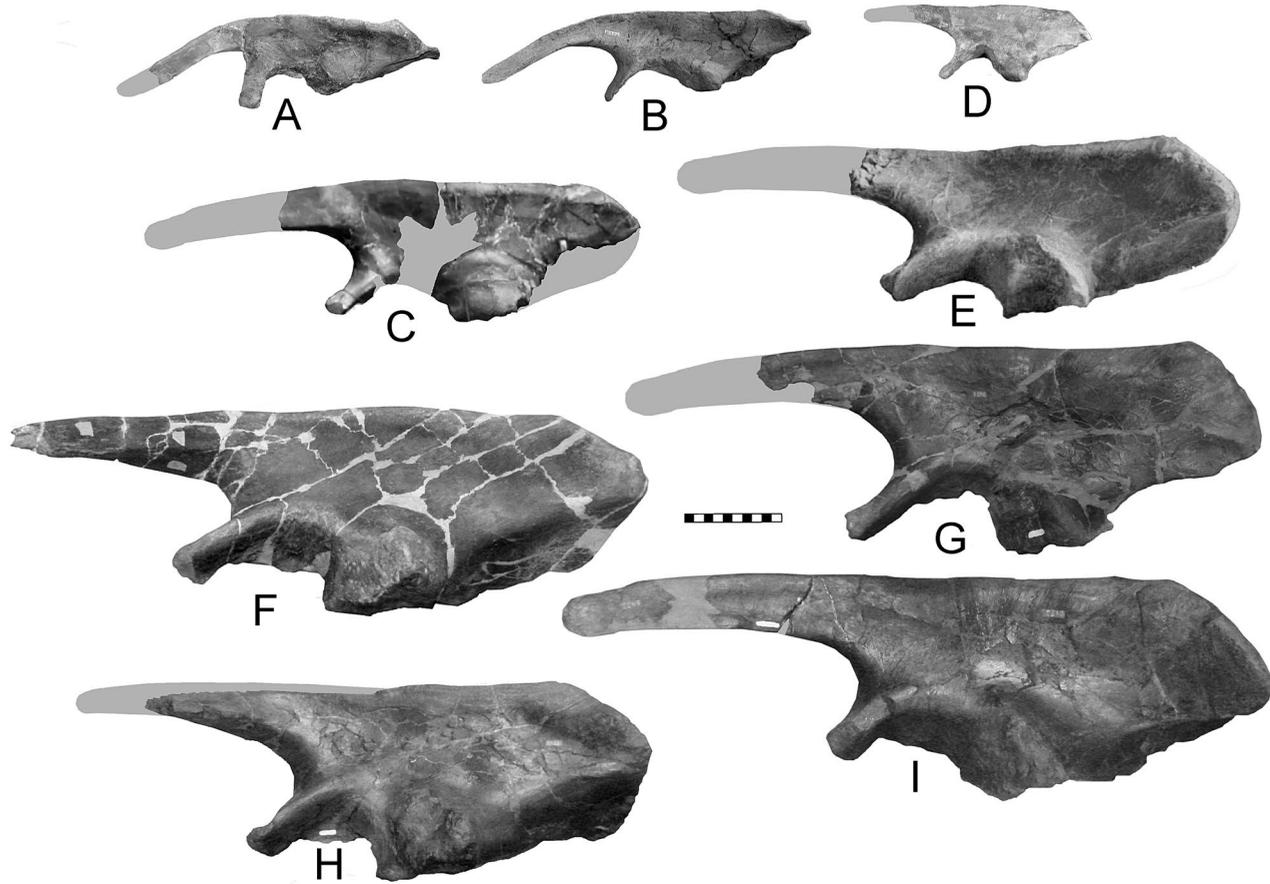


Fig. 11.—Comparison of ilia of *Camptosaurus aphanoecetes*, *Camptosaurus dispar*, and *Camptosaurus prestwichii* in lateral view showing how similar the ilium of *C. prestwichii* probably is to that of *C. dispar*. *Camptosaurus aphanoecetes* (A, CM 11337; B, DINO 4225). *Camptosaurus prestwichii* (C, OXFUM J.3303, reversed). *Camptosaurus dispar* (D, USNM 2210; E, YPM 1880; F, USNM 7631, reversed; G, USNM 5959, reversed; H, USNM 5818, reversed; I, USNM 5473, reversed). Missing areas shown in gray. B, courtesy of National Park Service. D, courtesy of M. Brett-Surman. Scale = 10 cm.

posterolateral view, which has the effect of foreshortening the acromial process, making it appear more triangular than it actually is. In addition, Carpenter and Wilson (2008: fig. 17) illustrated an array of acromial profiles in *Camptosaurus dispar*, including triangular, rounded, and truncated. As such, the shape of the acromial process cannot be used to distinguish *Camptosaurus dispar*, *Cumnoria prestwichii* (sensu McDonald 2011), and *Uteodon aphanoecetes* (sensu McDonald 2011), nor to separate the latter two taxa from the former. With regard to the shape of the dorsal margin of the scapular blade, Carpenter and Wilson (2008: fig. 17) illustrated a wide range of shapes of this margin in *Camptosaurus dispar*, ranging from straight (e.g., USNM 4282) to curved (USNM 5473), the latter as in the right scapula of *Cumnoria prestwichii* (sensu McDonald 2011; which is restored as more curved than the left) and the scapulae of *Uteodon aphanoecetes* (sensu McDonald 2011). Therefore, the range of variation in the dorsal contour of the scapula of *Camptosaurus dispar* indicates

that the curved dorsal margin of this bone in *Cumnoria prestwichii* (sensu McDonald 2011) and *Uteodon aphanoecetes* (sensu McDonald 2011) does not distinguish the latter two taxa from the former.

The morphology of the ilium also does not reliably separate *Cumnoria* and *Uteodon* from *Camptosaurus*. As with the scapulae of the *Cumnoria prestwichii* (sensu McDonald 2011) holotype (OXFUM J.3303), both ilia of this specimen are damaged, as illustrated by Galton and Powell (1980). This damage includes the loss of the central portions of both iliac bodies. An alternative reconstruction of the ilium of OXFUM J.3303 is possible, in which the dorsal margin is straight as in *Camptosaurus dispar* rather than convex (compare Fig. 10A to 10B). The preacetabular process of OXFUM J.3303 is also incomplete, and it too can be reasonably restored to resemble that of *Camptosaurus dispar* (Fig. 10C). The morphology of the resultant restoration of the ilium of OXFUM J.3303 is difficult to separate from that of *Camptosaurus dispar*, given the wide

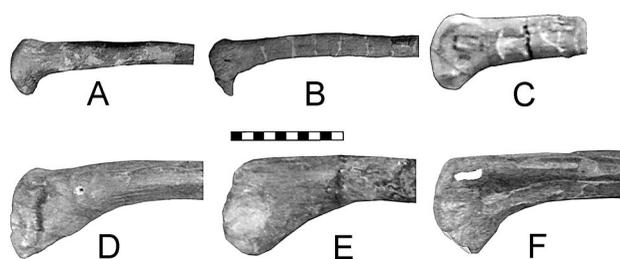


Fig. 12.—Comparison of the distal ends of the ischia of *Camptosaurus aphanoecetes* (A, CM 11337; B, CM 79050); *Camptosaurus prestwichii* (C, OXFUM J.3303); and *Camptosaurus dispar* (D, USNM 4282; E, USNM 5818, reversed; F, USNM 5818) in lateral view. C, courtesy of Jerry Harris. Scale = 10 cm.

range of variation in the latter (see Fig. 11). Both forms share the deep preacetabular notch of Carpenter and Ishida (2010), an anteroventrally projecting pubic peduncle, and a large, laterally facing ischial peduncle, characters that are widespread among iguanodontians. Furthermore, an ilium (DINO 4225) referable to *Camptosaurus aphanoecetes* that remains in situ on the quarry face at Dinosaur National Monument (Fig. 10D) has a straight dorsal margin and a deeper preacetabular notch than those of the holotype of this species (Fig. 10E). Therefore the curvature of the iliac dorsal margin varies among specimens of *Uteodon aphanoecetes* (sensu McDonald 2011), and the convex condition of the dorsal margin of the ilia of the holotype is less taxonomically significant than McDonald (2011) proposed. Additionally, the two other characters of the ilia of *Cumnoria prestwichii* (sensu McDonald 2011) and *Uteodon aphanoecetes* (sensu McDonald 2011) that McDonald (2011) included in the combination that supposedly separates these taxa from *Camptosaurus dispar*—the mediolateral thickening of the dorsal margin and the tapering of the postacetabular process with an associated break in slope along the dorsal margin—also occur in the latter (Fig. 10C).

Incidentally, the morphology of the isolated ilium DINO 4225 corrects some misinterpretations made by Carpenter and Wilson (2008) regarding the shape of this bone in *Camptosaurus aphanoecetes*. First, the preacetabular process is ventrally curved, not subhorizontal as is currently restored in the holotype of this taxon (CM 11337) and as was illustrated by Carpenter and Wilson (2008: fig. 24a). Judging from the orientation of the grain of the bone at the base of the preacetabular process of the holotype, this process was originally much more strongly curved, as shown in Figure 10E. However, due to a crack and a missing piece along its dorsal margin, it was assumed that this process was damaged, and it was reconstructed too straight. Consequently, the considerable ventral curvature of the preacetabular process should be added to the diagnosis of *Camptosaurus aphanoecetes* provided by Carpenter and Wilson (2008). Second, the postacetabular process is proportionally shallower than in *Camptosaurus dispar*

(Figs. 10–11). Gilmore (1925) noted that the ilium of CM 11337 was generally dorsoventrally lower than that of *Camptosaurus dispar*, including ilia of juveniles of the latter (Fig. 11D), contrary to what was claimed by Carpenter and Wilson (2008). Third, as seen in lateral view, there is a ‘step’ along the posterodorsal edge of the posterior end of the postacetabular process of *Camptosaurus aphanoecetes*, which is formed by the dorsal margin of the posterior projection of the brevis shelf (Figs. 10D–E). The apparent prominence of this ‘step’ partly depends on the orientation of the ilium relative to the viewer. Moreover, the relative width of the brevis shelf is variable in *Camptosaurus aphanoecetes*. The brevis shelf of the left ilium of the holotype is considerably wider than that of the right, but this is due to taphonomic distortion (Carpenter and Wilson 2008: fig. 13). The impact of this distortion on the appearance of the shelf is confirmed by the undistorted ilium DINO 4225, which shows that this shelf is not significantly wider than that in *Camptosaurus dispar* (Figs. 11D–I). Fourth, the ischial peduncle is less laterally prominent than it is in *Camptosaurus dispar*, including juvenile specimens of the latter (Fig. 11C). Finally, and contrary to Carpenter and Wilson (2008), the morphology of the preacetabular notch is variable in *Camptosaurus aphanoecetes* and therefore it is no longer considered taxonomically significant.

Turning to the last of the allegedly unique combination of characters shared by *Cumnoria prestwichii* (sensu McDonald 2011) and *Uteodon aphanoecetes* (sensu McDonald 2011), the distal end of the ischium does have an anteriorly expanded boot in these taxa (McDonald 2011). Nevertheless, this anterior expansion of the distal ischium is also present in some specimens of *Camptosaurus dispar*; indeed, the ischial boots of the three taxa are difficult to distinguish from one another (Fig. 12). Consequently, the combination of characters that McDonald (2011) claimed to be limited to *Cumnoria* and *Uteodon* also occurs in *Camptosaurus*, and therefore it cannot be used to justify the continued separation of the former genera from the latter.

Several other putative distinctions between the appendicular skeletons of *Camptosaurus dispar*, *Cumnoria prestwichii* (sensu McDonald 2011), and *Uteodon aphanoecetes* (sensu McDonald 2011) are doubtful as well. For instance, the broken coracoids of *Cumnoria* (sensu McDonald 2011) were reconstructed as having a rounded anterior margin, but their component pieces can also be reconstructed to have the blockier, more squared shape of *Camptosaurus*. In overall proportions, the humerus of *Cumnoria* (sensu McDonald 2011) resembles that of *Camptosaurus aphanoecetes*, but it also falls with the morphological range seen in *C. dispar*. Indeed, the humerus of the latter taxon shows a wide range of variation in anterior view (Carpenter and Wilson 2008): from straight (USNM 5473) to bowed laterally (USNM 4282); from having the proximal end only slightly wider than the distal end (USNM 5473) to having it significantly wider (USNM 4281); from having the proximal end flat (USNM 4282), to

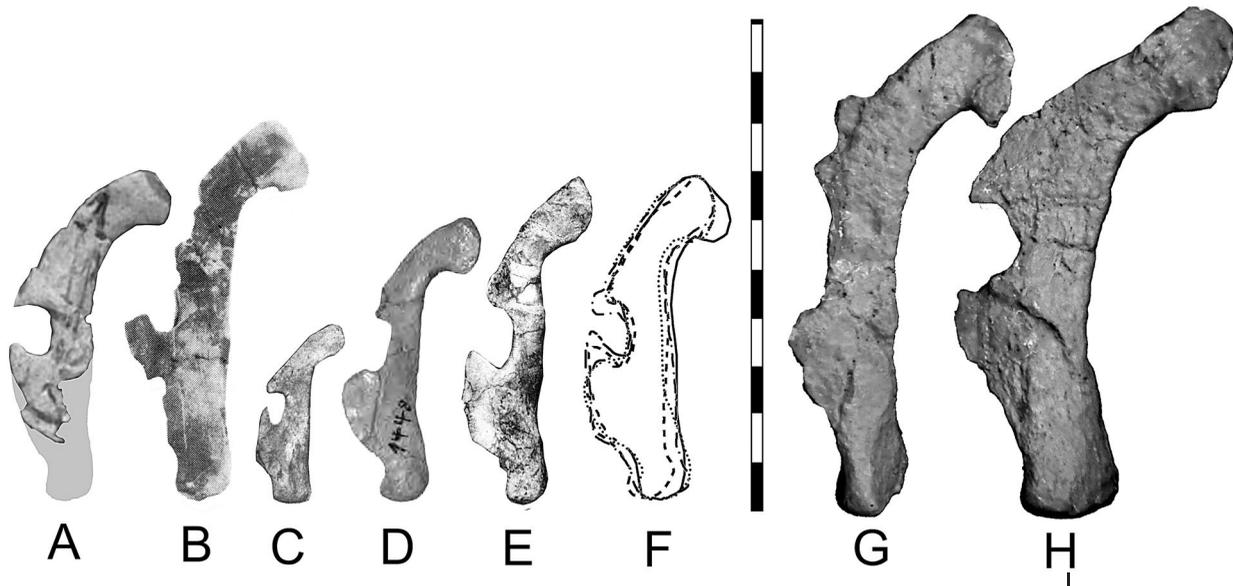


Fig. 13.—Comparison of basal iguanodontian quadrates in left lateral view. *Dryosaurus* cf. *D. altus*: A, CM 3392 (missing ventral portion restored after YPM 1876). *Dryosaurus altus*: B, YPM 1876 (reversed, modified from Galton [1983]). *Dysalotosaurus lettowvorbecki*: C, MB.R.1326 (adapted from Janensch [1955]); D, GPIT/RE/3608 (adapted from Hübner [2011]); E, MB.R.1320 (adapted from Janensch [1955]). F, range of variation in the quadrates of *Dysalotosaurus lettowvorbecki* evident in outlines of C–E. *Camptosaurus dispar*: G, DMNH 50131 (left quadrate); H, DMNH 50131 (right quadrate, reversed). Note the variation of the quadrates of *Camptosaurus dispar* (DMNH 50131) from both sides of the skull.

slightly convex (USNM 2210), to strongly convex (USNM 5473). The deltopectoral crest of *Cumnoria prestwichii* (sensu McDonald 2011) has a blocky outline, as in *Camptosaurus dispar*, as opposed to the more rounded contour of *Camptosaurus aphanoeetes*. In addition, it extends proportionally less anteriorly than in large specimens of *Camptosaurus dispar* (e.g., USNM 4281, USNM 5473) but more so than in juveniles (USNM 2210). Whether the ischial shaft of *Cumnoria* (sensu McDonald 2011) was straight as in *C. aphanoeetes*, or bowed as in *C. dispar*, cannot be determined from the fragments of this element that are known.

In summary, based on the osteological evidence presented above, we regard the few distinctions between *Camptosaurus dispar*, *Cumnoria prestwichii* (sensu McDonald 2011), and *Uteodon aphanoeetes* (sensu McDonald 2011) as indicative of separation at the specific rather than the generic level, and the genera *Cumnoria* and *Uteodon* as junior subjective synonyms of *Camptosaurus* (***Cumnoria* as revised synonymy, and *Uteodon* as new synonymy**). The species *Cumnoria prestwichii* and *Uteodon aphanoeetes* are returned to *Camptosaurus*, as ***Camptosaurus prestwichii*, revised combination, and *Camptosaurus aphanoeetes*, revised combination**, respectively.

Upper Jurassic Dryosaurid Taxonomy

The *Dryosaurus* cf. *D. altus* specimen described above also prompts brief comments on the taxonomy of Upper Juras-

sic members of Dryosauridae. *Dryosaurus altus* was erected by Marsh (1894) for material he had previously named as *Laosaurus altus* (Marsh, 1878). Galton (1977) referred a second species to *Dryosaurus*, *D. lettowvorbecki*, for material previously named *Dysalotosaurus lettowvorbecki* by Virchow (1919). Galton (1977) was partially influenced by the then-emerging field of plate tectonics, and sought to show connections of the North American, European, and African plates that could allow for intercontinental dispersal of this terrestrial genus (Galton pers. comm.). Although Galton (1981, 1983) later elaborated upon the proposed synonymy of *Dysalotosaurus* and *Dryosaurus* based on a suite of cranial and postcranial characters, this has recently been challenged by Hübner and Rauhut (2010) and Hübner (2011, 2012). Hübner (2011:9) stated that most anatomical differences between *Dryosaurus* and *Dysalotosaurus* are “not explainable by intrageneric variation.” Among other lines of reasoning, he claimed that the differences in the postcrania of *Dryosaurus* and *Dysalotosaurus* are greater than those between many accepted hadrosaur genera, and interpreted this as evidence that supports the generic separation of these two dryosaurids (Hübner 2011). Nevertheless, although lambeosaurine hadrosaurids (and chasmosaurine ceratopsids) do indeed have very conservative postcrania that render generic identification based solely on this part of the skeleton difficult (Carpenter 2010), similar morphological conservatism has not been demonstrated for non-hadrosaurid iguanodontians and there is no a priori reason to assume that it existed.

Hübner (2011) based another part of his argument for

generic separation on the quadrate, noting that the only preserved quadrate of the *Dryosaurus* specimen CM 3392 (the left) has a “concave posterior edge of the shaft and a consistent transition between the shaft and cotylar head,” thus resembling the quadrate of *Camptosaurus* in these regards (Hübner 2011:10). However, computed tomographic images of the CM 3392 skull reveal that the ventral (distal) third of the quadrate is reconstructed in plaster (Witmer pers. comm.), and as such, this purported concavity is at least partly an artifact. An alternative reconstruction is possible (Fig. 13A) that more closely resembles the quadrate of the *D. altus* holotype (YPM 1876; Fig. 13B). Consequently, the differences between these two *Dryosaurus* quadrates are probably less substantial than Hübner (2011) maintained, and would appear to fall within the range of variation of quadrates assigned to *Dysalotosaurus* (Figs. 13C–F). As for the quadrate of *Camptosaurus*, it can show considerable bilateral asymmetry: for instance, the left quadrate of DMNH 50131 has a comparatively straight shaft, thereby resembling that of *Dysalotosaurus*, whereas the right quadrate is concave posteriorly (Figs. 13G–H). There is no doubt that these two *Camptosaurus dispar* quadrates belong to the same individual, because they were found as part of a single associated skeleton.

One major but perhaps underappreciated difference between dryosaurid specimens from the Morrison Formation and the Tendaguru Beds is that the latter come from a single locality and stratum and therefore probably represent a single population (Hübner 2011, 2012). In contrast, the Morrison specimens come from multiple stratigraphic intervals that collectively span at least five million years. It seems inconceivable that no evolution would have occurred in *Dryosaurus* during this long temporal interval. Nevertheless, whether the lower Tithonian Carnegie Quarry specimens (e.g., CM 3392, CM 87688) represent a species distinct from the lower Kimmeridgian Como Bluff Quarry 5 specimen (YPM 1876), a possibility acknowledged by Hübner (2011), cannot be resolved without a thorough reanalysis of *Dryosaurus* (sensu stricto) that includes the numerous new specimens that have been found since Galton’s (1977, 1981, 1983) seminal studies. In light of the great similarities between *D. altus* and *D. lettowvorbecki*, it is still possible that the differences between these taxa cited by Galton (1981, 1983) and Hübner (2011) could reflect specific rather than generic separation. Ultimately, this distinction is a semantic one that hinges on the philosophical argument of what constitutes a morphological genus versus what constitutes a species (Carpenter 2010).

CONCLUSIONS

As it was described by McDonald (2011), the iguanodontian ornithopod *Uteodon* is a chimera consisting of a braincase of *Dryosaurus* cf. *D. altus* and the dentary and postcrania of *Camptosaurus aphanoeetes*. The braincase in

question provides new information on this part of the skeleton in *Dryosaurus*, especially the parasphenoid. Based on anatomical evidence, we regard the iguanodontian genera *Cumnoria* and *Uteodon* as subjective synonyms of *Camptosaurus* (***Cumnoria* as revised synonymy, and *Uteodon* as new synonymy**), and return the species *Cumnoria prestwichii* and *Uteodon aphanoeetes* to *Camptosaurus*, as ***Camptosaurus prestwichii*, revised combination, and *Camptosaurus aphanoeetes*, revised combination**, respectively.

ACKNOWLEDGMENTS

We thank A. Henrici (Carnegie Museum of Natural History) for access to CM 87688, CM 3392, and CM 15780, and for providing archival data. The late E. Hill (Carnegie Museum of Natural History) completed the arduous task of transcribing Earl Douglass’ records. MCL acknowledges A. McDonald (University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.) for discussions on basal iguanodontian anatomy and systematics. M. Brett-Surman (National Museum of Natural History, Washington, DC, U.S.A.) provided loan of USNM 5473, a braincase of *Camptosaurus dispar*, as well as the image of the ilium of USNM 2210 (also *Camptosaurus dispar*) used in Fig. 11D. Thanks also to J. Harris (Dixie State University, St. George, Utah, U.S.A.) for an image of the *Camptosaurus prestwichii* skeleton at the Oxford University Museum of Natural History, D. Chure (National Park Service, U.S.A.) for images of the *C. aphanoeetes* ilium DINO 4225, and R. Benson (University of Oxford, England) for images of the pelvis of *C. prestwichii*. L. Witmer (Ohio University, Athens, Ohio, U.S.A.) shared information from a computed tomographic scan of the skull of *Dryosaurus* cf. *D. altus* (CM 3392). Special thanks to C. Miles (Western Paleontological Laboratories, Lehi, Utah, U.S.A.) for the donation of DMNH 50131, a skull of *Camptosaurus dispar* from Bone Cabin Quarry West, Wyoming, to the Denver Museum of Nature and Science. Finally, we are grateful for review comments by A. McDonald and an anonymous reviewer, which improved the original manuscript, and comments by editors J.R. Wible and J.E. Rawlins, which greatly improved the revisions.

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APPENDIX 1

Selected Carnegie Quarry at Dinosaur National Monument block numbers and contents listed by Earl Douglass (from his unpublished Record Book 1909–1923), with additional comments by the present authors provided in brackets. Number 310 is an articulated sequence of cervical and dorsal vertebrae and ribs of a large individual of the sauropod *Barosaurus lentus* (CM 11984).

NUMBER 310. BLOCK NUMBERS.

Block 310/A. Portions of three Cervicals, 310/1, 310/2 and 310/3. (F^a:e30). Box 416.

Block 310/B. Parts of two Cervicals. 310/4 and 310/5. (E^b:e33). Box 393.

Block 310/C. Cervicals. (E:e36). Probably greater portions of cervicals 310/6 and 310/7. Box 429.

Block 310/D. Cervicals. (E^a:e39). Probably Cervical 310/10, and part of 310/7. Box 396.

Block 310/E. Cervical. (C^c:e40). Probably Cervical 310/11 and part of 310/12. Box 373A. Box 408.

Block 310/F. Cervical, and two small Limb Bones. (C^a:e42). Cervical 310/12. Also No. 215 [sic]. Two small limb bones. Box 373A. [“215” is clearly erroneous here, and should have been written “315”]

Block 310/G. Cervicals. (B^b:e43). Cervical 310/13 and part of No. 310/15. Box 410. Box 426? Box 446. [includes left humerus, radius, and ulna of *Stegosaurus* sp. CM 21765]

Block 310/H. Two Vertebrae. (B:e45). Probably last Cervical and first Dorsal. Parts. Other portions in Block 310/I. [includes *Campotossaurus aphanoecetes* fibula, dorsals; partial small centrum]

Block 310/I. Vertebrae. (B:e45). Connects with Block 310/H and with that block contains larger portion of Nos. 310/15 & 310/16. Box 374.

Block 310/J. Vertebrae. (A^b:e48). Apparently posterior portion of the last Cervical, and the three anterior Dorsals. Small portions of Centra of one or two Dorsals in Block 310/M. Box 397. [includes *Dryosaurus* cf. *D. altus* vertebra CM 41684]

Block 310/K. Vertebrae. (A^c:e50). Two Dorsals. Probably fourth and fifth. Box 392.

Block 310/L. Toe Bones etc. (A^c:e43). Toe Bones and parts of small Ribs. Box 402.

Blocks 310/La,b,&c. (A^b:e44). Belongs with Block 310/L. Box 402.

Block 310/M. Vertebrae etc. (A^a:e46). Contains small portions of anterior Dorsals. Also a Claw. Part of Neck of “*Uintasaurus*” No. 325. Part of Jaw probably belonging to the same. Box 374. [includes Sauropoda indet. pes CM 42294; *Stegosaurus* sp. caudal vertebra and hemal arches CM 41683]

Block 310/N. Toe Bones etc. (A^b:e44). Toe Bones probably belonging with 310 Portions of Neck and Skull of No. 325. Box 395. [includes partial jaws with teeth, cervical vertebrae, and cervical ribs of *Camarasaurus* cf. *C. lentus* field number 325/CM 11969; right ulna of juvenile *Camarasaurus* sp. CM 42275; braincase and cervicals of *Dryosaurus* cf. *D. altus* CM 87688]

NUMBER 315.

DINOSAUR. (B^b:e42). Box 373A Two small limb bones. [Includes right femur, tibia, fibula, astragalus, and metatarsal IV of *Campotossaurus aphanoecetes* CM 15780]