HADROSAUR LOCOMOTION AND HERDING BEHAVIOR: EVIDENCE FROM FOOTPRINTS IN THE MESAVERDE FORMATION, GRAND MESA COAL FIELD, COLORADO [1]

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ABSTRACT: Dinosaur footprint casts from a Mesaverde (Campanian) coal mine near Gunnison, Colorado resemble those of the notorious "mystery dinosaur, *Xosaurus*" which was probably a giant hadrosaur. Existing footprint descriptions, although obscure and hard to verify, are too important to overlook, particularily since debate over hadrosaur speeds currently focuses only on a single, apparently ambiguous trackway. Hindlimb/foot ratios and stride-length estimates based on comparisons with other animals should be modified using actual measurements of hadrosaurs. Mesaverde trackway data indicates that hadrosaurs were usually slow moving, although this does not imply that they were incapable of running. The frequency and preferred orientation of their prints suggests high relative abundance and gregarious group activity (herding), which was probably an effective defense strategy. Footprints of a carnosaur are also associated with those of the hadrosaurs.

INTRODUCTION

Dinosaur footprints from the Mesaverde Formation occur at a number of localities in the western United States, particularly in western Colorado and eastern Utah. At least five authors have published illustrations. These are Peterson 1924, Lull *in* Strevell 1932, Brown 1938, Look 1955, and Balsley 1980. Other authors have referred to "abundant dinosaur tracks" (Young 1976). Brown (1938) also collected and described footprint casts from two now-abandoned mines near Cedaredge, Colorado and attributed them to the "Mystery Dinosaur," subsequently dubbed *"Xosaurus"* by Look (1955). These prints attract attention because of their large size (32 to 38 inches in width); the correspondingly long stride estimates remain the subject to a lively debate (Russell and Beland 1976, and Thulborn 1981) which will probably continue until more reliable maps (cf. Balsley 1980 and Hickey 1980) are available to elucidate trackway patterns. Well preserved foot print casts occur in coal mines such as the one to which we were given access. Operations in this mine in the eastern portion of the Grand Mesa coal field near Gunnison (Fig. 1) have exposed 7800 sq ft of cast studded mine roof.

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METHODS:

Cast-bearing portions of the roof were mapped using tape measure and Brunton compass. The majority of casts are clearly defined, enabling accurate measurement of heel-toe azimuth, length, maximum width, and depth. Indistinct prints

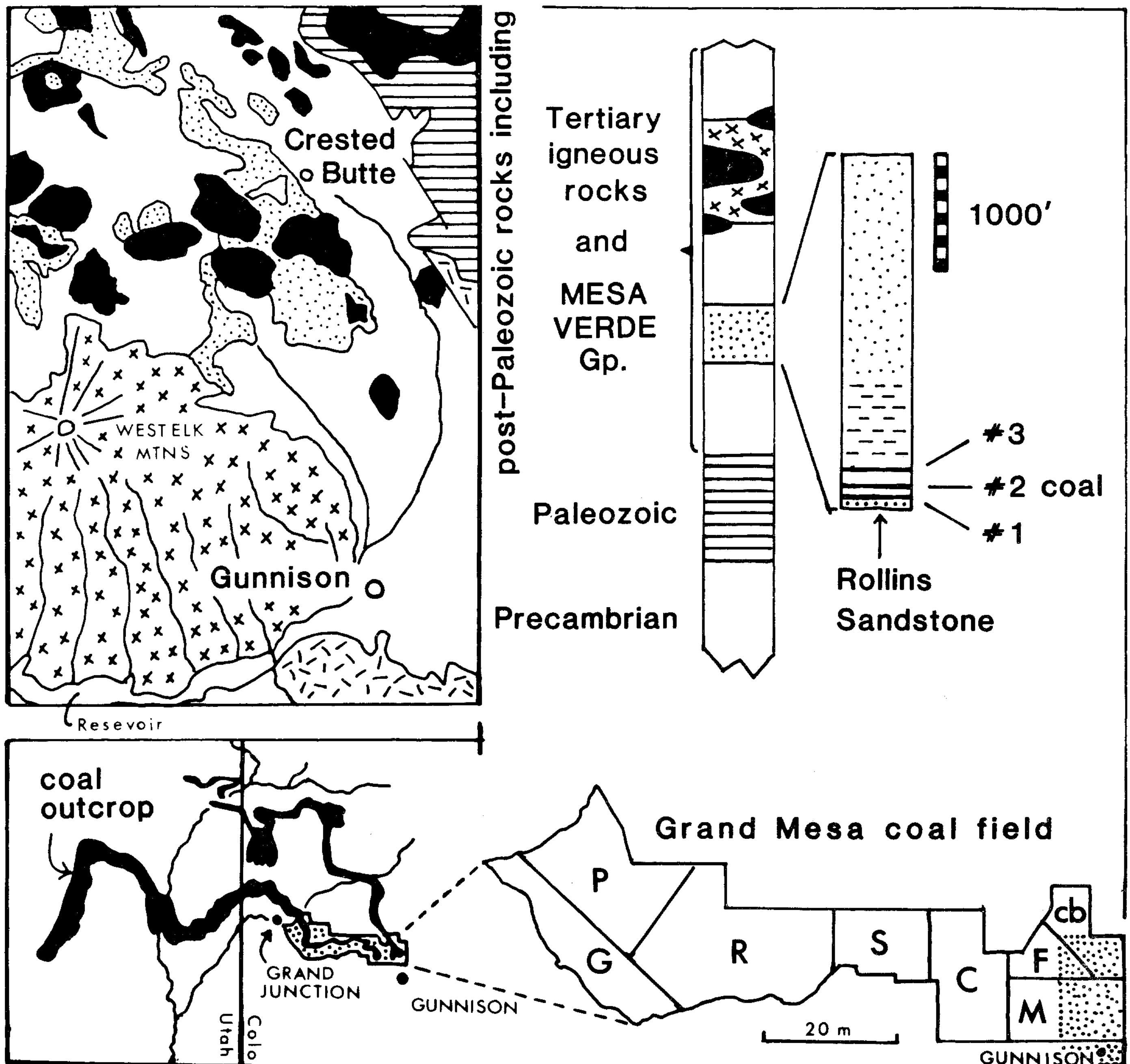

Figure 1. Simplified geological map and section for the eastern part of the Grand Mesa coalfield (stippled). Local fields: G, Gunnison; P, Palisades; R, Rollins; S, Somerset; C, Coal Creek; M, Mount Carbon; F, Floresta and; cb, Crested Butte. Footprints occur in the top of the #2 coal.

are rare, so speculative interpretations can be avoided. However, since the limitations of the underground working mean we cannot claim to have recorded and differentiated every print unequivocally, we relied on extensive photography (Fig. 2), obtaining optimum results with oblique shots. Prominent casts were numbered with 4" square scale cards. Adjacent prints were designed with appropriate suffixes (a-d) or n (north), s, e, and w orientations. This scheme allows each print to be identified individually (Table 1). For convenient comparison with historical records, measurements in Table 1 are given in feet and inches. Museum abbreviations are explained in the Acknowledgements.

Table 1. Measurements of Tridactyl Prints
(toe direction, in degrees; length, width and depth, in inches)

Cast No.	Toe Dir.	L	W	D	Cast No.	Toe Dir.	L	W	D	Cast No.	Toe Dir.	L	W	D
1	150	32	30	8.0	17a	140	29	25	4.5	35a	15	(24)	(23)	2.5
2	190	30	34	4.5	18	195	27	30	4.5	35b	0	27	24	-
3	10	40	30	4.5	19	195	28	28	7.0	35c	15	(24)	23	-
4	0	30	34	3.5	20	195	33	28	5.0	36a	0	(21)	24	1.5
5	170	33	31	4.5	22	160	29	31	-	36b	35	(22)	24	-
6	195	34	32	6.0	23	160	(28)	28	4.0	37	150	24	22	3.5
7	155	(28)	32	6.0	24a	175	27	33	4.5	38n	165	(25)	28	-
*7a	340	22	19	-	24b	205	29	32	6.0	38s	170	17	18	3.0
7b	205	32	34	5.0	24c	350	33	30	-	38w	170	(28)	28	-
8	160	30	32	4.5	24d	20	29	30	-	38a	195	(15+)	17	-
8a	160	28	25	-	25w	175	30	32	5.5	38a,n	195	33	34	-
9	155	32	31	5.0	25e	185	27	34	-	39a	155	(19)	19	-
9a	350	25	21	5.0	26a	10	31	32	-	39b	145	22	17	3.5
10	20	28	29	5.5	26b	195	30	30	4.0	40a	135	18	17	3.0
10a	170	19	26	-	26c	165	(28)	(27)	-	40b	125	16	16	-
11	5	27	30	-	26d	30	31	32	-	41a	150	36	34	5.5
11a	25	25	28	3.0	27	170	28	25	2.5	41b	40	20	18	-
11b	70	20	21	-	28a	0	30	33	3.0	41c	165	36	32	-
12	190	27	30	5.5	28b	0	(24+)	36	-	42	170	(27)	27	-
12a	185	28	28	-	29	160	32	34	6.0	43a	200	(15)	15	-
12b	185	22	22	-	30	170	(28)	26	5.5	43b	160	(31)	27	-
12c	190	26	26	-	31a	15	31	32	5.0	44a	165	(36)	32	-
*13	45	19	21	2.0	31b	150	33	32	3.0	44b	150	(18)	16	-
*14	110	16	17	2.0	31c	25	31	31	6.0	45a	150	26	24	-
15s	185	–	30	7.0	32a	0	30	30	-	45b	145	32	30	-
15n	155	–	30	-	32b	5	25	(25)	-	45c	145	32	30	-
16	135	34	29	6.5	33	150	30	32	3.5					
17	185	30	29	5.5	34	355	25	22	3.0					

*?*Albertosaurus*

NATURE OF THE PRINTS:

Preservation

All prints are preserved as fine sandstone or siltstone casts, with mud drapes, infilling the original impressions in the coal. This relationship is seen only at the tunnel edges (Fig. 2), where the coal has not as yet been mined. Such relationships have been interpreted by Look (1955), who noted that "the sand must have come in rather suddenly." Similarly, Balsley (1980) referred to "rapidly deposited flood sediments" and noted that the contact between coals and overbank sediments indicated "decreasing scour away from channels towards the swamp where foot prints are well preserved." Although most of the coal has stripped cleanly away from beneath the overlying sandstone, a little adheres at the print margins, conveniently outlining the grey casts. In places it is evident that the animal slid in the mud, elongating its print and undercutting the anterior rim, thereby causing an overhang, resulting in separation of toe cast from ceiling. Such cast portions are likely to drop out during or after mining.

Morphology, Size, and Distribution

The majority of prints are remarkably large (average width 31") and strikingly reminiscent of the "Mystery Dinosaur" casts illustrated by Brown (1938); they probably represent "an ornithopod of the family Hadrosauridae" (Thulborn 1981), which were the largest and most abundant Late Cretaceous ornithopods known from North America. They are also the same size as prints described by Peterson (1924) and attributed to *Tyrannosaurus*. However, the generally broader toes (Fig. 2) and absence of sharp claw impressions indicate great weight bearing and weight distributing adaptations. None of the footprints give any clear indication of interdigital webbing frequently said to have existed in hadrosaurs (Osborn 1912, Colbert 1945, Langston 1960 and Ratkevich 1976). However, the apparent absence of this feature, based on footprint observations, is not inconsistent with evidence from hadrosaur mummies which show "no recognizable traces of webbing" on the hind feet (Lull and Wright 1942). Although webbing of the manus may be inferred from the famous *Anatosaurus* specimen described by Osborn (1912), it is possible as Osborn himself noted, that "the skin may have slipped down over the hand before the drying and hardening occurred" (Lull and Wright 1942). Although Ostrom (1964) is prepared to accept that the webbed manus "interpretation is almost certainly correct," he has forcefully put the case for terrestrial adaptations amongst hadrosaurs. In light of Ostrom's em-

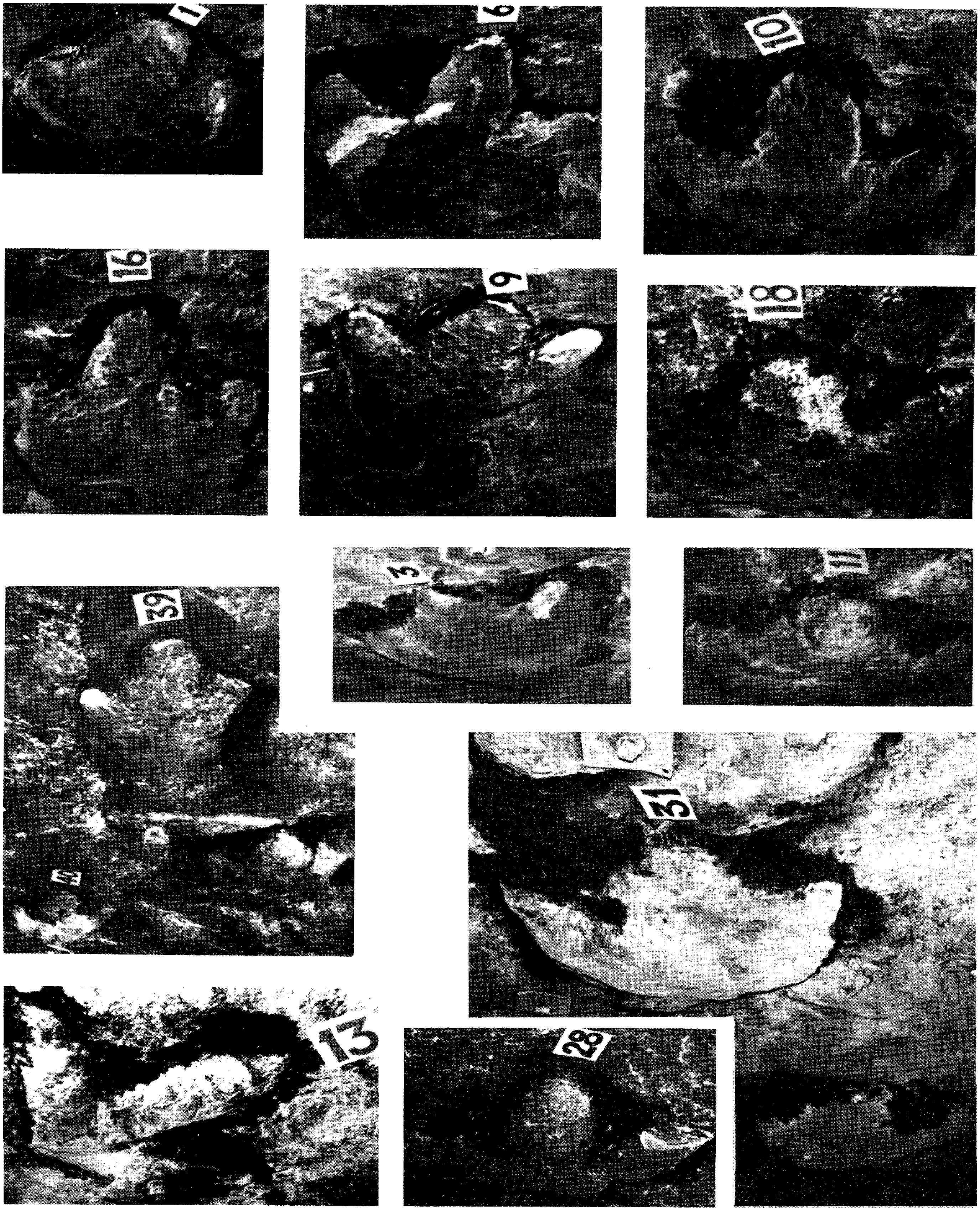

Figure 2. Photographs of representative tracks including ?Albertosaurus (# 13). Other tracks are provisionally assigned to the Hadrosauridae. 4-inch-square number cards provide scale. Measurements detailed in Table 1. Track locations on Figure 3.

phasis on anatomical evidence against aquatic adaptations and the uncertainty surrounding the interpretation of Langston's weathered ichnite (1960), evidence for a webbed pes is weak.

We recorded 82 tridactyl prints (Table 1) of which only three smaller examples (numbers 7a, 13, 14) are distinctly different (Fig. 2), exhibiting slender and elongated divergent toes apparently tipped by sharp claws. This print morphology is probably attributable to a large carnosaur, possibly *Albertosaurus*, which is well known in Campanian terrestrial sediments in North America.

Since the heel outline is indistinct in many prints, width measurements are more reliable for size analysis. The majority of prints exceed 28 inches in width; the remainder, arbitrarily subdivided into medium (21-27") and small (15-19") categories, are mainly restricted to localized areas (Fig. 3) and apparently represent smaller juveniles rather than manus impressions of a different species. The smallest prints are confined to the western entry (Fig. 3) and average 17 inches in width. Similarly, a distinct cluster of medium sized (22-24") prints occurs at the western end of the south entry; in all 21 prints fall in the 21-27" size bracket (average 24"). The remaining 48 prints average 31 inches in width (range 28-36"), indicating a preponderance of large individuals traversing this area. The overall mean width is 27.6 inches. Print depths (Table 1) which vary from less than 2 inches to 8 inches (average 5") probably indicate variable hadrosaur gait and/or substrate consistency. One animal stepped on a piece of wood (Print 41c). It is worth noting that many Utah footprints exhibit "a long heel mark" (Strevell 1932), also observed by Balsley (1980); the former author suggested that this feature indicated that the "animals had walked flat footed." The absence of such distinctive features in the Gunnison prints might alternatively indicate that a different substrate consistency prevented the preservation of such posterior traces.

Orientation

A plot of anterior, mid-toe azimuths of all tracks reveals a striking pattern of preferred orientation (Fig. 3). The majority of tracks (62%) are directed southwards between 145 and 205 degrees, while 26% point in the opposite directions, northwards, between 340 and 30 degrees. The remaining 12% mainly form NE and SE components of this pattern. No prints occur in the 135 degree western sector between 205 and 340 degrees. Such nonrandom, bimodal distribution patterns are reminiscent of those described by Ostrom (1972) and likewise suggest gregarious behavior amongst the Hadrosauridae (Dodson 1971, Currie and Sarjeant 1979, Balsley 1980). The bimodal distribution pattern can perhaps be considered indicative of "two distinct events of group activity" (Ostrom 1972).

We noted five obvious cases of overlapping prints (numbers 15, 25, 38, 38a and 44b) all of which align with the preferred direction. In the latter three examples from the west entry cluster, small 16-18" prints overlap larger prints suggesting that juveniles may have been following adults as a herd traversed the area. Two of the three *?Albertosaurus* prints (numbers 13 and 14, Fig. 3) point away from either of the other two trends, so the carnosaur(s) were probably not stalking this herd.

Stride Patterns

Conventionally a stride (Fig. 4) is regarded as two steps (Alexander 1976). Recently Russell and Beland (1976), Russell (1981) and Thulborn (1981) have debated the significance of the three Mesaverde footprints extracted by Brown (1938) for the American Museum of Natural History. Thulborn questioned the estimate of a 15 foot stride (one step) proposed by Brown (1938) and accepted by Russell and Beland (1976) by suggesting that this distance actually represents two steps. Brown had evidently ignored a partial imprint midway between two distinct footprints, thus doubling the step estimate. However no mention was made by Thulborn, Russell or Beland of a 16'3" "stride" (step) discovered in 1944 "in the same coal mine" (Look 1955). Similarly other figured trackways (Peterson 1924, Strevell 1932, and Balsley 1980) have not been considered (Fig. 5). Our study suggests that most prints were made by hadrosaurs similar in size to Brown's "mystery" ornithopod, but that the stride length was variable, occasionally reaching the maximum lengths that have been recorded.

In several areas prints appear to form part of a trackway sequence. Specifically, print pairs 10 and 11 in the east entry, 33 and 31b, 41c and 29 at the west entry show an average spacing of 14' (range 13-15') and match well for size. Elsewhere there is a tendency for crowding, which allows wider scope in interpretation. Although this will no doubt generate some debate, it is worth noting that several prints in the south tunnel (27, 31a,c, 32a, and b) apparently left only a single print when traversing the 20 feet of exposed area (roof).

A hadrosaur with feet up to 3 feet in length would, according to Alexander (1976), stand 11-12 feet at the hip, hip-height (h) being equal to about four times length, l, cf. Russell and Beland (1976). Using Alexander's formula for stride length (λ = two steps) and hip-height ratio as an indication of the animals' speed ($\lambda/h \leqslant 2$ = walking; $\lambda/h \geqslant 2$ = running), it would appear that the largest animals could have stepped 11-12' without running. However, Alexander's formula ($h = 4x1$) may not be applicable to hadrosaurs. Measurements of *Anatosaurus* (D.M.N.H. 1493) collected by Brown in 1908 from the Hell Creek Beds (Maastrictian) of Montana indicates that a foot length (and width) of around 50 cm corresponds to a hip height (h) of 2.90 m ($\simeq$ 9.5'); this gives a l:h ratio of between 1:5 and 1:6. Even when using reconstructions (cf. Langston 1960, Fig. 2) which increase the estimate of footsize to allow for flesh, the ratio still remains well in excess of that proposed by Alexander. Combining these empirical observations with Alexander's rationale, we arrive at the conclusion that an animal with 3' footprints might stand as

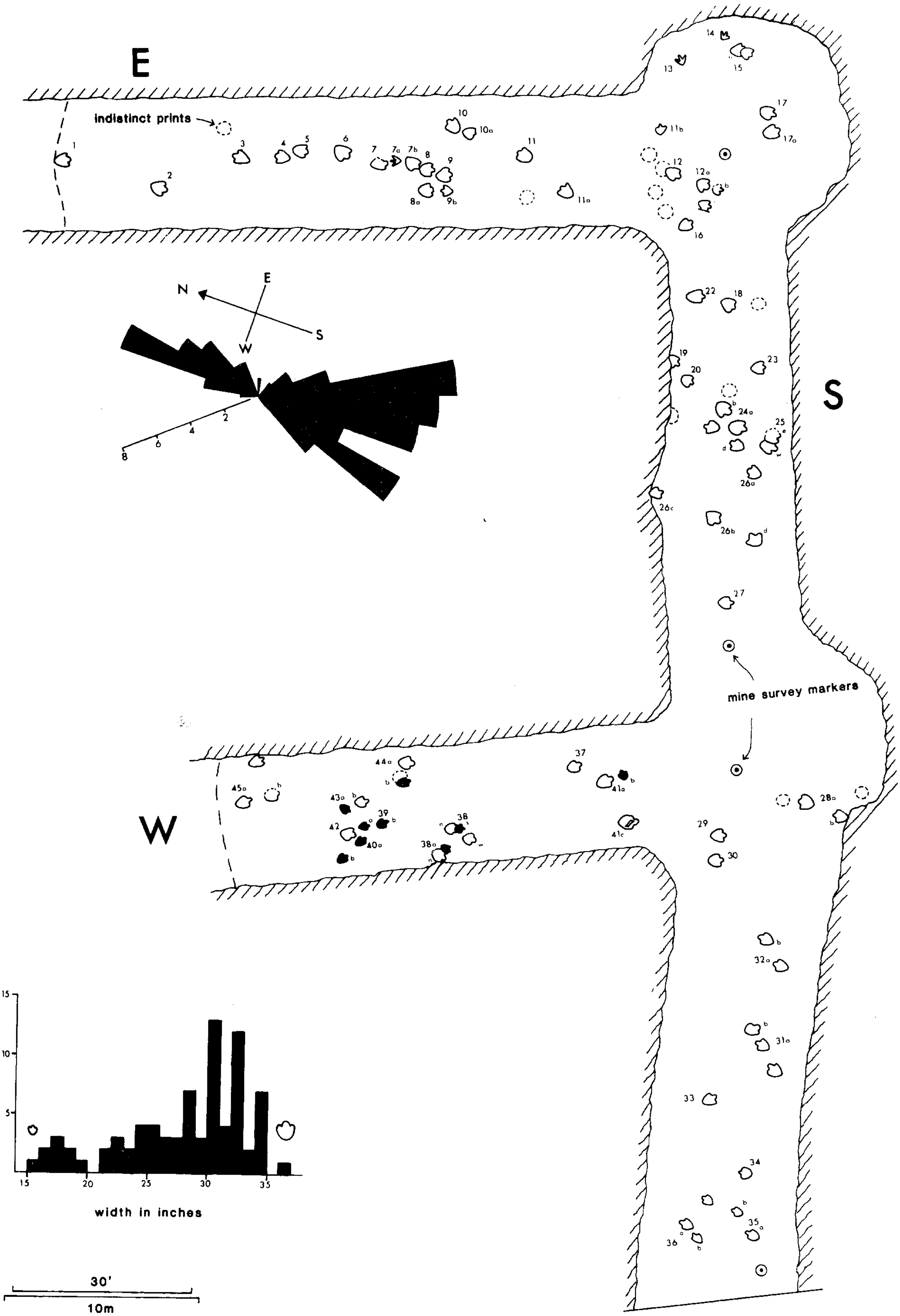
E
indistinct prints
S
W
N
mine survey markers
width in inches
15
20
25
30
35
5
10
30'
10m

Figure 3. Map of cast studded mine roof with tracks drawn to scale (measurements for individually numbered prints given in Table 1). Rose diagram shows mid toe direction for all tracks; histogram gives maximum width. Small (15-19") prints shown in black are attributable to juveniles.

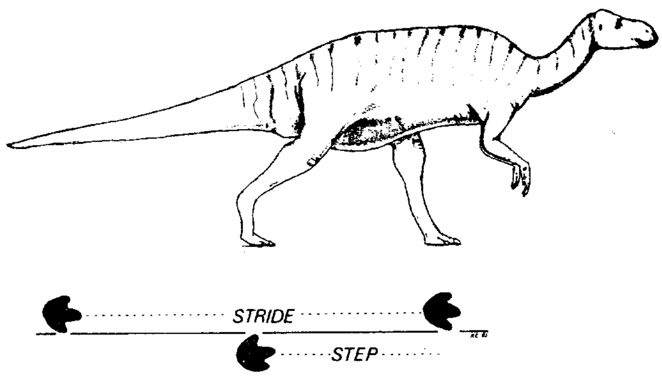

Figure 4. Reconstruction of a Campanian Hadrosaurus to illustrate the difference between step and stride. Drawing by Ken Carpenter.

high as 15' at the hip (h) and **step** the same distance without running. Surprisingly, Russell and Beland (1976) and Thulborn (1981) made no mention of other available data. Peterson provides evidence of a 9'4" (2.84 m) stride for an animal with a 30" foot length, and Strevell (1932) recorded a 12' (3.66 m) stride (Fig. 5); both of these examples conform to patterns noted by Balsley (personal commun.) where λ = 10'. By contrast the 1944 discovery near Cedaredge (Look 1955) implies a 32'6" (9.90 m) stride! Although Alexander's formula suggests that Peterson's animal was walking (λ /h = 0.93) whereas the one referred to by Look (1955) was running (λ /h = 2.57), respective estimates based on a 1:5 ratio for estimating h suggest slower movement (i.e., 0.75 and 2.06). Brown even referred to 28" long tracks of an animal "had leisurely walked along covering 8 feet in each stride." Alexander's formula and our revised estimate confirm that the creature was indeed walking (λ /h = 0.85 or 0.69); even if we assume that Brown meant "step" not stride, the values (1.71 or 1.37) still indicate walking. Print pairs 3 and 4, 5 and 6, 11 and 11a, 12 and 12a, 18 and 22, 26c and 26b, 26a and 24d, and 24d and 24c in the Gunnison mine **might be** considered parts of consecutive sequences where step lengths averaged between 7 and 8 feet but varied considerably (range 5-11'). Prints 35a, b, c, and 40 b, a, 39b also appear to represent trackways of smaller individuals.

Debating the significance of single step or stride dimensions seems somewhat fruitless since locomotion formulae simply imply that the dinosaurs responsible for making these tracks were moving at variable speeds. Balsley's excellent account indicates that in densely wooded areas the tracks are randomly orientated; this strongly implies that the animals were moving slowly, perhaps browsing, and not purposefully transversing the area as in our example. Such evidence suggests that most known hadrosaur trackways indicate slow movement; it even seems reasonable to speculate that hadrosaurs would only have spent a minimal proportion of their time in running activity and that foot prints indicative of walking would therefore dominate the geologic record. Similarly, "prints made by animals travelling at greater speed are unlikely to be complete, often comprising digit impressions only" (Sarjeant 1975).

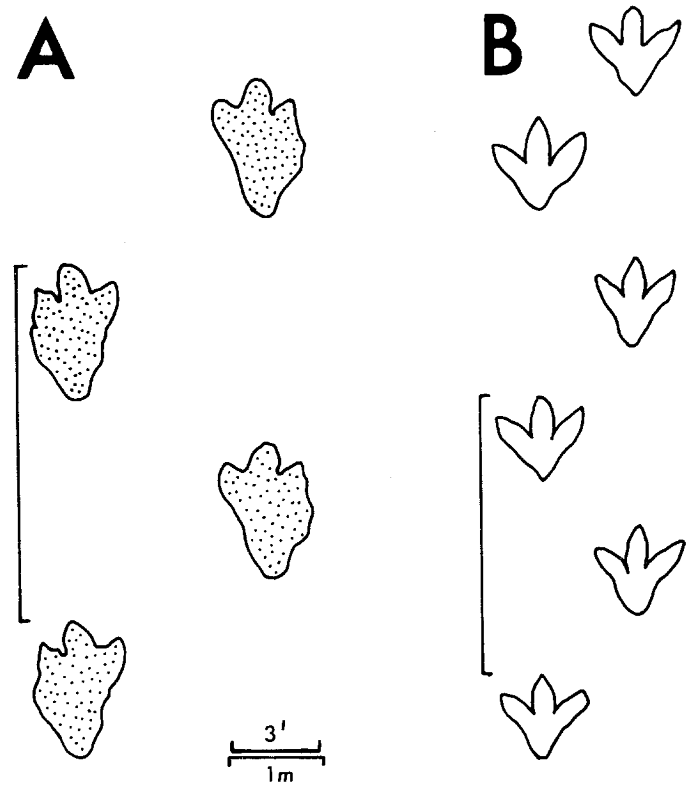

Figure 5. Documented trackways: A. "Stride . . . of Dinosauropodes" after Strevell (1932), B. "Consecutive tracks" after Peterson (1924); both drawn to same scale.

CONCLUSIONS:

Distribution of Footprint Sites

Our data indicates the wealth of underground footprint evidence that has been or is potentially available in Cretaceous coal mines of Colorado and Utah. Peterson (1924) referred to five specific mine locations where prints were known; this is in addition to locations noted by Strevell (1932), two mines referred to by Brown (1938), three described by Look (1955) including one where a dinosaur apparently stood on "an animal faintly resembling a crocodile," Balsley's examples (1980), D.N.M.H. footprint specimens #1186, Young's account (1976), our current example, and numerous other unauthenticated but no doubt valid reports. Peterson (1924) stated that he had observed tracks "over an area more than 100 miles in extent and in different seams of coal, which represent a stratigraphic thickness of more than 200 feet of sandstone including three or four beds of coal.

Affinity of Footprints

Ultimately our inference that the creatures, responsible for most of the abundant large tracks were hadrosaurs is unproven. However, several authors (Langston 1960 and Thulborn 1980) have ascribed such tracks to the Hadrosauridae which were the largest ornithopods of the day. This inference is also consistent with the evidence of gregariousness and vegetarianism (cf. Ostrom 1964, Balsley 1980, Young 1976, Currie and Sarjeant 1979, and Dodson 1971), and with Brown's undescribed American Museum of Natural History femur from Wyoming (Look 1955). Peterson's interpretation of a contemporary *Tyrannosaurus* may be open to question, but since we have not had the opportunity to examine the cast he figured we have no basis for refuting his original observations. Our data and that of Balsley (1980) and Parker also indicate the presence of a variety of non-hadrosaur tracks.

Step and Stride Length

Current debate (Russell and Beland 1976 and Thulborn 1980) is based only on data provided by Brown (1938) from a single mine. Our observations, which suggest several other sources of trackway information excluding our own, indicate that these presumed, giant hadrosaurs showed significant variation in stride pattern as might be expected if they ever varied their speed. However, any re-assessment of hadrosaur speeds on the basis of new and existing trackway data should address the need for modification of Alexanders' locomotion formulae. As shown, recalculation using revised ratios indicates slower movement. Data presented by Balsley (1980) and Parker suggest that in densely vegetated areas hadrosaurs took short 5 foot steps presumably while slowly browsing, avoiding trees, and each other; other Utah examples (Fig. 5) show very similar dimensions indicating slow movement. Our observations suggest that elsewhere step and stride length was often longer; our 11 examples of probable print pairs show a step size ranging from 5 to 15 feet. Such observations suggest that records of 15-16 foot steps (Brown 1938 and Look 1955) are not unreasonable as maximum observations (evidence of running based on locomotion formulae). It also appears that no one has seriously considered the probable differences in morphology between prints made by running and walking hadrosaurs.

Ecological Inferences

Our observations like those of Balsley (1980) suggest that these presumed bipedal hadrosaurs were gregarious and abundant. Dodson (1971) arrived at a similar conclusion in a study of contemporary faunas from Alberta and suggested that there was evidence of "a large or at least dense population of animals." He also pointed out that the carnivore/herbivore ratio seemed "indicative of the Eltonian balance of a living fauna;" the same appears to be true for our *?Albertosaurus*/hadrosaur footprint ratio. The localized occurrence of both small and large prints might indicate an age-mixed herd, implying parental care (cf. Horner and Makela 1979). Evidence of gregarious group activity (herding) is important since it provides an alternative defense hypothesis. It has previously been assumed (Lull and Wright 1942; Ostrom 1964) that hadrosaurs fled into water to avoid predators, although there is no factual basis for this assumption. It seems more probable in light of the abundant footprints from the Mesaverde Formation, that hadrosaurs traveled in herds and thus were mutually protected much like African ungulates today. This hypothesis is consistent with the evidence of large, gregarious populations and helps explain how the hadrosaurs, lacking any armorment, survived abundantly for so long. Only one of the three penecontemporaneous carnosaur prints could be inferred to represent a predator stalking a hadrosaur herd; the other two prints orientations militate against such direct inferences. Although further conclusions seem premature at present, it is evident, Balsley (1980) and Parker (personal commun.) that numerous paleoenvironmental and paleoecological inferences can be made at sites where dinosaur footprints and plant fossils occur together. Unlike Balsley's map ours shows no indication of standing trees; this implies that the animals were traversing an open area without hinderance, hence the preferred orientation pattern.

ACKNOWLEDGEMENTS:

We should like to thank the H. L. Weaver family of Gunnison for allowing us access to their mine and for their cooperation in enhancing the scientific investigation of this material. We especially thank Mr. Bob Weaver, whom we must credit with this discovery, for his on-site advice and cooperation. It would be an abuse of our access privilege not to warn those with a genuine scientific interest to avoid any follow-up investigation likely to interfere with mine operations. In order to deter footprint hunters who might otherwise interfere with working operators or endanger themselves in abandoned mines, we have avoided referring to specific locations. We also thank John Balsley, Lee Parker, Don Lindsay and William J. Morris for their advice and help. (D.N.M.H. refers to Denver Museum of Natural History. American Museum of Natural History material purportedly collected by Brown (Look 1955) from the Mesaverde but apparently still encased in the original plaster, (W. J. Morris, and J. B. Horner, personal commun.).

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