

Behavior of hadrosaurs as interpreted from footprints in the "Mesaverde" Group (Campanian) of Colorado, Utah, and Wyoming

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ABSTRACT

Dinosaur footprints are common in the ceiling rocks of many coal mines in the "Mesaverde" Group of Colorado, Utah, and Wyoming. Bones from the "Mesaverde" Group provide a clue as to the possible identity of the footprint makers. The bone collections are dominated by an unidentifiable genus of lambeosaurid hadrosaur. The hadrosaurid *Maisaura* is also present, although it is rare. Ceratopsids also occur, and a skull is tentatively referable to *Anchiceratops*. Theropods are rare and include dromaeosaurids and tyrannosaurids. Thescelosaurids, ankylosaurids and nodosaurids are extremely rare and are known only from the shed teeth.

A comparison of the "Mesaverde" Group footprints with the foot bones of representatives of the families known from the "Mesaverde" bone assemblages identify the footprints as being made by hadrosaurs, a tyrannosaurid, and a ceratopsid. As yet no dromaeosaurid, thescelosaurid, ankylosaurid, or nodosaurid footprints are known from the "Mesaverde" Group, suggesting that they rarely, if ever ventured into the swamps.

The abundance of hadrosaur footprints at two localities, one near Price, Utah and the other near Grand Mesa, Colorado, are interpreted as evidence of herding for group protection. Such conclusions appear to be supported by mass accumulations of skeletons that have been interpreted as evidence of herding. Azimuth plots of hadrosaur footprints from the two localities show that most of the animals were traveling south, and, based on footprint speeds from one of the mines, were not traveling rapidly. Because so many animals from two separate sites were traveling in the same direction, it is suggested that these animals might have been migrating. The shallowness of the footprints, even of twenty ton animals, the incompleteness of trackways due to missing footprints, the presence of hatchling hadrosaur footprints, and charcoal due to fires indicate that the hadrosaurs ventured into the swamps late in the dry season, and probably during a drought when the substrate was dried out.

The presence of hatchling footprints suggests that egg hatching in hadrosaurs coincided with the start of the rainy season when new plant growth would be available. That the rainy season during the Campanian did not always occur on schedule may explain why the swamps were not inundated at the time the tiny footprints were made (otherwise the hatchlings would have floated). The lack of rain and absence of new plant growth may also explain the high mortality rates for juvenile hadrosaurs in upland nesting sites. This suggests the possibility that regions affected by droughts were occasionally widespread during the Campanian just as they are today.

INTRODUCTION

Numerous dinosaur footprints are known from the ceilings of many coal mines in the "Mesaverde" Group of Colorado, Utah and Wyoming. An early account of these footprints by Brown (1938) was very brief and tended towards sensationalism. These footprints played an important role in a recent debate about the speed of hadrosaur locomotion (Russell and Beland, 1976; Thulborn, 1981; Russell, 1981; Thulborn, 1982, 1984; Lockley and others, 1983). The history behind the collecting of this trackway was recently given in the posthumous memoir of R. T. Bird (1985) who assisted Brown in their excavation. Other reports of footprints from the "Mesaverde" are even more brief: Peterson (1924), Strevell (1932, 1940), Look (1951, 1955), Rigby and others (1966), Wilson (1969), Collins (1976), Lockley (1984, 1986a), Parker and Balsley (1986), Rowley and Parker (1986), Lockley and Jennings (1987), Lockley and Conrad (1989), Parker and Balsley (1989), and Rowley and Parker (1989).

These reports indicate how abundant and inadequately studied are most "Mesaverde" footprint sites. Two additional reports, by Balsley (1980) and Lockley and others (1983), are more informative, giving maps of the footprints in the mine ceilings. These maps are reproduced in Figures 1 and 2 and form the basis, in part, of this study.

STRATIGRAPHY, AGE, AND DEPOSITIONAL ENVIRONMENT OF THE "MESAVERDE" GROUP

The two main footprint localities used in this study are about 290 km apart, while the main dinosaur localities of B. Brown near Rock Springs, Wyoming, are about 360 km from both footprint localities (see Fig. 3). The name of the coal mine and seam represented by Figure 1 was not given by Balsley (1980), although it is most certainly in the Blackhawk Formation in the vicinity of Price, Utah. These footprints will be referred to as the Price footprints. The footprints of Figure 2 occur in the Number Two Coal Seam in the Bowie Member of the "Mesaverde" Formation in the Grand Mesa Coal Field, Colorado (Lockley and others, 1983). These will be referred to as the Grand Mesa footprints.

The term Mesaverde has frequently been applied to many Upper Cretaceous coal-bearing rocks outside the San Juan Basin (Reeside, 1924). The problems of this application are numerous and have been discussed in detail by Lillegraven and McKenna (1986). They concluded such usage is incorrect; therefore "Mesaverde" will be used for those rocks in the Colorado-Utah-Wyoming area.

The "Mesaverde" Group or Formation records the eastward regression of the Late Cretaceous seaway across Utah, Colorado and Wyoming. This withdrawal of the sea (R8 of

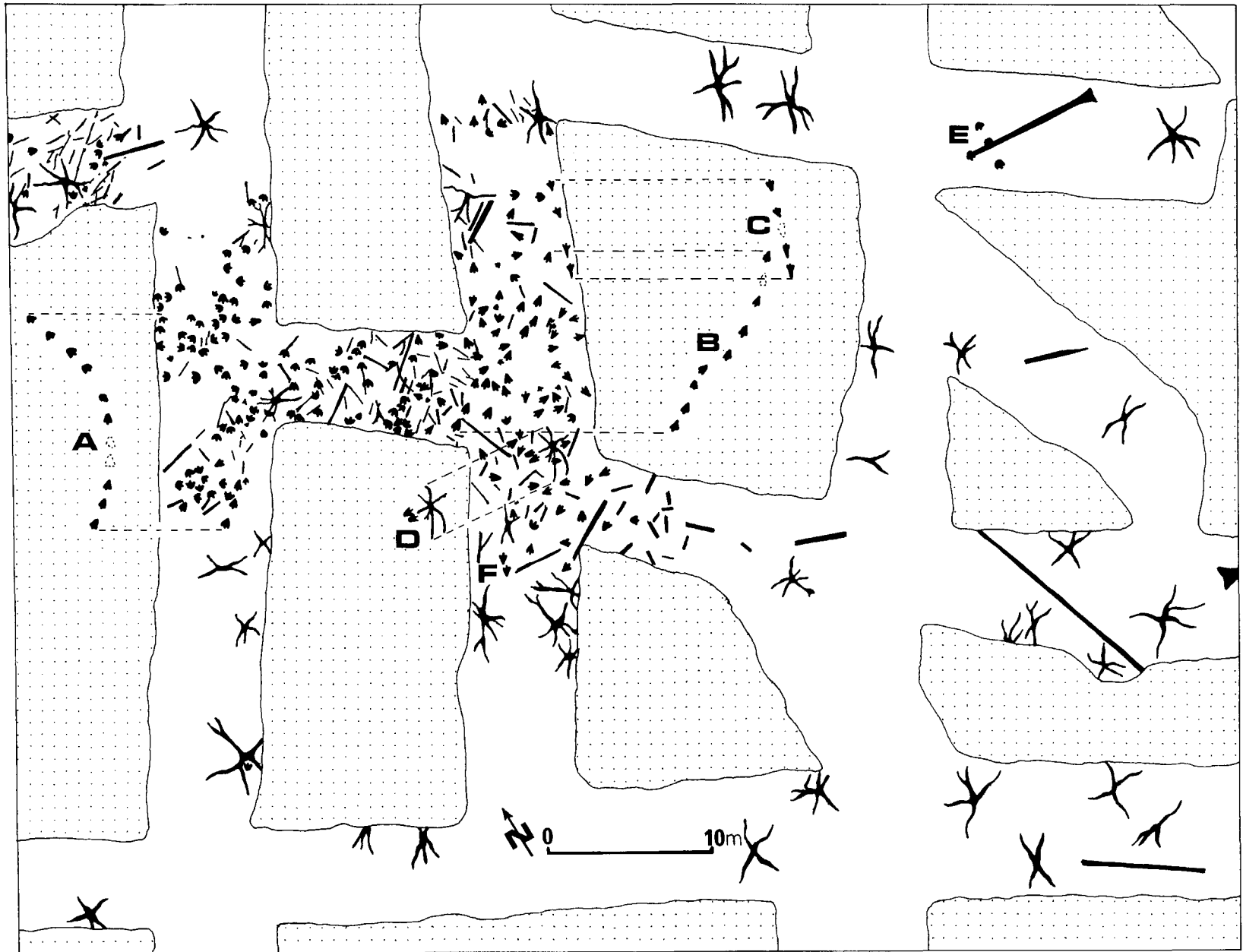


Figure 1. Map showing the distribution of footprints from the Blackhawk Formation, Mesaverde Group, Utah. Possible trackways shown in insets A, B and C. D, paired footprints suggesting a hadrosaur feeding from a tree. Other features include major roots of erect trees, logs and other tree debris. Stippled areas are unmined coal pillars. Modified from Balsley, 1980.

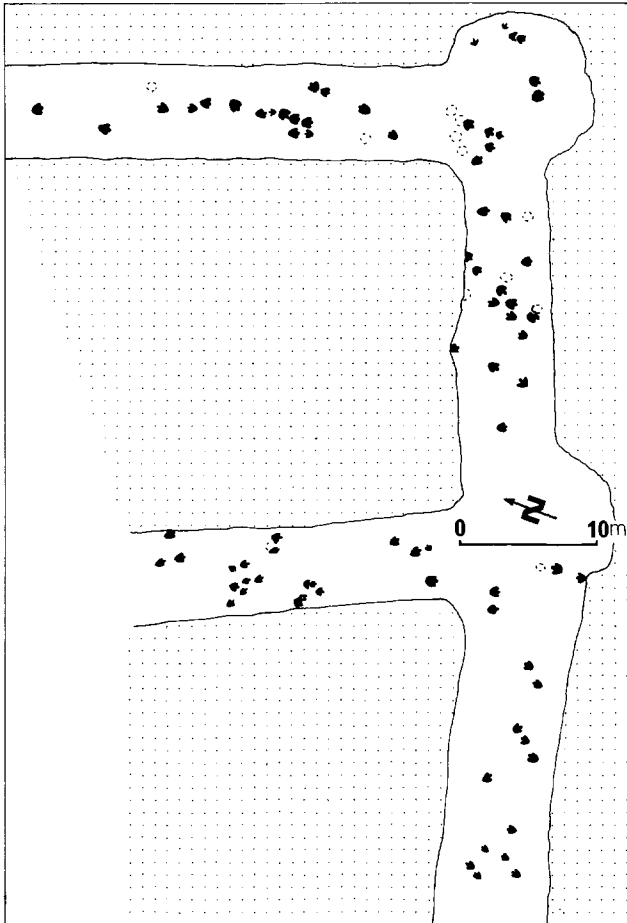


Figure 2. Map showing the distribution of footprints in the Bowie Shale Member, Mesaverde Formation, Colorado. Stippled areas are unmined coal pillars. Modified from Lockley and others, 1983.

Kaufmann, 1977) was erratic, as indicated by the brief pulses of transgression (Fig. 3) that serve to separate formations or members. In Wyoming and parts of northwestern Colorado, deposition of the "Mesaverde" ended with a final transgression of the seaway (T9 of Kaufmann, 1977), but in central-western Colorado and Utah, deposition of the "Mesaverde" apparently continued uninterrupted to the end of the Cretaceous. The start of this regression is believed to coincide with renewed tectonism in western Utah with the sediments shed eastward. The regressive phase is preserved as a complex of facies interpreted as accretionary ridges, barrier island, lagoonal, prodelta, delta front, delta mouth bars, distributary, interdeltic, and fluvial coastal plain (Balsley, 1980; Flores and others, 1982; Kiteley, 1983; Kirschbaum, 1986).

The footprint-bearing Blackhawk Formation in the vicinity of the Price footprints is bracketed between the underlying *Scaphites hippocrepis* (= *Haresiceras montanaense*) zone (Cobban, 1977) of the Aberdeen Sandstone and overlying *Baculites asperiformis* zone of the Castlegate Sandstone (Gill and Hail, 1975). Radiometric dates of these zones (82 Ma - 77.5 Ma, Kaufmann, 1977) indicate a span of 4.5 my. The Grand Mesa footprints are more recent, occurring just above

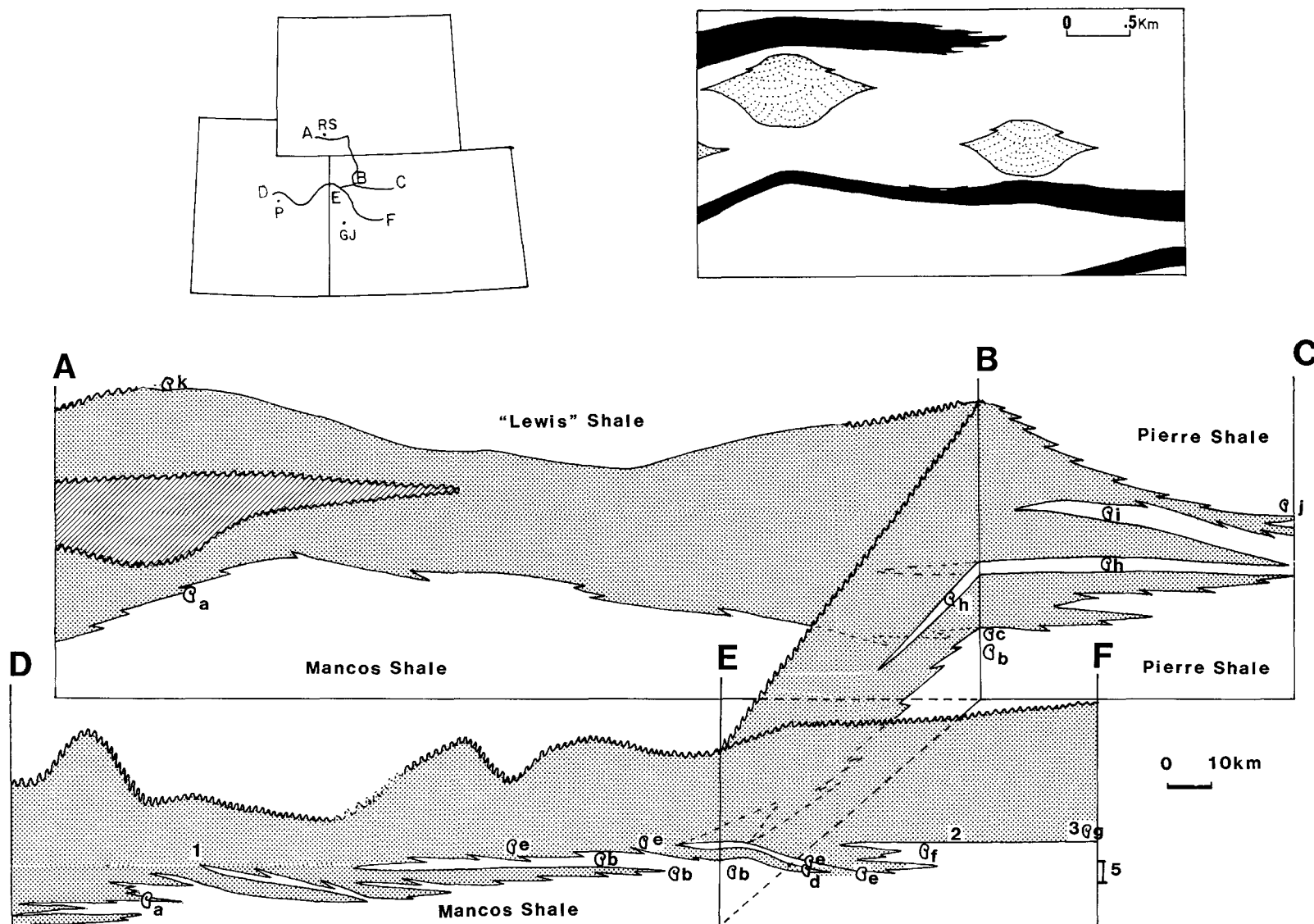
the *Didymoceras stenosoni* zone of the Rollins Sandstone (Gill and Hail, 1975). Towards the north and northeast, the lateral equivalent of the Bowie Member is overlain by a tongue of the Pierre Shale with *Baculites reesidei* (Izett, Cobban and Gill, 1971). Radiometric dates (72.75 Ma - 69 Ma) indicate a span of 3.25 my separate these two zones (Kaufmann, 1977).

In the Rock Springs area, *S. hippocrepis* is also present immediately below the "Mesaverde" Group, while *Baculites baculus* occurs at the base of the overlying Lewis Shale (Kirschbaum, 1985, 1986). A major regional unconformity occurs within the "Mesaverde" Group (Gill and Cobban, 1973) with possibly 18 ammonite zones missing near Rock Springs (*Haresiceras placentiforme* - *Baculites cuneatus* zones); this represents 11 my (Kaufmann, 1977). The dinosaur bones collected by Brown occur in the Almond Formation, which correlates to the east between the *Baculites reesidei* zone (Gill and Cobban, 1973) and the top of the *Baculites eliasi* zone. Radiometric dates of 69 Ma and 68.75 Ma separate these zones (Kaufmann, 1975).

This bracketing by ammonite zones indicate that the Price footprints correlate with the lower Two Medicine Formation dinosaur fauna of Montana (see Horner, 1984b). The Grand Mesa footprints correlate with the Judithian dinosaur faunas of the upper Two Medicine and Judith River formations of Montana and Alberta (see Horner, 1984b, and Dodson, 1983). And the Brown dinosaur collection from Rock Springs correlates with the Horseshoe Canyon Formation dinosaur fauna of Alberta (see Russell, 1985). An "Edmontonian" age for part of the "Mesaverde" is in agreement with the conclusions reached by Archibald (1987), Lillegraven (1987), and Lillegraven and Ostresh (1990) based on mammals.

During the deposition of the "Mesaverde" Group, coal swamps developed in the interdeltic, sea level deltaic, and especially the coastal plain environments (Balsley, 1980; Parker and Balsley, 1989). Most of the coals are freshwater in origin, although the proximal ends of the interdeltic swamps may have had some brackish water influence. As may be seen by the inset to Figure 3, most of the coals of the coastal plain occur in a sequence of overbank sediments with offset lenticular channel bodies. The overbank sediments are massive to weakly bedded and show penetration by roots. Some laminated lacustrine sediments also occur. The lenticular sandstones (shoestring channels) are typically 17 to 200 m wide and 1 to 3.3 m thick. The virtual absence of fine-grained channel-filled cutoffs suggests that most of the streams were not very sinuous, and that avulsion onto the lower floodplain was frequent (Balsley, 1980).

The floral composition of the Blackhawk Formation swamps has been determined by Parker (1975; see also Parker and Balsley, 1989) and may indicate the diet of the herbivorous dinosaurs that entered the swamps (e.g. Price footprints). Based on the co-dominance of two trees, these swamps may be referred to as *Sequoia cuneata*-*Rhamnites emimens* swamps, and are analogous to the extant bald cypress-water tupelo swamps of Mississippi and Louisiana. Subordinate trees include the conifers *Protophyllocladus polymorpha*, *Brachyphyllum macrocarpum* and *Moriconea cyclotoxan*, and the angiosperms *Cissus marginata* and *Plata-*



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Figure 3. Stratigraphic cross-section of the "Mesaverde" Group (stippled) in northeastern Utah, northwestern Colorado and southwestern Wyoming; intraformational unconformity in the Rock Springs area shown by cross-hatching. Upper contacts of the Lewis Shale and Pierre Shale along line A-C not shown. Base line corresponds to the top of the Niobrara Formation *Haresiceras montanaense* zone. 1, approximate level of footprints shown in figure 1. 2, approximate level of the State-Hall Mine (see text). 3, approximate level of footprints shown in Figure 2. 4, approximate level of bones in Figure 4. 5, relative position of the type Mesaverde Group for comparison. This corresponds to Regression 7, whereas the "Mesaverde" mostly corresponds to Regression 8 (see Kaufmann, 1977). Ammonites: a, *Scaphites hippocrepis*; b, *Baculites asperiformis*; c, *B. perplexus*; d, *B. gregoryensis*; e, *B. scotti*; f, *Didymoceras nebrascense*; g, *D. stevensoni*; h, *Exiteloceras jenneyi*; i, *B. reseedei*; j, *B. eliasi*; k, *B. baculus*. Abbreviations: GJ - Grand Junction, CO; P - Price, UT; RS - Rock Springs, WY. Data for cross-section from Fisher, Erdmann and Reeside (1960); Miller (1970); Gill and Hail (1975); Johnson and Finn (1986). Inset: relationship of sandstone bodies to overbank and coal deposits (black), lower Blackhawk Formation, Wasatch Plateau, Utah (modified from Sanchez and Brown, 1986).

nus raynoldsii. A common understory shrubby tree, which actually may have occurred along the margins of the swamps, was the palm, *Phoenicites imperialis*. Two cycad-like plants also occurred, but were rare: *Nageiopsis* sp. and *Podozamites* sp. Herbaceous understory plants consisted of the ferns *Cyathea pinnata* and *Onoclea hebridica*. Such ferns probably did not live on inundated soil, but along the better drained swamp margins, as well as on tree buttresses, floating logs, and decaying stumps. The water lily, *Nymphaeites dawsoni*, and the water chestnut, *Trapa paulula* are the only two aquatic plants known from the swamps.

Most of the dinosaur footprints occur in the lower part of the Blackhawk Formation (lower "Mesaverde" Group) in Utah and the Bowie Shale Member (lower Williams Fork Formation) in Colorado. The footprints occur as siltstone and fine sandstone casts in the ceilings of the mines and occasionally in the mine floor. These sediments of the mine ceilings indicate that their deposition is linked to the infilling of the footprints pressed into the coal peat. The thin, tabular nature of most of these siltstone and sandstones intercalated with coals and carbonaceous shales indicate crevasse splay or flood deposits (Balsley, 1980).

AFFINITIES OF THE FOOTPRINTS

One of the earliest attempts to determine the footprint maker in the "Mesaverde" Formation was by W. D. Matthew (in Peterson, 1924). He concluded that the track maker was a tyrannosaurid, although he did not elaborate. I suspect the major reason was the large size of the tridactyl tracks observed by Peterson (1924). At the time of Peterson's description, the tyrannosaurid *Tyrannosaurus* was the largest tridactyl dinosaur known from North America. Recently, Haubold (1984) formally recognized the footprints by calling them *Tyrannosauripus*.

Barnum Brown disagreed with Matthew, concluding that the footprint maker was not a tyrannosaurid, but a giant iguanodontid, and he spent a field season looking for its skeleton (Brown, 1983; Bird, 1985). Brown had little success in Colorado, but did considerably better in Wyoming finding several partial skeletons and skulls of dinosaurs. None, however were of the giant "mystery dinosaur" despite allusion to it by Brown (1938). Field notes of E. Schlaikjer in the archives of the American Museum of Natural History refer to the specimens from Wyoming as coming from the Almond Formation of the "Mesaverde" Group.

Brown was evidently not aware that the "Mesaverde" at Rock Springs was many millions of years younger than the "Mesaverde" in Colorado (see discussion above). Thus, it would have been doubtful that any of the skeletons found by Brown at Rock Springs could have been that of the footprint maker in Colorado.

A list of the materials collected or seen in the field by Brown and his party is presented in the Appendix along with locality data and some measurements. A few of the specimens are illustrated in Figure 4. Additional dinosaur material from the "Mesaverde" is also listed (see also Breithaupt, 1985, for a composite list based on other sites).

As with most North American Late Cretaceous dinosaur faunas, hadrosaurs dominate the material collected by Brown.

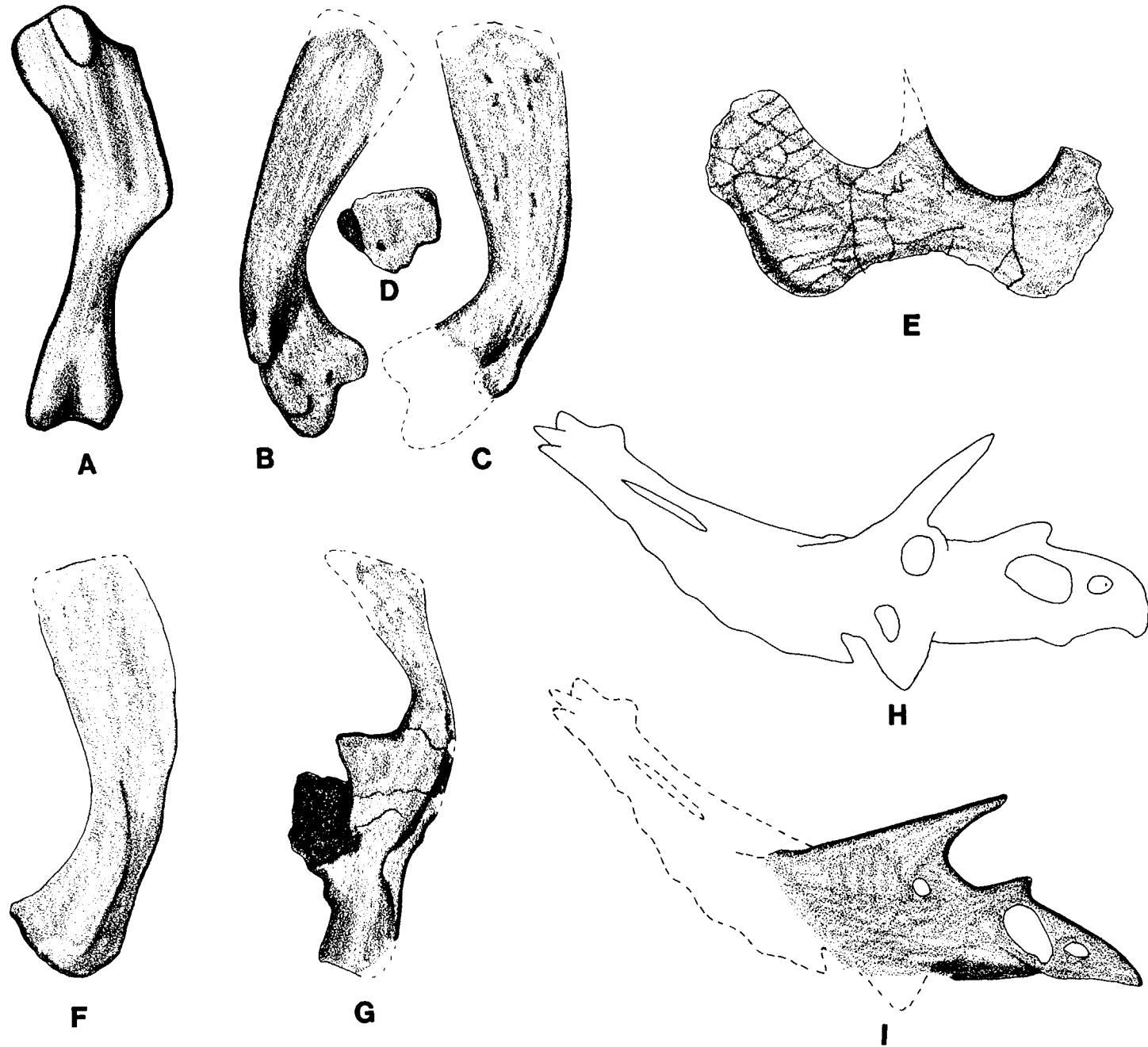
Except for a lambeosaurid, most of the hadrosaur material is not identifiable. Identification of the lambeosaurid is based upon the characteristic short, deep-bodied jugal (Fig. 4E).

A partial ceratopsian skull was also found, which Brown (1938) believed to be a new species. Unfortunately, I have been unable to locate the specimen in the American Museum of Natural History (AMNH). A field photograph of the specimen in the archives of the AMNH was used to make Figure 4H. The skull is encrusted in limonitic matrix. However, it does show that the orbit is rather small and oval, that the brow horns project forward, that the nasal horn is small, projects forward and is located over the posterior portion of the external nares, and that the muzzle is long. The skull closely resembles that of *Anchiceratops* sp. from the Horseshoe Canyon Formation of Alberta (see figure 4G), and I tentatively refer it to that genus. Langston (1959) notes that the distribution of *Anchiceratops* in Canada suggests that it preferred low lying, possibly swampy environments, where other ceratopsians were excluded. Its presence at Rock Springs is another indication of an Edmontonian age for the top of the "Mesaverde" (see additional discussions by Russell and Chamney, 1967, for dinosaur biostratigraphy of the Edmontonian).

The field notes of E. Schlaikjer suggest that a partial skeleton of a theropod had been found (see Appendix); however I was unable to find the specimen in the collections of the AMNH. Isolated teeth have been reported from Utah and Colorado, including tyrannosaurid and dromaeosaurid teeth (Parker and Balsey, 1989; Carpenter, field notes, 1983; Archibald, 1987).

At least three major types of footprints are known from the "Mesaverde"; these are shown in Figure 5. The most common are those ascribed to hadrosaurs (Fig. 5A). These footprints differ from that described and figured by Langston (1960) in lacking the isolated "heel" (see Langston, 1960, Fig 1; this footprint is from the Saint Mary River Formation which is equivalent to the uppermost part of the "Mesaverde" Group and basal "Lewis" Shales). The footprint is actually very shallow and not very distinct, and I am not convinced that the "heel" impression belongs to the footprint. Furthermore, I am unable to confirm the presence of webbing between the toes as Langston suggested.

The "Mesaverde" footprints and the footprint described by Langston were made by a short, broad, tridactyl foot with broad, somewhat blunt toes. Trackways of these footprints from the "Mesaverde" (Lockley and others, 1983) indicate that the print maker was a very large bipedal dinosaur. Assuming that we know the major late Cretaceous dinosaur groups in North America, the only dinosaur with the correct foot morphology is a hadrosaur, and, as may be seen in Figure 5A, the correspondence between the foot bones and footprint is very close. Unfortunately, it is not known which genus of hadrosaur is the footprint maker because no skeleton has been recovered associated with the footprints. It is probable, in light of the great diversity of Judithian and "Edmontonian" hadrosaurs in North America, that more than one genus of hadrosaur was involved. The presence of *Maisaura* in the Williams Fork Formation suggests that it may be one of the footprint makers (see Appendix).



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Figure 4. A-H, dinosaur bones from the "Mesaverde" Formation collected by the American Museum of Natural History's Sinclair Expedition of 1937. A, lambeosaurid humerus, AMNH 3653, from the Green Valley Mine. B-G all Lambeosaurid, AMNH 3651, from Cedar Canyon, Sweetwater County, Wyoming: B, left scapula; C, right scapula; D, coracoid; E, jugal; and G, left ilium. F, hadrosaur right scapula, AMNH 3660, Long Canyon, Sweetwater County, Wyoming. H, ?*Anchiceratops* sp. partial skull, AMNH 3652, Sweetwater County, Wyoming (drawn from a field photograph). G. *Anchiceratops* sp. for comparison with H (modified from Russell and Chamney 1967). See Appendix for measurements of elements.

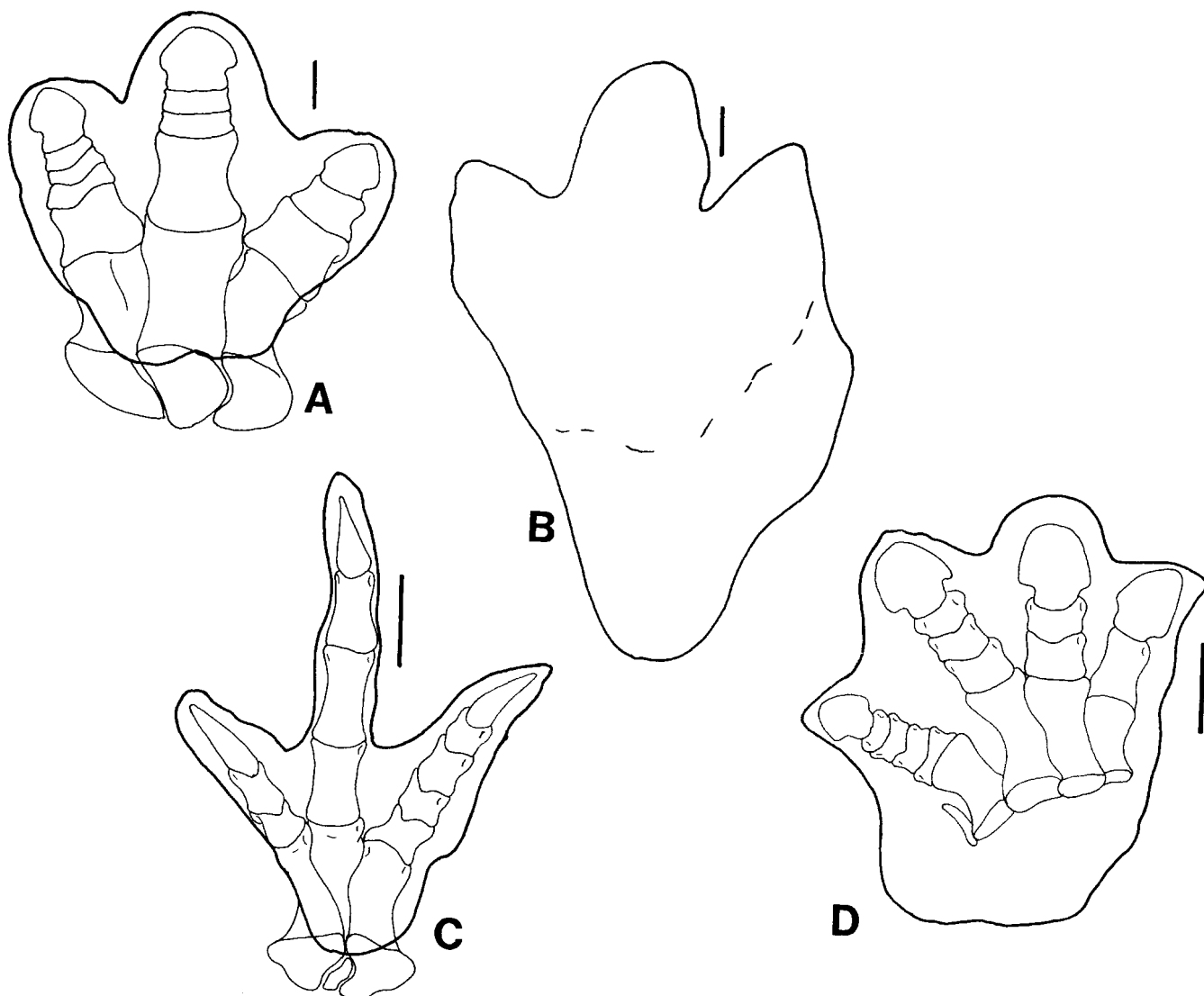


Figure 5. Pes footprints from the "Mesaverde" Group with foot skeletons for comparisons. A, hadrosaur footprint with foot skeleton of *Kritosaurus* (modified from Parker and Rowley, 1989, and Parks, 1920). B, hadrosaur footprint with elongated heel due to slipping on mud (holotype of *Dinosauro-podes magrawii*, modified from Strevell, 1940). C, tyrannosaurid footprint with foot bones of *Albertosaurus* (ROM 1237). D, ceratopsian footprint with foot skeleton of *Styracosaurus* (modified from Rowley and Parker, 1989, and Brown, 1917). Heavy bar = 10 cm.

Langston (1960) noted an absence of digital pads, a condition confirmed in the well defined footprints from the "Mesaverde." This supports Langston's suggestion that hadrosaurs had very limited inter-phalangeal motion; i.e., they could not curl their toes. The shortness of the phalanges (Fig. 5A) supports this observation. The broad heel of the "Mesaverde" footprints and the lack of digital pads suggests the presence of an elephantine-like pad (Langston, 1960). However, Brown (1916) reports that a "mummy" of *Corythosaurus* shows lobes beneath the metatarsals and proximal phalanges. Whether these are truly pads or the distal ends of the metatarsals cannot be resolved at this time. Regardless, such a pad(s) would cushion the step on hard ground, and would make interdigital movement very limited.

There is a considerable amount of variation in the hadrosaur footprints, but most of these differences can be explained by the consistency of the original substrate, peat

rebound, and peat compaction during coalification, how the animal stepped, or the size of the individual. For example, elongated heels are common (Fig. 5B) and indicate slipping of the animal as it walked. This interpretation is based on several features: the "heel" is shallower than most of the footprint and the tips of the toes frequently extend obliquely down into the coal; striations show the direction the foot slipped; and presence of the "heel" on footprints along a single trackway is inconsistent. Slipping on mud can only occur when the substrate is less than saturated with water, thus indicating the absence of standing water.

Other footprints do not show the toes well defined (eg., Balsley, 1980, Figs. 95 and 96). These footprints are moderately deep, suggesting the substrate had a high water content, so when the foot was removed the substrate was not able to retain the impression well. With other footprints, however, the substrate may have stuck between the toes. Still

other footprints differ from the large hadrosaur prints by their minute size (Figs. 6, 7; Lockley, 1986A reports smaller prints 3 cm x 2 cm). Except for size, these prints compare well with the larger prints (compare Figs. 5A and 6). Not unexpectedly, elongated heels due to slipping are also seen in these small footprints (see Lockley, 1986a, Fig. 11B, upper right).

Another large tridactyl footprint known from the "Mesaverde" is shown in Fig. 5C. This type of footprint was made by a long, slender foot with long, slender toes. The heel is typically narrow and rounded, although if not impressed deeply, it may assume a V-shape (see Lockley and others, 1983, Fig. 2) or be almost absent (Lockley, 1986a, Fig. 11D). Interdigital pads are present or may be inferred from swellings of the toe impressions. Frequently the tips of the toes are sharp indicating the presence of claws, but sometimes the impressions are blunt, possibly because of substrate sticking to the claw. The presence of sharp claws, the large size of these footprints, and the slenderness of the foot and toes indicates the track maker was probably a tyrannosaurid, because a giant ornithomimid, such as *Gallimimus*, is not yet known from the Upper Cretaceous of North America. The slenderness of the toe impressions is more like that expected for the tyrannosaurid *Albertosaurus*, rather than that for the heavier, slightly wider toed *Daspletosaurus*. As may be seen in Fig. 5C, the correspondence between the footprint and the foot skeleton of *Albertosaurus* is very close.

A third footprint type is that of a quadruped in which the manus possessed five digits and the pes four (Fig. 5D). The pes prints indicate a short, broad foot with blunt toes, or hooves. Digital pad impressions are absent indicating little movement of the toes. A large elephantine pad is inferred to have been present based on the very large heel impressions. This pad extended further posteriorly from the metatarsals than in hadrosaurs (compare Figs. 5A and 5D). These footprints have previously been identified as sauropod (Young, 1976), but this is certainly incorrect because the manus shows distinct toes, the pes heel is not as broad as in known sauropod tracks, and sauropods are absent from the better known contemporary dinosaur faunas of the Judith River and Two Medicine formations. Furthermore, the only well known Upper Cretaceous (Maastrichtian) sauropod from North America, *Alamosaurus*, is only known from upland sediment (Lucas, 1981).

These footprints in the "Mesaverde" were probably made by a ceratopsian because of the five manus and four pes digits. As may be seen in Figure 5D, there is a strong correspondence between the pes foot skeleton of a ceratopsian and that of the footprint. Lockley (1986A) previously reached a similar conclusion independently, but did not state his reasons for the identification (see also Lockley, 1989, Fig. 2K).

The footprints cannot be those of an ankylosaurid, because the pes of all known Upper Cretaceous ankylosaurids from North America have only three digits (Carpenter, in preparation). The feet of Upper Cretaceous nodosaurids are very poorly known, but here also there is indication of only three digits in the pes as well (Carpenter, 1990). This is in marked contrast with Lower Cretaceous nodosaurids, which have four pes digits (Carpenter, 1984).

I suspect that the trackway of an ankylosaurid, aside from the relatively larger manus print, will be difficult to separate from that of a medium-size hadrosaur walking quadrupedally if distinct digits are not present on the manus impression. Another distinction may be that hadrosaur trackways show that the animal walked pigeon-toed (positive rotation), while ankylosaur trackways show slight negative rotation (Carpenter, 1984).

Although skeletal remains of giant hadrosaurs are not known from the "Mesaverde" Group, the presence of these animals is demonstrated by footprints up to 91.4 cm wide (width is used because many footprints in the "Mesaverde" are elongated due to slippage of the animal on the soft substrate). (I am skeptical of Collins' [1976] report of a 121 cm wide footprint; I suspect length is meant). This contrasts with a footprint described by Langston (1960), which is, at 55 cm wide, the size expected from contemporaneous skeletons.

It is possible to approximate the size of the "Mesaverde" Group giant hadrosaur based on the correlation between foot width and the length of the leg as determined from mounted hadrosaur skeletons (Lockley and others, 1983). This indicates that a 91.4 cm wide print was made by an animal 416.8 cm tall at the hips. Such an animal would have had a femur length of about 165 cm. The largest hadrosaur from North America is known from a 95 cm long lambeosaurid humerus from the mid-Campanian El Gallo Formation of Baja California (Morris, 1976). Based on the proportions of the humerus to the femur in complete lambeosaurid skeletons from the Judith River Formation of Alberta, this animal from the El Gallo Formation would have had a femur 179 cm long. Thus, lambeosaurid large enough to have made the widest of the "Mesaverde" footprints are known to have existed in North America during the Campanian. The mounted skeleton of *Shantungosaurus giganteus* at the Beijing Museum of Natural History, with a 169 cm femur, is 14.72 m long (Hu, 1973). This is the estimated length of Brown's "mystery" dinosaur.

FOOTPRINTS AND HADROSAUR BEHAVIOR

The importance of footprints for interpreting dinosaur behavior has been discussed before (summarized by Lockley, 1986b), and the theoretical conclusions will not be repeated here. With regards to the footprints sites in the "Mesaverde" Group, they provide a unique "snapshot" of the lives of some of the Campanian dinosaurs, particularly the hadrosaurs.

Hadrosaurs dominate Late Cretaceous dinosaur skeletal faunas in North America, and it is not surprising that they also dominate the "Mesaverde" footprint assemblages. Their great abundance and dominance of the Grand Mesa and Price footprint assemblages suggests herding. This agrees with the conclusion reached by Dodson (1971) based on multiple skeleton quarries in the Judith River Formation, and on colonial nesting by the hadrosaur *Maisaura peeblesorum* (Horner, 1982, 1984A). Herding is a very common antipredator mechanism among extant large ungulates because individuals rely upon group defense, group alertness, and anonymity within the group to avoid predators (Jarman and

Jarman, 1979). That this mode of behavior is very successful is demonstrated by the large number of ungulate species utilizing this method today. Mass accumulations of hadrosaurs, as well as other herbivorous dinosaurs, indicate this mechanism has had a long, successful history among herbivorous tetrapods.

The distribution map of the Price footprints is shown in Figure 1, and that of Grand Mesa is shown in Figure 2. Measurements for the Grand Mesa footprints were given by Lockley and others (1983). As yet measurements are not available for the Price footprints, although a representative sample illustrated by Balsley (1980) shows that prints as large as the Grand Mesa footprints are present (i.e. at least 62 cm wide). The width of the Grand Mesa footprints are between 38.1 cm and 91.4 cm, indicating individuals between 4.5 m and 16.6 m long. Such a size mixture indicates a herd composed of both subadults and adults (Lockley and others, 1983). The apparent absence of small juveniles among the Grand Mesa footprints may be an artifact of preservation because many of the smaller footprints at this site are shallow. This suggests that the smaller, lighter juveniles may not have depressed the peat enough to leave a distinct print (Lockley and others, 1983).

In at least one mine in the Price area, however, very small juvenile footprints are known (see Table 1 and Figs. 6 and 7; see also Lockley, 1986A). These footprints have been artificially enhanced (Lockley, personal communication 1990). However, there is reason to believe that the enhancement reflects the correct dimensions and morphologies based on comparisons with foot bones of juvenile hadrosaurs from Montana.

The size of these juvenile trackmakers can be reconstructed by comparison with the reconstructed skeleton of a baby *Maiaasaura peeblesorum* at the Museum of the Rockies (MOR). This 98.5 cm long skeleton, with a 12.1 cm long femur, has a foot 5.5 cm wide. With the foot fleshed out,

the footprint is estimated to have been about 5.7 cm to 5.8 cm wide. The age of the juvenile is unknown, but is probably less than a year old (Horner and Gorman, 1988). Another skeleton, recovered from a deeply weathered egg and believed to belong to a hatchling-sized individual, is 39.8 cm long, has a 6.7 cm long femur, and has a foot 3.2 cm wide. A footprint made by this animal is estimated to have been about 3.4 cm. Thus, the small "Mesaverde" footprints could have been made by baby hadrosaurs less than a year old and between 40 cm - 98.5 cm long. This small size suggests a nearby hadrosaur rookery (Horner and Gorman, 1988) and reinforces a previous suggestion that lowland dinosaurs nested in the lowlands (Carpenter, 1982; Fiorillo, 1987).

In order to determine the directions the animals at the Price and Grand Mesa sites were walking, an azimuth of the middle digit was taken. Although hadrosaur trackways show that they are pigeon-toed, a plot of both feet should show the general direction the animal was walking. Ideally, azimuths for trackways should be plotted, rather than individual tracks. However, this was not possible with the Price and Grand Mesa sites because so few distinct trackways are present. The results are presented in Figure 8 using the Late Cretaceous north magnetic pole of Smith and Briden (1977).

As may be seen in Figure 5A, the Price footprints are not randomly oriented as reported by Lockley (1986a). There are at least two axes set at right angles to one another. The Grand Mesa footprints, however, show only a single axis. In both plots most of the footprints trend in a southerly direction. Both plots are combined and compared in Figure 5C, emphasizing the general southerly trend of the two sites. The wide spread of the azimuths is probably due to the pigeon-toed walk of the hadrosaurs, so that the azimuth of digit III changes from left foot to right foot.

The result of the plots suggests that the majority of the animals were heading in the same direction, possibly for the same purpose, despite the considerable time gap separating them. Figure 5A shows some footprints in almost all of the quadrants, indicating that the direction of travel was not hindered despite the presence of trees or stumps. Therefore, the southerly trend cannot reflect travel by the hadrosaurs through a restricted passage. Freedom of travel was also inferred from the Grand Mesa footprints (Lockley and others, 1983). In an interesting contrast, Strevell (1940) stated that many tracks he observed headed in an easterly direction. Unfortunately, Strevell did not state on which mines he based this observation, and it is not possible to verify his comment.

Considering the abundance of footprints at both the Price and Grand Mesa sites, it is surprising how few trackways there are. Part of this is due to the difficulty of isolating the tracks of a single individual from the confusion of other prints. Three possible trackways among the Price footprints are shown in Figure 1, insets A-C. Admittedly, other interpretations of footprint pairs are possible for A and B. Another reason why trackways are not common is due to missing footprints. This may be seen in Figure 1 at E and F. Elsewhere isolated footprints occur, indicating that many intervening footprints are also missing.

Why so many footprints should be missing at both footprint sites is puzzling considering how soft extant swamp

TABLE 1. MEASUREMENTS (CM) OF BABY HADROSAUR FOOTPRINTS ILLUSTRATED IN FIGURES 6 and 7 (FIG. 7C SAME AS FIG. 6, SPECIMEN J).

Specimen	Length	Width
A	3.8	3.2
B	4.4	4.1
C	3.4	4.1
D	>4.6	3.8
E	4.8	4.8
F	4.6	5.2
G	4.3	4.6
H	-	5.5
I	4.2	4.6
J	4.6	4.9
K	4.2	6.1
Fig. 7A	9	8.5
Fig. 7B	9.3	8.1

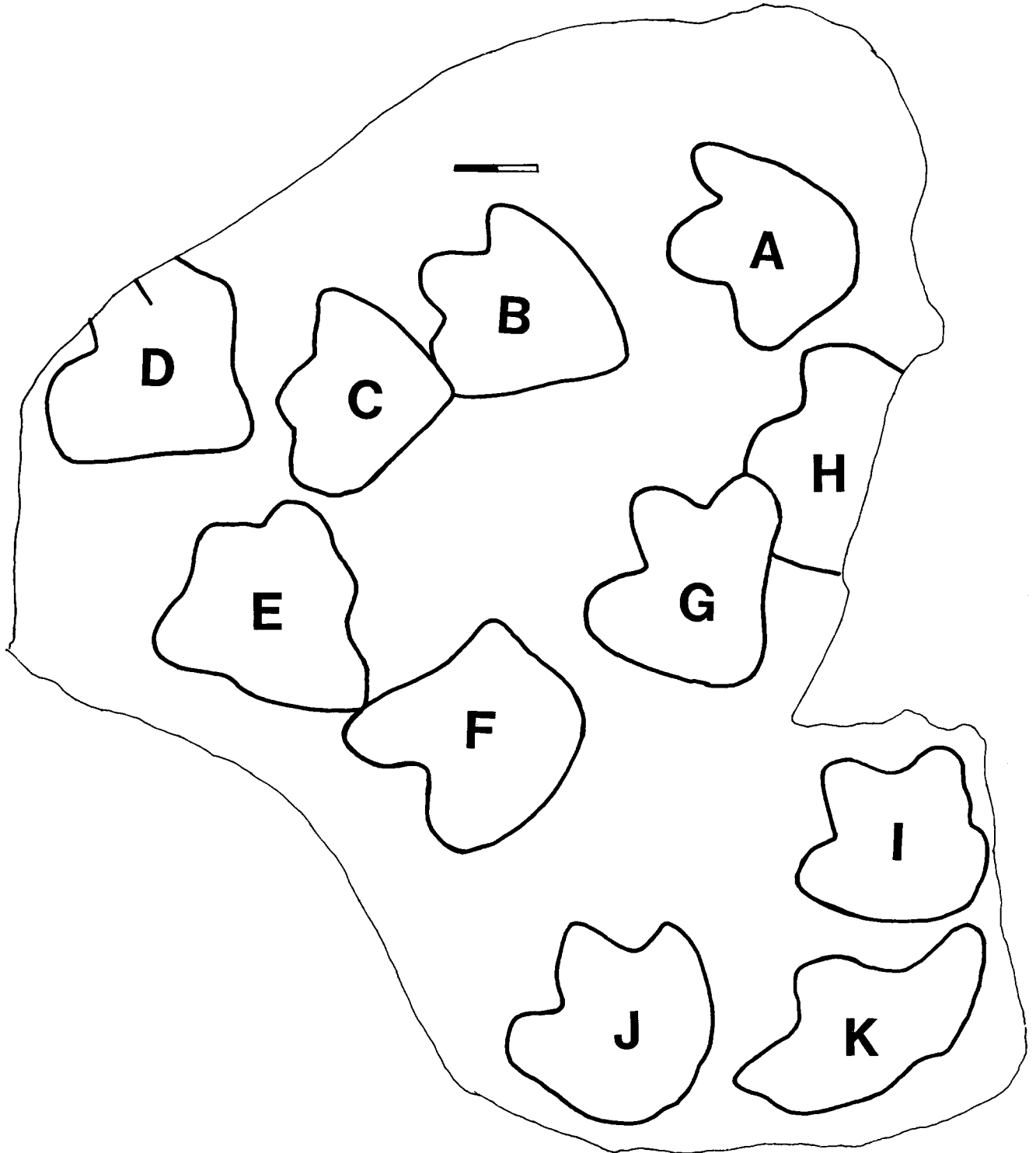


Figure 6. Baby hadrosaur footprints (Utah Department of Antiquities, Paleontology Collection (UDA PC) 85.5.1) from the Blackhawk Formation, Utah. See Table 1 for measurements. Scale = 2 cm.

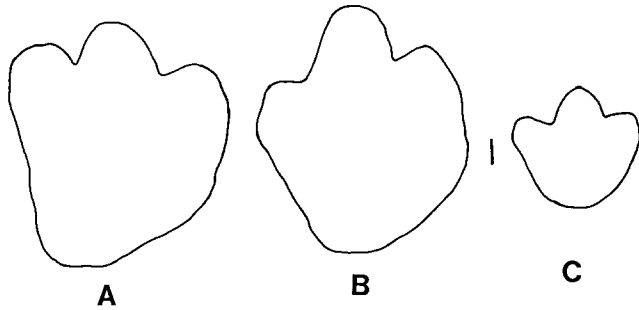


Figure 7. Juvenile hadrosaur footprints A (UDA PC 85.4.1) and B (UDA PC 85.4.2) compared to a baby footprint (J of figure 6). See Table 1 for measurements. Scale = 1 cm.

substrate is (personal experience in Mississippi). It is difficult to imagine a 18,000 kg (20 ton) hadrosaur leaving 91 cm wide footprints only 9 cm -15.25 cm deep in soft swamp peat (see Lockley and others, 1983; weight estimate provided by G. Paul). Such an animal would exert about 3 kg/cm² to the substrate in mid step (foot treated as a circle with two interdigital wedges removed, because foot width = foot length in hadrosaurs). It is possible that the absence of some footprints can be the result of peat rebound after a hadrosaur had passed, but as Balsley (1980) has noted, many of the footprints are well defined and must have been formed just prior to the influx of sediment.

I suspect that the swamps were not inundated, and that the swamps were undergoing water stress due to a severe dry season or drought. Subaerial exposure is indicated by mudcracks reported by Parker and Balsey (1989). Uneven dryness of the peat would explain the varying depths of the footprints observed by Lockley and others (1983), why the animals frequently slipped, why in many places footprints are missing, and why only isolated prints occur in some places. Also, the presence of hatchling footprints indicates that most, if not all, of the standing water was gone; otherwise the tiny hadrosaurs would have floated. On the other hand, the substrate at this particular site must have been moist enough to be deformed under the weight of the baby hadrosaurs.

Additional evidence for the drying out of the swamps is the presence of charcoal (Balsley, 1980), indicating that forest fires swept through the swamps (Carpenter, 1987a) as sometimes occurs today (Cypert, 1961). That the climate was conducive for an occasional drought is demonstrated by growth rings in silicified wood within the coals (Balsley, 1980). These growth rings indicate rapid growth during the wet or rainy season, and slowed growth during the dry season. If the dry season became prolonged, then a drought would result. Such a climatological interpretation is contrary to Wolfe and Upchurch (1987), who argue for low Late Cretaceous rainfall spread evenly throughout the year.

The presence of hatchlings in a dried out swamp suggests that, under ideal conditions, egg hatching coincided with the start of rainy season when new, protein rich, low fiber growth would be available. If the rainy season was delayed, then the hatchlings would be severely stressed, and, as I have suggested elsewhere (Carpenter, 1987a), this may

explain the high mortality of baby *Maisaura* as reported by Horner (1984). The presence of eggs with embryos at Horner's sites suggest that hatching may have aborted when conditions were exceptionally severe.

On a regional scale, it is possible that some of the droughts recorded in the "Mesaverde" swamps coincided with those recorded at the contemporary *Maisaura* nesting grounds in Montana. If true, then this indicates that some of the droughts were geographically very extensive. It remains to be seen, however, if the scale of resolution in dendrochronology of fossil wood will ever allow us to make such long distance climatic correlation.

The terrestrial nature of hadrosaurs, as demonstrated by Ostrom (1964) and reinforced by the upland nesting sites of *Maisaura*, contradicts the theory that swamps were the preferred habitat of the "Mesaverde" hadrosaurs. As Western and Van Praet (1973) have noted, many large mammals in East Africa seek refuge in swamps during the dry season because this habitat retains water longest. This water is especially important for animals highly dependent on drinking water and relief from the heat. In addition, swamps often remain green during the dry season, providing a food source for the animals.

Possible evidence for feeding by the hadrosaurs in the "Mesaverde" swamps was reported by Balsley (1980). Footprints have been found at the base of several trees as if the individuals were browsing (see Fig. 1, inset D). These trees have been identified as *Sequoia cuneata* on the basis of needle mats around them. That hadrosaurs did feed on conifers is demonstrated by a wad of *Cunninghamites elegans* needles in the stomach region of a "mummified" *Edmontosaurus* (Krausel, 1922). However, unlike Ostrom (1964), I do not believe this indicates the typical diet of hadrosaurs. All we know for certain is that the last meal eaten by this animal included conifer, which is high in fiber and low in protein.

The utilization of high fiber, low protein plants by animals increases as the dry season progresses. This occurs because plants under water stress begin to remove the protein from their leaves and to store them in the roots, and because high protein, low fiber plants are selectively depleted by the herbivores first (Carpenter, 1987a). In light of the suggestions for droughts at the time the hadrosaurs were in the swamps, it is more likely that they were there to seek water and to feed on what green vegetation they could find.

Once the rainy season started, deposition of silt and sand by floodwaters would infill the footprints, thus preserving them. If the dry season was not too severe and water remained in the swamps, then the dry season migration of hadrosaurs into the swamp might be recorded as the bioturbation reported by Parker and Balsley (1989).

The movement or migration of the hadrosaurs into and through the swamps may explain why most of the footprints trend towards the south as indicated by Figure 8. The herd represented by the Price footprints must have travelled at a more leisurely pace than the herd represented by the Grand Mesa footprints, because their footprints occur in most of the azimuth sectors. At least some of the animals may have stopped to feed (eg. Fig. 1D).

Bimodal distribution and speed estimates of the Grand Mesa footprints suggests purposeful, although leisurely

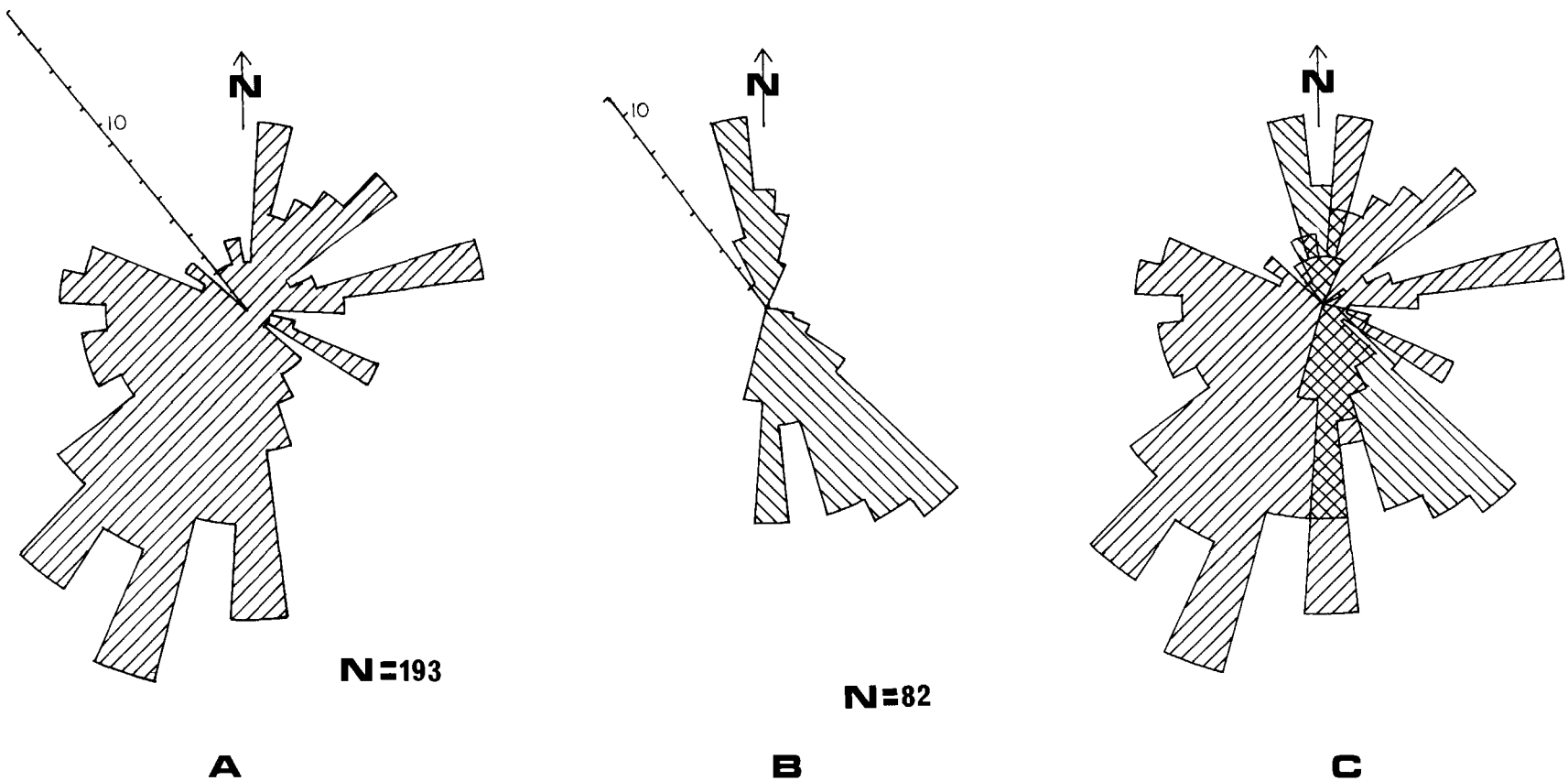


Figure 8. Azimuth plot of digit III for hadrosaur A, Price footprint site and B, Grand Junction footprint site. C, combination of plots in A and B emphasizing that most animals at both sites traveled in a southerly direction. Trackways are approximately parallel to shoreline at this time. North is corrected for the Cretaceous pole as determined from Smith and Briden (1977).

movement of these animals in two directions (see discussion above). The north-trending footprints are a little shallower ($x = 3.7$ cm) than the south-trending footprints ($x = 4.8$ cm), suggesting a passage of time between the two events during which the swamp substrate dried more. One scenario is that the north-trending footprints record the return migration at the end of the drought immediately before flooding. This flooding, which typically accompanies the rainy season (Foster, 1965), would bury the footprints with sediment. The prediction from this hypothesis would be that north-trending, or wet season footprints would always be less common than south-trending, or dry season footprints. This would occur because the substrate would quickly be saturated by the presence of standing water, and any prints made in such mud would not be infilled later with silt or sand. The possible seasonal migration of dinosaurs has been discussed by Hotton (1980), and the footprints from the "Mesaverde" may eventually provide support for this hypothesis.

Footprints in the "Mesaverde" are very abundant and geographically widespread, but most remain unstudied. Detailed analysis of these footprints and their sedimentological context may modify some of the conclusions I have made here, but the result will be a more detailed and accurate picture of Campanian hadrosaur behavior, as well as those of other dinosaurs. Yet to be resolved is the odd distribution of footprints reported by Wilson (1969) in the Blackhawk Formation near Castle Gate, Utah. He noted that footprints occur in the "lower" and "upper" coal seams, but apparently not in the "middle" seams. It is possible that the "middle" coals had a brackish water influence (Balsley, 1980) that dinosaurs avoided, but this needs to be studied.

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APPENDIX

Dinosaurs from the "Mesaverde" Group.

I. Specimens collected by the American Museum of Natural History.

A. Almond Formation, Sweetwater County, Wyoming.

1. AMNH 3651 (field no. 10), lambeosaurine: weathered skull and lower jaws, both scapulas, one coracoid, both femurs, a hindlimb, 12 ribs, pelvis, sacrum, 30-35 vertebrae, chevrons, ossified tendon, and skin impression. South side of Cedar Canyon in NW1/4, Sec. 24, T. 22N, R. 104W. See figs. 4B-E, G. Length of left jugal = 28 cm; length of left scapula = 72 cm; length of left ilium = 77 cm, and length of preacetabular blade = 37 cm; length of six sacrals = 48.5 cm; length of right femur = 93 cm; length of tibia and astragalus = 73 cm.
2. AMNH 3652 (field no. 3), ?*Anchiceratops* sp.: skull lacking most of the frill, ilium, ribs, vertebrae, and fragments. NE1/4 Sec. 11, T. 19N, R. 105W, about 30.5 m above the Ericson Sandstone. See figure 4H.
3. AMNH 3654 (field no. 9), hadrosaur: humerus, tibia and fragments. Two miles south of Songster's Coal Mine. (not seen)
4. AMNH 3656 (field no. 4), ceratopsian: frill. South side of a prominent hill in Sec. 13, T. 20N, R. 105W, about 30.5 m above the Ericson Sandstone. (not seen)
5. AMNH 3657 (field no. 5), hadrosaur: sacrum, hindlimbs, ribs, and vertebrae. North side of U.S. Highway 30, beneath airport beacon in SW 1/4, Sec. 26, T. 20N, R. 101W. About 23 m above Ericson Sandstone. Identified as a possible ankylosaur in the field.
6. AMNH 3658 (field no. 6), ceratopsian: frill fragment. NW1/4, Sec. 21, T. 20N, R. 101W, about 30.5 m - 46m above Ericson Sandstone. A note attached to the specimen card states this specimen was discarded in April, 1941.
7. AMNH 3660 (field no. 2), hadrosaur: partial skeleton. North Slope of a ridge extending from the first hill north of Long Canyon in NE1/4, Sec. 21, T. 21N, R. 104W. About 30.5 m above the Ericson Sandstone. Length of scapula = 110 cm, length of femur = 105.5 cm. See figure 4F.

The following data are from the field notes of Erich Schlaikjer. These specimens may or may not have been collected. If collected, they may still be in field jackets as no specimen cards are available for them.

8. Field no. 1, bone fragments in SE1/4, Sec. 27, T. 19N, R. 105W.
9. Field no. 8, ceratopsian: limb bones in N1/2, Sec. 25, T. 20N, R. 105W.
10. Field no. 10, theropod?: south facing escarpment along a creek near where the railroad tracks curve north in NW1/4, Sec. 13, T. 19N, R. 104W, about 30.5 m above the Ericson Sandstone.

B. Bowie Shale Member, Delta County, Colorado

1. AMNH 3653 (field no. 13), lambeosaurine: humerus. Green Valley Coal Mine in SE1/4, NE1/4, SW1/4, Sec. 12, T. 13S, R. 95W (see figure 4A).
2. AMNH 3655 (field no. 14), bone fragments. Green Valley Coal Mine, same location as previous.
3. AMNH 3659 (no field no.), ceratopsian: horn core. Three miles north of Cedaredge.

II. Dinosaur specimens in the Denver Museum of Natural History. DMNH 1657, ceratopsian, four fused anterior cervicals (25 cm long along midline), and a tibia missing the proximal end. Hayden Mine No. 4 (Haybro Mine), Oak Creek, Colorado.

DMNH 1658, rib fragment, genus unknown. Pinnacle Mine, Oak Creek, Colorado.

DMNH 1669, distal end of hadrosaur radius. Hayden Mine No. 3. Oak Creek, Colorado.

DMNH 2128, hadrosaur pes phalanges III-1, III-2, III-3, and partial phalanx. Ten miles north of Fruita, Colorado.

III. Dinosaur specimens in the Museum of Western Colorado. Uncatalogued, *Maiasaura* middle pes phalanx ungual from the Williams Fork Formation, Garfield County?, Colorado. The ungual shows the characteristic ventral keel and short, broad shape seen only in *Maiasaura* (Horner, personal communication, 1989).