Four-toed theropod footprints and a paleomagnetic age from the Whetstone Falls Member of the Harebell Formation (Upper Cretaceous: Maastrichtian), northwestern Wyoming

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The Harebell Formation is a syntectonic sequence of conglomeratic sediments deposited in a narrow, rapidly subsiding trough that formed in the latest Cretaceous along the eastern margin of the ancestral uplift of what are today the Teton and Gros Ventre Mountains of northwestern Wyoming. On at least two occasions subsidence temporarily exceeded the rate of sediment supply and the area was flooded by a brackish or marine incursion from the Western Interior Seaway that lay to the east. The age of the Harebell Formation is Maastrichtian, corroborated by $^{40}K/^{40}Ar$ isotopic ages, vertebrate and palynomorph biostratigraphy, and a preliminary magnetostratigraphic analysis which correlates it to the geomagnetic reversal time scale from the upper part of C31R to the base of C30N. Sandstone slabs collected from the lower Whetstone Falls Member contain nine partial and complete footprints attributable to a theropod (Dinosauria: Saurischia). The footprints were formed as surface tracks in the tabular-bedded sandstone by dinosaurs that roamed the burrowed and leaf-littered sand flats and shallow waters along the margins of a low-energy, brackish-water embayment. Eight of the nine footprints represent a hitherto unknown ichnogenus, representing a four-toed pedal morphology for a theropod dinosaur which is unprecedented in the Late Cretaceous. The theropod nature of the tracks is implied by the length and narrowness of the digits and the sharp claw impressions. The tracks have clearly defined impressions of four toes, none of which appears to be a hallux in the traditional theropod sense of a small, retroverted hallux. The metapodial impression is also unlike that of other known theropod tracks: greater in relief than the digits but quite small in area. The tracks represent at least two individuals, although no clear trackways are available. *Exallopus lovei*, gen. et sp. nov., represents a type of theropod not currently recognized from body fossils.

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1. Introduction

Numerous tracks of a four-toed theropod dinosaur that represent a previously unknown Late Cretaceous (Maastrichtian) dinosaur ichnotaxon were collected from the lower part of the Harebell Formation in the Bridger-Teton Wilderness of northwestern Wyoming. The tracks were found in sandstone talus blocks on the east side of Whetstone Creek. The Harebell Formation has previously produced isolated dinosaurian bone fragments and teeth and is thought to be Maastrichtian in age on the basis of palynomorphs and radiometric dating (Love, 1956, 1973, 1977; McKenna & Love, 1970). In order to constrain further the

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age of this formation and date the track-bearing level, we sampled a reconnaissance magnetostratigraphic section through the Harebell Formation.

Four-toed dinosaurian footprints with very long, slender toes, claws, and compact metapodial impressions are remarkable because this footprint morphology is inconsistent with body fossils of any adequately known dinosaur pes. The digital lengths and widths, the presence of sharp claws, and the small size of the metapodial impression are indicative of a theropod origin. These tracks represent evidence of a hitherto unknown group of large, gracile theropod dinosaurs in the Maastrichtian of North America. This discovery allows for a more accurate assessment of dinosaurian diversity immediately preceding the Cretaceous-Tertiary extinction event. The purpose of this paper is to describe these tracks and to constrain the age of the site.

Location of the Study Area

The Harebell Formation outcrops over an area of 680 km^2 in the northern Jackson Hole region of northwestern Wyoming (Figure 1). Here we focus on two main localities. The first is beside Whetstone Creek at Lat. 43°57′54″N, Long. 110°24′39″W, where we collected dinosaur footprints from talus blocks along the east side of the creek. The second locality encompasses a series of road-cut exposures of the Harebell Formation on the Togwotee Road (Hwy 26) east of Moran Junction. There we collected oriented hand samples at approximately 300 m intervals for paleomagnetic analysis.

2. Stratigraphy of the study area

The Jackson Hole region contains a succession of Upper Cretaceous foreland basin sediments that spans more than 20 my of geologic time from the Frontier and Cody Formations of Late Cretaceous (Coniacian) age, to the Pinyon Conglomerate of the early Tertiary (Figure 2). The Harebell and Pinyon Conglomerates are composed of sediments eroded from the mountain blocks uplifted during the onset of the Laramide orogeny in the Jackson Hole region. The Harebell Formation was named by Love (1956) after Harebell Creek, located near the southern boundary of Yellowstone National Park some 20 km northwest of the study area. The Harebell Formation is a syntectonic succession of sandstone, mudstone, and auriferous conglomerate (Lindsey, 1972) that was deposited on alluvial fans next to rapidly rising highlands to the west and north of Jackson Hole. The Harebell ranges from 20 to 3350 m in thickness and is bounded above and below by unconformities.

At its base, the Harebell lies with angular unconformity on a succession of rocks of Late Cretaceous age. The youngest units to underlie the Harebell Formation are the tuffaceous sediments of the Meeteetse Formation, which have been dated by $^{40}K/^{40}Ar$ at 74.9 Ma (Love, 1977; recalculated with the updated IUGS constants of Dalrymple, 1979). This age determines the minimum age of the onset of uplift and erosion of the Upper Cretaceous sediments in the Jackson Hole region. Love (1973) defined two members of the Harebell: a lower unnamed member about 600 m thick consisting of fine-grained sediments, herein named the Whetstone Falls Member, and a sequence of quartzite conglomerates that he named the Bobcat Member.

The type section of the Harebell Formation contains pollen of Maastrichtian age and theropod dinosaur teeth, again of latest Cretaceous age, which are
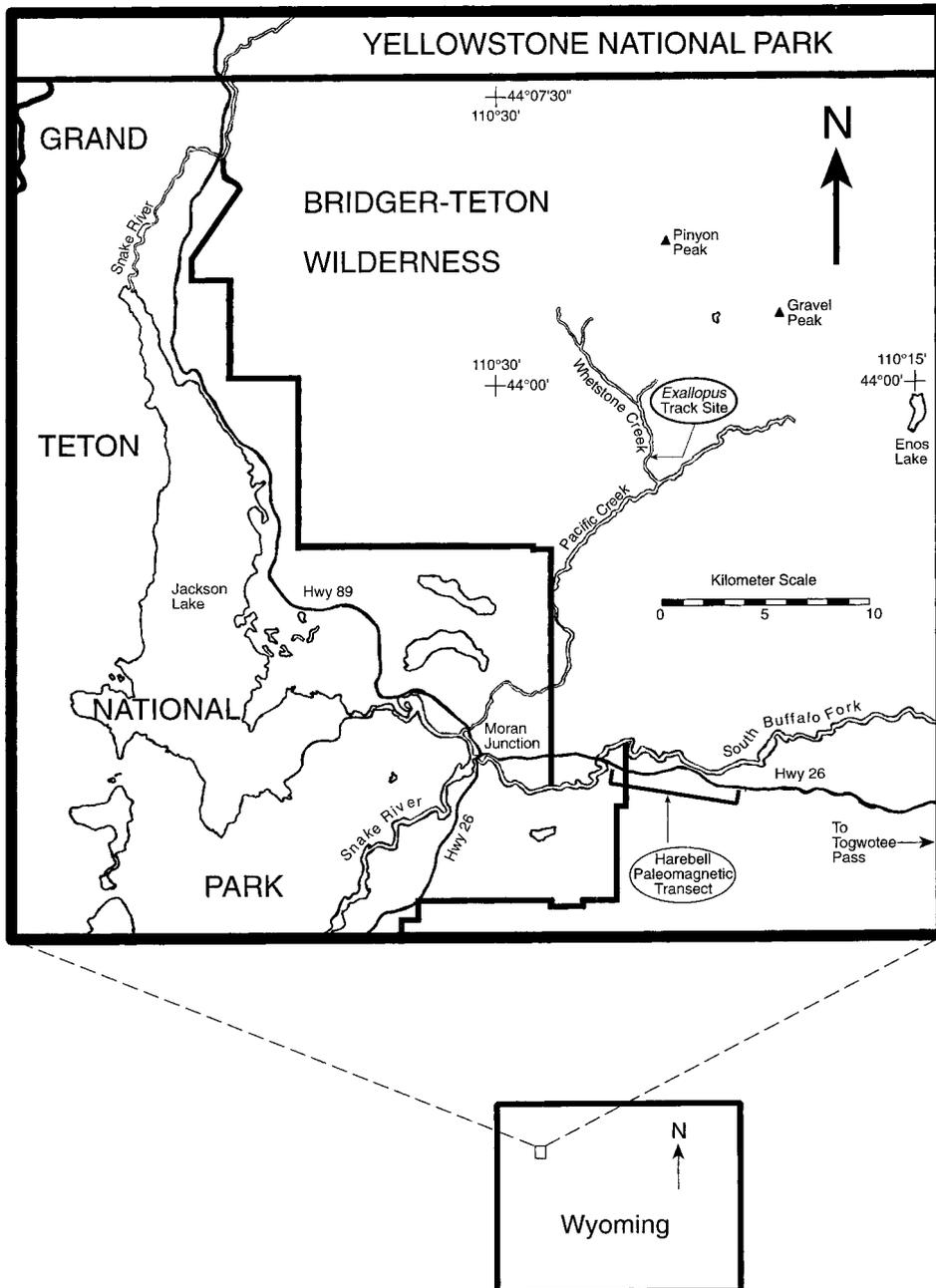
Figure 1. Map showing location of study area. The location of the trackway site is marked at Whetstone Fall at N. Lat. 43°57′54″N, W. Long. 110°24′39″W. The magnetostratigraphic section was sampled along the Togwotee Road.

attributed to the family Tyrannosauridae (Love, 1973). Ceratopsian teeth have also been reported from conglomerate lenses about 76 m below the top of the Whetstone Falls Member. They are described as a form that have dental battery grooves less arcuate and more closely spaced than *Triceratops* (Love, 1973). The invertebrates found in these units are dominantly fresh-water clams (e.g.,
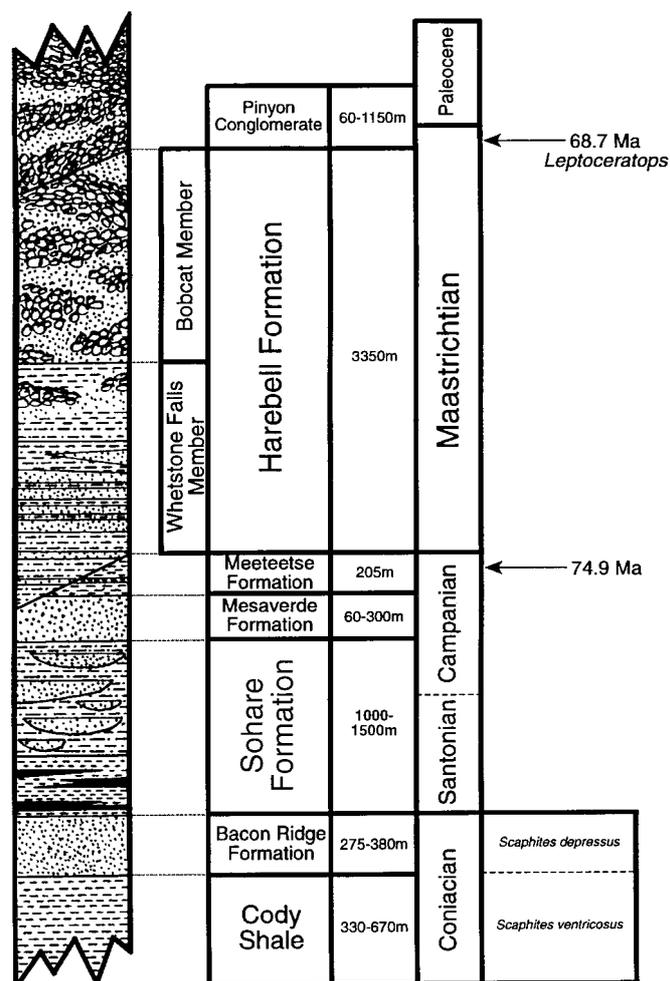
Figure 2. Stratigraphy of the Upper Cretaceous rocks in the Jackson Hole area, Teton County, Wyoming. Based on Love (1956, 1992).

Sphaerium and *Eupera*) and gastropods (e.g., *Viviparus, Reesidella, Physa,* and *Bellamya tulotomops*).

The contact of the Bobcat Member with the underlying Whetstone Falls Member is gradational and placed at the level where lenses of conglomerates begin to predominate (Love, 1973). The conglomerate layers are very thick, but pinch out rapidly to the north, east, and southeast into finer grained sediments. They were deposited in a southeasterly flowing river system (Lindsey, 1972) that was confined within a narrow subsiding trough. The uplift of the ancestral Teton-Gros Ventre Mountains lay on the western margin of the downwarp, suggesting that the high rate of subsidence was linked to lithospheric loading to the west.

Within the Bobcat Member there is a unit of dark grey carbonaceous shale which contains a brackish water fauna and a Late Cretaceous pollen assemblage (Love, 1977). The fauna contains numerous specimens of *Mytilus* that are found in association with ostracodes of a large fresh to brackish water genus resembling

the Early Cretaceous form *Paracypridea* sp. (Sohn, 1969), acritarchs, and dinoflagellates. The occurrence of these forms indicate that the area subsided to sealevel and was invaded by an embayment of the Western Interior Seaway.

The Harebell Formation is overlain with sharp angular unconformity by the Pinyon Conglomerate. The lower part of the Pinyon Conglomerate in north-eastern Jackson Hole contains a 30-m-unit of white biotite-rich tuff that has been dated at 68.7 Ma (K-Ar, Love, 1977; recalculated with the updated IUGS constants of Dalrymple, 1979). A *Leptoceratops* tooth was found 45 m above the base of the type section of the Pinyon Conglomerate (McKenna & Love, 1970). Both the isotopic age and the dinosaur fossil suggest that at least the lowermost part of the Pinyon Conglomerate is Late Cretaceous in age.

3. Paleomagnetic analysis

3.1. Procedure

Two oriented hand samples for paleomagnetic analysis were taken from each of seven sites spaced an average of about 300 m apart, which ranged from the base to the top of the Harebell Formation where it is exposed along the Togwotee Road east of Moran Junction, Wyoming (Figure 1). Two additional samples were collected from a single site at the level of the tracks at the Whetstone Creek locality. The samples were dry-sanded into 2-cm^3-cubes for paleomagnetic analysis. Both samples from each site were initially measured at room temperature for their natural remnant magnetization (NRM), and then demagnetized in a stepwise fashion in an alternating field in ten steps of 2.5 mT, 5 mT, 10 mT, 15 mT, 20 mT, 25 mT, 30 mT, 40 mT, 50 mT, and 60 mT. Additional thermal demagnetization steps were then carried out at temperature steps of 120°C, 150°C, 200°C, 250°C, 300°C, 350°C, and 400°C or until the maximum unblocking temperature was reached for that sample. The demagnetization processes and magnetic measurements were carried out in a magnetically shielded room at the Scripps Institution of Oceanography on a CTF three-axis cryogenic magnetometer.

Figure 3 displays all the bedding-corrected demagnetization data available from the section, plotted as vector end-point or equal-area diagrams as appropriate. As the section is preliminary, and only two samples were collected and measured for each site, a statistical analysis that checks for the consistency of the directions from each sample and computes the average magnetic direction for each site could not be undertaken.

The seven sample sites are represented by seven plots, numbered 1 to 7 and arranged on the diagram in stratigraphic order from bottom to top, left to right. The two samples analysed for each site, 'A' and 'B', are both plotted on a single diagram, except for site 1 where one sample was lost during sample preparation. On the vector end-point diagrams, the NRM direction of the sample at room temperature is marked by a cross. The horizontal and vertical components at each temperature step are plotted with square symbols for the A sample and as triangles for the B sample. On the equal-area projections the A sample data are shown as squares and the B data as stars. The stratigraphic position of the sample sites with respect to the Harebell Formation section is shown in Figure 4.
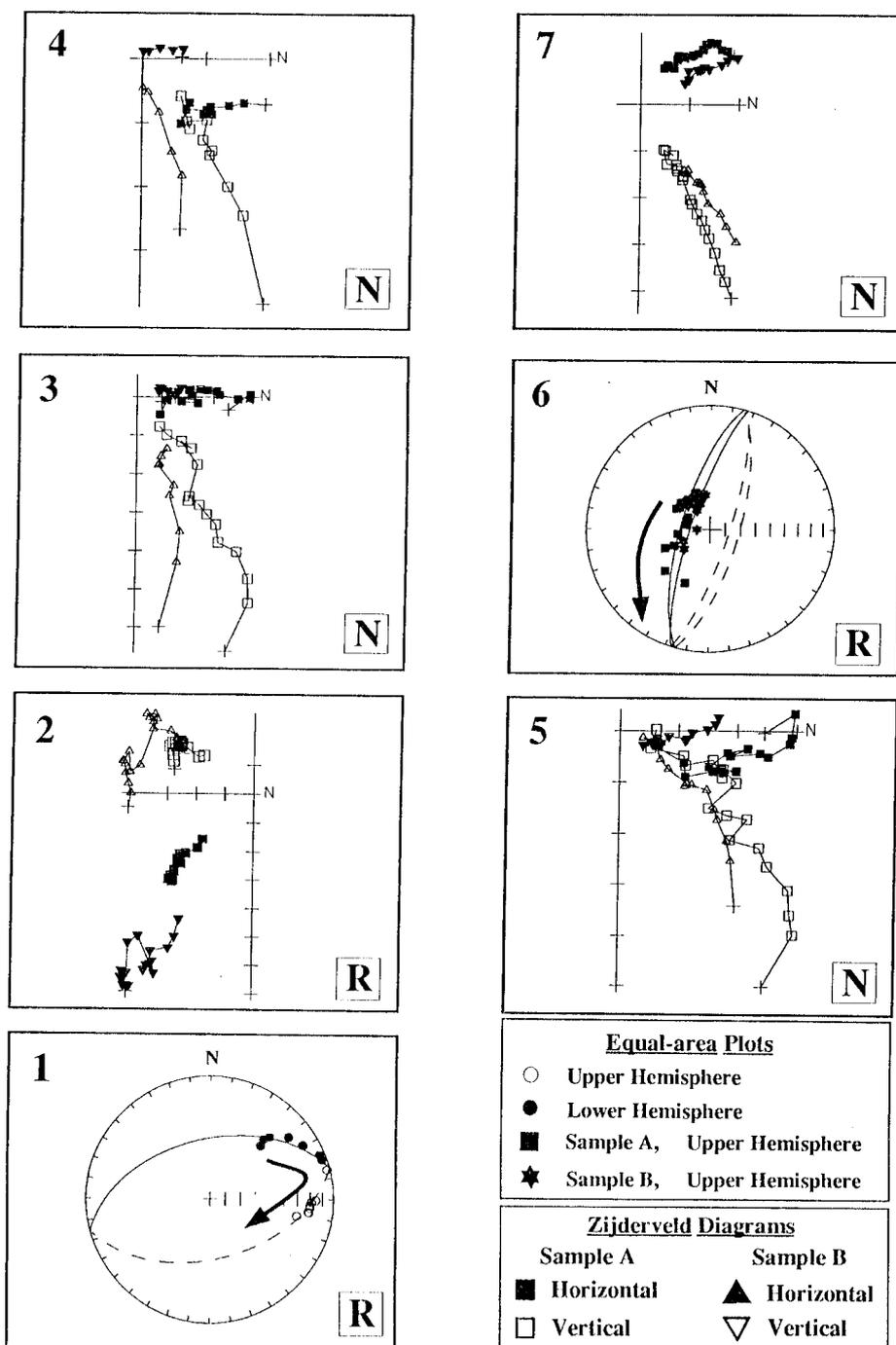
Figure 3. Vector end-point diagrams and equal-area projections of the sample behavior during step-wise demagnetization. Arranged in stratigraphic order from site 1 to site 7, the interpreted polarity of each site is shown in the bottom right of each frame.

3.2. Reversed polarity interval R1

The demagnetization data for site 1 closely follows a great circle toward a reversed polarity direction (as shown by the arrow in Figure 3) but a single characteristic component has not been isolated. This site is believed to be a reversed polarity site. The samples in site 2 show considerable differences in intensity, but they too define a consistent reversed polarity direction. These two sites together define a reversed polarity interval R1 which occupies the lower 700 m of the section (Figure 4). Two samples taken from the Whetstone Falls dinosaur trackway site were also reversed. The trackway site can be projected to lie in the upper part of the Whetstone Falls member of the Harebell Formation section, which correlates the trackways to this lower polarity interval, R1.

3.3. Normal polarity interval N1

Sites 3 and 5 all contain several components of magnetization but a final normal characteristic component has been isolated that shows a very consistent normal polarity direction. Samples from site 4 may be bypassing the origin, suggesting the presence of a ghost reversed component, but on balance we prefer a normal direction for these data. The interval comprising sites 3, 4, and 5 is defined as N1 and ranges from approximately 700 to 1500 m in the section.

3.4. Reversed polarity interval R2

Both samples in site 6 shows a consistent demagnetization trajectory that initially clusters in a present day field direction then moves on a great circle path towards a reversed polarity. This site may be considered questionable but it is certainly not a normal remanence direction. For the purposes of this preliminary study it is considered to be a reversed polarity site.

3.5. Normal polarity interval N2

The topmost site in the section displays a high intensity normal polarity direction with a single component of magnetization.

4. Correlation to the geomagnetic reversal time scale

Although these results are considered to be preliminary because of the wide spacing of the sample sites, the paleomagnetic evidence points to a major reversal boundary, from reversed to normal in the Whetstone Falls Member, and a shorter more questionable reversal in the Bobcat Member of the Harebell Formation. Within the broad time period defined by the stratigraphy (Figure 2) and the bracketing isotopic ages (74.9 and 68.7 Ma) there are two possible polarity intervals in the geomagnetic reversal time scale (GRTS) of Cande & Kent (1992) to which the polarity sequence R1 to N2 can be correlated. The first possibility we have labeled Hypothesis 1 in Figure 4; it correlates to Chron C32, which ranges from 73.781 to 71.722 Ma (Cande & Kent, 1992) straddling the Campanian/Maastrichtian boundary (as defined in the Western Interior by Kennedy *et al.*, 1992). The second possibility, Hypothesis 2 in Figure 4, is the polarity sequence of Chrons C31 and C30, which range from 71.72 to 66.60 Ma (Cande & Kent, 1992) and lies entirely within the Maastrichtian. These two
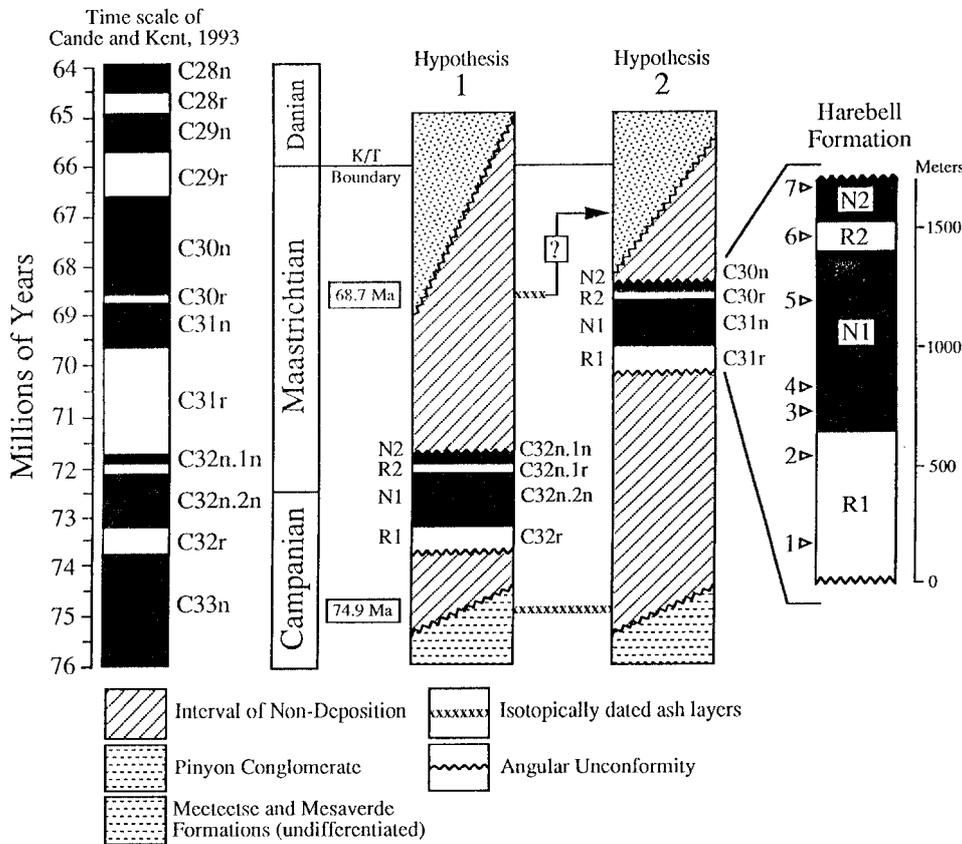
Figure 4. Correlation diagram showing the geomagnetic reversal time scale (GRTS) of Cande & Kent (1992); latest Cretaceous stage boundaries as defined by Kennedy *et al.*, (1992); isotopic ages (Love, 1977); alternative correlations of the Harebell Formation polarity sequence to the GRTS, hypotheses 1 and 2 and the correlation favored by this study to the Maastrichtian, Chrons 31 and 30 .

polarity intervals each fit equally well with the tentative magnetostratigraphy of the Harebell Formation (Figure 4).

We evaluate Hypothesis 1 (assuming that the polarity sequence R1 through N2 is Chron C32) by comparing it with the available chronologic and geologic information. The date of 74.9 Ma from the Meeteetse Formation beneath the basal unconformity of the Harebell Formation (Figure 2) places only a minimum age on the onset of the Laramide orogeny in the Jackson Hole region. Correlated to the GRTS, the date establishes that the beginning of the uplift could have occurred no earlier than, but most probably somewhat later than, the upper part of C33n (Figure 4). For Hypothesis 1 to hold true, the regional uplift and erosion, which exposed Late Cretaceous sediments as old as 88 Ma (Love, 1977), *and* the deposition of 700 m of the Harebell Formation would have had to have occurred within a time period of about 1.6 my (the difference between the age of the Meeteetse bentonite at 74.9 Ma and the top of C32R at 73.288 Ma; Cande & Kent, 1992).

Kennedy *et al.* (1992) place the Campanian/Maastrichtian boundary in the Western Interior at the biostratigraphic level of the ammonite range zone of *Baculites eliasi*, which ranges chronologically from 71.35 to 72.08 Ma, and is

known from regional magnetostratigraphic studies to lie in the upper half of C32n.2n (Hicks, Tauxe & Obradovich, 1991; fig. 3.14 of Hicks, 1993). If Hypothesis 1 is true and N1 correlates to C32N, then the Campanian/Maastrichtian boundary can be projected to lie approximately in the middle of the Harebell Formation (Figure 4) and the whole of the lower unnamed member would therefore lie in the Upper Campanian. However, this hypothesis is in conflict with the palynomorph and vertebrate biostratigraphy (Love, 1973), which indicates that the Harebell Formation is entirely Maastrichtian in age.

The preponderance of geologic, biostratigraphic, and chronologic information correlates the lower Harebell reversal R1 with the upper part of C31R, and the overlying normal polarity interval N1 with C31N (Hypothesis 2, Figure 4). This would place the Harebell Formation entirely within the Maastrichtian and in concordance with the biostratigraphy. The reversed interval R2 correlates with the short reversed interval C30R, and the topmost part of the Harebell within N2 can be inferred to lie in C30N. The upper radiometric age of 68.7 Ma chronologically correlates the base of the Pinyon with the base of C30R (Cande & Kent, 1992). However that isotopic age lies more than 300 m stratigraphically above C30R (as indicated by the arrow and question mark in Figure 4) which suggests either that the age of the C30N/C30R reversal may be somewhat younger than indicated in the GRTS, or that this age is anomalously old. This isotopic age was obtained from biotite crystals, and due to ^{39}Ar recoil effects (Hess & Lippolt, 1987), biotites extracted from bentonites often yield uninterpretable heating spectra or total fusion ages that are too old when compared to sanidine phenocrysts from the same unit. The younger correlation to the GRTS of Hypothesis 2 implies that the period of uplift and erosion between the underlying Upper Cretaceous strata and the Harebell Formation occurred over a period of some 4 to 5 my, a more reasonable time span for such a large scale tectonic event (Love, 1977) than the 1.6 my implied by Hypothesis 1.

The chronologic range of the magnetic polarity sequence of the Harebell Formation is approximately 68.2 to 70.3 Ma, which gives a calculated sedimentation rate of around 800 m/my, in the same range as the 920m/my proposed by Love (1973). The reversed trackway site most probably lies in the upper part of C31r and can thus be dated at approximately 70 Ma.

5. Paleoenvironment of the track site

The dinosaur tracks are found at a single level in the Whetstone Falls Member in a two-meter-thick tabular sandstone unit that lies in an interbedded succession of fine-grained sandstone and mudstone. The tracks are found on a planar surface within the fine-grained sandstone. The tracks are occasionally overlain by leaf impressions and the sinuous tracks of an invertebrate ichnofossil cf. *Neonereites biserialis* (Seilacher, 1960). This ichnofossil is also known from the Bearpaw Shale in the Bighorn Basin (Hicks, 1989), which was deposited in a relatively confined marine embayment in western Montana and Wyoming (Lillegraven & Ostresh, 1990). The Bearpaw Shale contains the ammonite *Baculites reesidei,* whose range zone is dated at 72.5 ± 0.4 Ma (Baadsgaard *et al.*, 1993), in a normal polarity interval correlated to C32N (Hicks, 1993).

In the Bighorn Basin, the ichnofossil *Neonereites biserialis* is found near the top of a regressive succession of subtidal marine sediments that lies just beneath the

tidal and shoreface sandstones of the Fox Hills Formation. It is found in
stratigraphic association with *Rhizocorallium* sp., *Thalassinoides* sp., and
Diplocraterion sp. The ichnofossils occur in rippled, tabular and hummocky,
cross-stratified sand layers that are heavily bioturbated. The interbedded shales at
this level are carbonaceous with abundant macerated plant material, suggesting
that a fluvial source of terrigenous organic debris was nearby and the environ-
ment may have been partially brackish (e.g., near a river mouth). The
well-defined ichnofossil levels may have been formed by opportunistic species
and mark brief marine incursions in a dominantly brackish water environment.

The occurrence of this ichnofossil in the Whetstone Falls Member of the
Harebell Formation is additional evidence to support Love's (1973) contention
that the northern Jackson Hole region was flooded by a marine or brackish
incursion. At a time when the rate of subsidence exceeded the rate of sediment
supply and the land surface fell below sea level, an arm of the Bearpaw Sea
probably invaded the drainage system that flowed to the southeast along the
rapidly subsiding linear downwarp in which the Harebell Formation con-
glomerates are confined.

The association on the same sandstone slabs of a nearshore marine ichnofossil
with dinosaur tracks allows the paleoenvironment to be reconstructed very
precisely as the sand-flats at the margins of a shallow marine or brackish
embayment. This is the earliest recorded instance of such a marine incursion in
the Harebell Formation, but at least one other is known from the overlying
Bobcat Member (Love, 1977).

6. Systematic paleontology

Theropoda Marsh 1881
Family uncertain
Genus *Exallopus*, gen. nov.
Etymology. Greek *exallos*, meaning different; Greek *pous*, meaning foot.
Diagnosis. Apparently bipedal tracks with four long, slender functional pedal
digits. Average divarication between outermost digits (I and IV) is 111.4°.
Footprint width greater than length. Digits II and IV subequal in length; both
shorter than digit III. Digit I shortest digit, and not a reversed hallux. Impression
of distal end of metatarsals impressed deeper than the digits and is semicircular in
shape. Claw marks compressed laterally. Track maker apparently bipedal,
although possibility exists that pes prints completely overlie manus prints.

Exallopus lovei sp. nov.
Etymology. In honor of J.D. Love, whose geologic mapping of the Jackson Hole
area provided the stratigraphic framework for this study. The attempt to relocate
one of Love's fossil plant localities led to the discovery of the track site.
Holotype. DMNH 5989, natural cast of left print.
Paratype. DMNH 5996, natural cast of right print.
Plesiotypes. DMNH 5990, fragmentary print, possibly two overlapping tracks;
DMNH 5992, partial print of right pes, overlapped by DMNH 5993; DMNH
5993, virtually complete left print; DMNH 5994, partial left print; DMNH
5995, partial right print; DMNH 5997, virtually complete left print. Each track
has been given its own catalog number. Abbreviations used: DMNH—Denver
Museum of Natural History, Denver, Colorado
Type Locality. DMNH Locality #443: Whetstone Falls Member of the Harebell

Formation, Upper Cretaceous (Maastrichtian), in the Bridger-Teton Wilderness on the east side of Whetstone Creek, 1067 m upstream from confluence of Whetstone and Pacific Creeks, at an elevation of 2304 m (NW 1/4 of NE 1/4 of SW 1/4 of Sec. 10, T46N, R113W; 43° 57′ 54″ N, 110° 24′ 39″ W).

Description. Eight footprints referable to *Exallopus lovei* on four slabs (Figures 5a, b, 6, 7) were removed from the locality. The prints are all natural casts; actual prints were discovered but not collected. All the tracks have a great deal of relief, implying that the original tracks were relatively deep. The tracks have clear outlines, although they are not so well-defined that digital nodes ('pads') can be distinguished. Measurements of each track are given in Table 1.

The holotype, DMNH 5989, is the only complete track of the eight collected. The print, that of a left pes, clearly demonstrates the existence of four digits plus an impression made by padding beneath the distal end of the metatarsals. The footprint length (FL) was measured from the tip of the longest digit (digit III) along its axis to the opposing edge of the metatarsal impression (method 'b' of Thulborn, 1990, p. 82). Digital lengths (DL) were measured from the distal end of each digit along its axis to the intersection of the axis and a line drawn perpendicular to the axis and tangent to the most recessed point of the hypex (method 'c' of Thulborn, 1990, p. 83). Digits II and IV are subequal in length, while digit I is markedly shorter than the other digits. Footprint width (FW) was measured perpendicular to footprint length (per Thulborn, 1990, p. 82). Digital widths (DW) were measured perpendicular to DL near the bases of the toes. Digit III is the widest; digits II and III appear to be roughly the same width, and digit I has the smallest width. Divarication of the digits seems to be greater overall in the holotype than on the other prints, although most of the other prints are too incomplete for a decent comparison. Average total divarication seems to be roughly 111°, which is greater than that of most other known theropod tracks, although it must be noted that total divarication measurements for most other tracks are for tridactyl, not tetradactyl, prints. The average total divarication excluding digit I is 76.8°.

Overall, the tracks display a suite of characteristics that are unique among known theropods tracks. *Exallopus* tracks are characterized by four toes radiating directly from the small and rounded impression of the distal end of the metatarsals. This indicates that the foot possessed four metatarsals, approximately subequal in length, supporting four functional digits. The small area of the metapodial impression indicates that the metatarsals are closely appressed, and perhaps even fused, along their entire length. The relief of the metapodial impression is greater than those of the digits. The metapodial impressions have an average relief of 3.8 cm, but collectively, the bases of digit III average only about 2.4 cm. The metapodial impression is rounded distally, in a circular manner inconsistent with the parabolic, elongate, 'wedge-shaped' configuration seen in most theropod tracks (Thulborn, 1990). All digits, including the hallux, radiate directly from the forward margin of the metapodial imprint in a stellate pattern. The hallux is impressed along the entirety of the digit, rather than indicating its presence merely with a claw mark. The hallux is not in a reversed position.

Three of the tracks (DMNH 5989, 5996, and 5997) suggest an additional feature: areas between digits II and III and between III and IV have greater relief than the surrounding substrate, but less relief than the digital impressions. J. Farlow (written commun., 1993) has suggested that this might indicate webbing
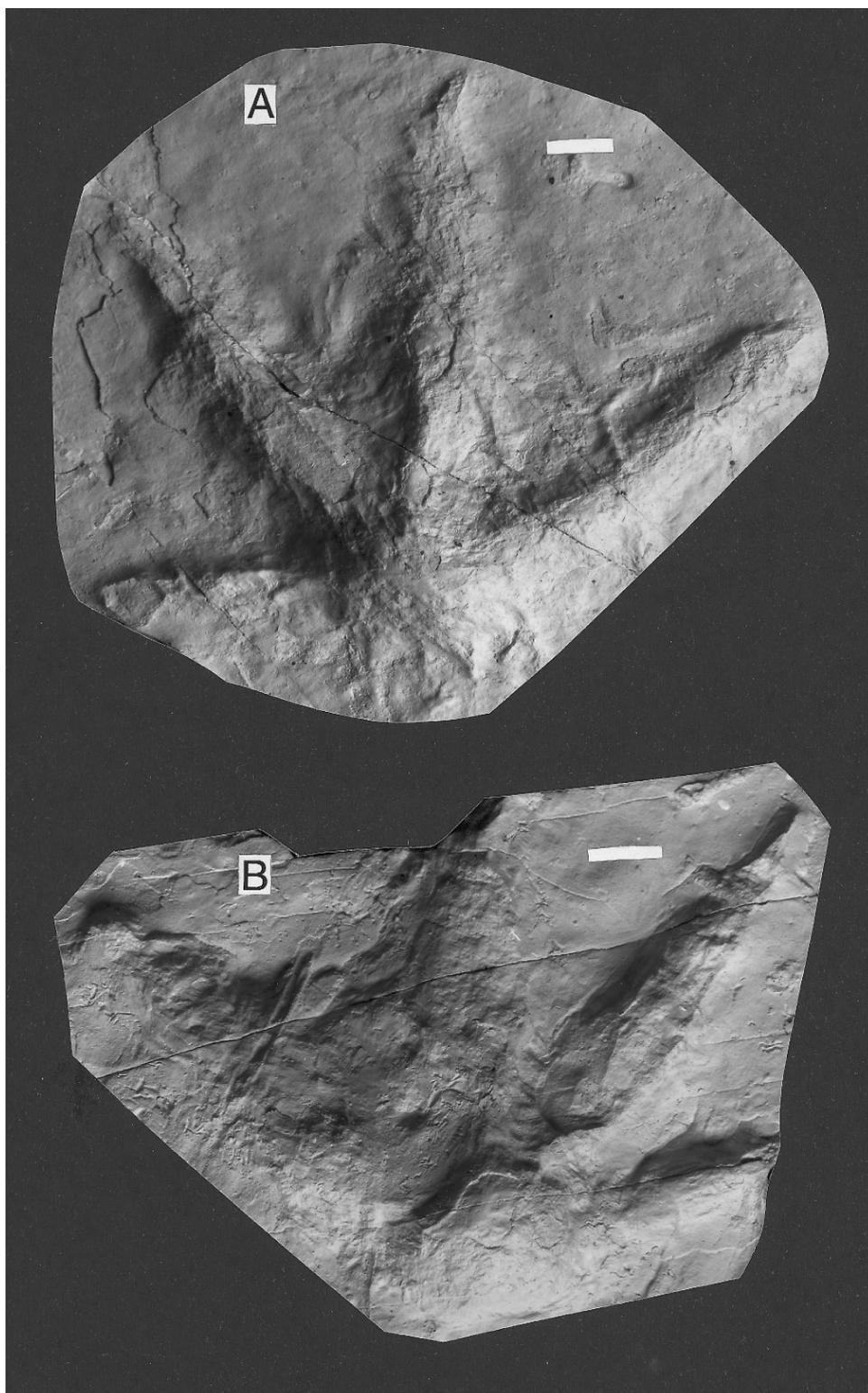
Figure 5.   A, *Exallopus lovei*, holotype (DMNH 5989), natural cast of left pes print. B, *Exallopus lovei*, paratype (DMNH 5996), natural cast of right pes print. Scale = 3 cm.
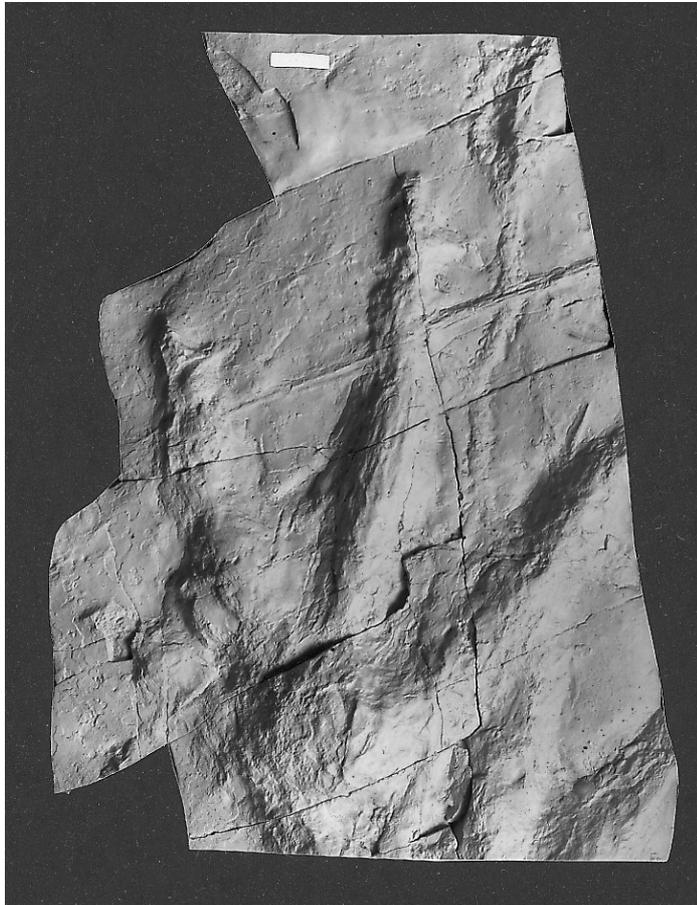
Figure 6.   *Exallopus lovei* track (DMNH 5993) with cf. *Neonereites biserialis* burrow (upper right). Scale = 3 cm.

between the toes. The terminal margins of the ''webbing'' impressions extend horizontally between the digits. The webbing impressions observed in the *Exallopus* tracks begin at the hypex and terminate roughly one-third the way up the toe. Whether or not this is a preservational feature or actual webbing between the digits is uncertain.

7. Discussion

The size of the *Exallopus* tracks and the apparent bipedal nature of the tracks shows that the track maker was a dinosaur, although which dinosaur is somewhat of a conundrum. No known 'Lancian' or 'Edmontonian' dinosaurian taxon shows the size range or foot structure of these tracks. The FL/FW ratios (of the only three tracks complete enough to provide this measurement) are of no assistance, as one (.90) falls within the range generally accepted for ornithopods but not theropods, another (.73) falls within the theropod range, and the third (.83) could be either ''carnosaurian'' or from a large ornithopod (Thulborn, 1990). Thus, only a comparison of the track morphology to the pedal skeletons of various dinosaurs will provide insight into the origin of the *Exallopus* tracks.

Table 1.   Measurements of *Exallopus lovei* tracks

	DMNH 5989*	DMNH 5990	DMNH 5992	DMNH 5993	DMNH 5994	DMNH 5995	DMNH 5996	DMNH 5997
Toes evident	4	3?	3	4	3?	4	4	4
foot	left	right?	right	left	left	right	right	left
FL	28.4	n/a	n/a	31.5	n/a	n/a	21.5†	19.8†
DL I	11.0	8.9?	n/a	8.0	9.3†?	4.7†	7.5	6.3
DL II	17.4	11.7?	9.9†	17.9	18.1†?	17.0	16.5	14.5
DL III	18.7	13.8†?	11.5†	22.4	18.5†?	16.0†	13.5†	12.7†
DL IV	17.3	n/a	8.0†	15.0†	n/a	17.7	16.0	11.5
FW	31.5	n/a	n/a	n/a	n/a	n/a	29.5	23.0
FS	34.5	n/a	n/a	n/a	n/a	n/a	29.5	25.3
DW I	3.4	3.7?	n/a	3.6	?	?	3.5	3.0
DW II	4.0	4.5?	4.2	3.2	6.6?	5.0?	4.3	5.6?
DW III	4.0	4.5?	3.7	3.6	5.3?	?	4.7	4.2
DW IV	4.7?	n/a	3.4	3.5	n/a	?	4.5	3.4
DIV I-II	58°	˜87°?	n/a	19°	80°?	40°	20°	30°
DIV II-III	40°	˜42°?	21°	28°	54°	36°	29°	45°
DIV III-IV	52°	n/a	50°	28°	n/a	33°	51°	48°
DIV II-IV	92°	n/a	71°	56°	n/a	69°	80°	93°
TTL DIV (I-IV)	150°	n/a	n/a	75°	n/a	109°	100°	123°
FL/FW	.90	n/a	n/a	n/a	n/a	n/a	.73†	.86†

FL = footprint length; DL = digit length; FW = footprint width; FS = footprint span; DW = digit width; DIV = angle of divarication; TTL DIV = total divarication (between outermost digits); n/a = not applicable. All length measurements in cm.
* holotype; † measurement based on preserved portion of track; part of digit missing from track.
Note: DMNH 5991 is a very faint, three-toed track of apparent theropod origin on the same slab as DMNH 5989 and 5990 and is not herein described; it represents a possible undertrack of another theropod ichnospecies.

Among the non-ornithopod ornithischians, the Thyreophora and the Marginocephalia, only the latter could be considered candidates for the *Exallopus* track makers, as it is generally accepted that the former were quadrupeds.

Of the ceratopsians, only the psittacosaurids and some protoceratopsians may have used bipedal movement. Psittacosaurids have tetradactyl feet, but digit I is very much reduced. Also, as far as is known, psittacosaurids are exclusively found in the Lower Cretaceous of Asia. Some of the smaller Asian protoceratopsians, such as *Microceratops*, and the North American Upper Cretaceous *Leptoceratops* [body fossils of which have been found in the Pinyon Conglomerate (Love, 1973)] are better adapted to bipedality, although this may not have been a favored stance. The feet of both *Microceratops* and *Leptoceratops* are tetradactyl with relatively long and narrow digits. All four digits are directed forwards and radiate from the base of the metapodium (digit I is very slightly elevated). The terminal unguals are not nearly as blunt as those of larger ceratopsians, although they are too broad to have made the narrow claw impressions seen in *Exallopus*. Morphologically, the pedes are very similar to those of the supposed *Exallopus* track maker, except that the ceratopsians are smaller: the foot of *Leptoceratops* is only 20 cm, and *Microceratops* is just under 10 cm, compared with around 30 cm for the larger prints of *Exallopus*. It is very nearly certain that *Leptoceratops gracilis* did not grow large enough to have made *Exallopus* tracks because the known skull is small and shows the completely fused sutures expected of an adult animal (Sternberg, 1951). Larger ceratopsians possessed a markedly different pedal morphology, and could not have made the *Exallopus* tracks.

Pachycephalosaurs are bipedal ornithischians, despite their apparent relations

to the ceratopsians (Sereno, 1986). Pachycephalosaurian feet are very poorly represented in the fossil record. What is known demonstrates a foot composed of four metatarsals, supporting a functionally tridactyl foot with a strongly reduced digit I (Maryańska, 1990).

Among the most common Late Cretaceous ornithopods were the hadrosaurids. The pes is tridactyl, with broad, short digits, terminating in blunt hooves (Thulborn, 1990). No hadrosaurid is known to have even a remnant of pedal digit I; thus, no hadrosaurid could have made the tetradactyl *Exallopus* prints.

Many Late Cretaceous ornithopods, especially the hypsilophodontids, possessed a tetradactyl pes. Hypsilophodontid pedal digits are relatively long and narrow, and terminate in 'hooves' which are long and narrow, and not as distinct from claws as the hooves of more graviportal forms, such as the hadrosaurids. They are distinguished from claws by their lack of curvature and medial compression, and blunter distal ends. Digit I is slightly reduced, but still very much present in the pes. Morphologically, the foot of a typical hypsilophodontid very closely resembles an expected form for the makers of *Exallopus*, except that all known hypsilophodontids are roughly one-third the size of the assumed *Exallopus* track maker. Also, the metatarsals in hypsilophodontids are not closely appressed at their distal ends, which would give a hypsilophodontid track a much broader 'heel' region.

The dinosaur *Tenontosaurus*, a primitive iguanodontid (Forster, 1990), has a similar foot to that of a hypsilophodontid. However, *Tenontosaurus* has toes much shorter than would be expected for the *Exallopus* track maker. The metatarsals of *Tenontosaurus* are widely spaced at their distal ends, and would have left a much broader 'heel' impression than is seen in *Exallopus*.

Some prosauropod tracks resemble *Exallopus* in that they have four clearly defined digital impressions. Farlow & Lockley (1993) figure a tetradactyl track, *Pseudotetrasauropus*, attributed to a prosauropod, which resembles those of *Exallopus* in morphology. The *Pseudotetrasauropus* print possesses four long, narrow digits with small claw impressions, like *Exallopus*, though they are not as narrow. However, the impression of digit I is longer than that of *Exallopus*. In addition, it does not seem to connect to the 'heel' imprint, unlike that of *Exallopus*. The 'heel' in *Pseudotetrasauropus* may, in fact, be an imprint of a digital node, rather than a true, combined metatarsophalangeal pad. Further, digits II, III, and IV in *Pseudotetrasauropus* are subequal, unlike those of *Exallopus*. Most importantly, no prosauropod is known to have survived beyond the Early Jurassic, and while not completely impossible, it is highly improbable that the *Exallopus* track maker is an Upper Cretaceous remnant of an otherwise completely unknown prosauropod line.

Therizinosauroids, suggested by Paul (1984) to be a relic lineage of prosauropod descent, are now known to be aberrant theropods, possibly close to the Maniraptora (Russell & Dong, 1993). The feet of *Alxasaurus* and *Erlikosaurus*, the only therizinosauroids for which the pes is almost completely known, are tetradactyl with large claws (Barsbold & Perle, 1980; Russell & Dong, 1993). Although therizinosauroid locomotion is uncertain, given the paucity of existing material, most reconstructions of these animals place them in a quadrupedal stance (e.g., Paul, 1988), though bipedality may have been quite possible (Russell & Dong, 1993). Even if therizinosauroids could move bipedally, the interdigital divarications of *Exallopus* tracks appear to be greater than is reconstructed for *Erlikosaurus* (Barsbold & Perle, 1980), although that reconstruction does not

account for the normal spreading of the digits that occurs when meeting resistance from a substrate. Nevertheless, the metatarsals of *Alxasaurus*, *Erlikosaurus*, and *Segnosaurus* are very massive and stocky, and do not articulate at their distal ends, as would be expected for the *Exallopus* track maker. A print made by a foot like this would have a very broad metapodial impression, unlike the small and compact form seen in *Exallopus*. The pedal phalanges of *Alxasaurus* and *Erlikosaurus* are likewise broad and thick and would leave an impression much less gracile than those of *Exallopus*. The pedal unguals are short in the Lower Cretaceous *Alxasaurus* but long in the Upper Cretaceous *Erlikosaurus*, whereas the claw impressions of *Exallopus* are extremely short. It does not appear likely that any known therizinosauroid was responsible for the *Exallopus* tracks.

With tracks attributed to other, more 'typical' theropods, *Exallopus* tracks share a number of features, including long, narrow digits (especially in 'coelurosaur' tracks), large interdigital divarication angles, small metapodial impressions, and distinct, laterally compressed claw marks (especially notable on DMNH 5989, 5990, 5993, 5994, and 5996). *Exallopus* tracks differ from most of their theropod counterparts in the tetradactyl nature of the pes, as well as the semicircular shape of the rear margin of the metapodial impression.

Fossil footprints attributable to theropod dinosaurs are relatively common in Upper Cretaceous strata around the world. The structure of the theropod pes is generally perceived as similar to many modern birds in predominant tridactyl morphology (Thulborn, 1990). Almost every theropod known from body fossils has four toes, digits I, II, III and IV, with digit V having been greatly reduced or lost early in theropod evolution (Gauthier, 1986). Recent analysis of *Herrerasaurus* indicates that a 5-toed condition is possibly primitive for the Theropoda (Novas, 1993). However, the loss of digit V was a rapid evolutionary trend, for only a few million years later, this digit was reduced to a splint of metatarsal V in *Coelophysis* (Colbert, 1989) and *Syntarsus* (Raath, 1977). From this point in the Late Triassic onward, theropods apparently had four pedal digits.

Digit I (the hallux) in the theropod pes is, in all generally accepted phylogenies, reduced in size and elevated to the point where it generally did not contact the ground in normal, digitigrade stance. Digit I is often reversed to a position in opposition to the three main, weight-bearing digits (II, III and IV) in later theropods (Gauthier, 1986). Tracks designated as having a theropod origin demonstrate a reversed hallux as far back as the Late Triassic (Thulborn, 1984; Gauthier, 1986), and possibly even the Middle Triassic (Haubold, 1971; Lockley, 1991); thus, theropods have been, almost since their beginnings, functionally mesaxonic, with a tridactyl pes. By far the majority of tracks associated with theropods are tridactyl as well. Thus, the discovery of tracks made by a functionally tetradactyl theropod in the Upper Cretaceous is quite unexpected.

In the instances where theropod tracks *do* have impressions of four digits, the fourth digit is almost always in the position expected of a hallux: medial or distal to the mesaxial digits (Thulborn, 1990). Since theropods are assumed to be functionally digitigrade, the metatarsals do not often leave an impression, except under certain circumstances.

Exallopus tracks depart from most theropod track-making scenarios (Figure 7a–e), as they are both shallow and possess a definite and complete hallux impression but no elongate 'heel' imprint. This demonstrates that the first digit
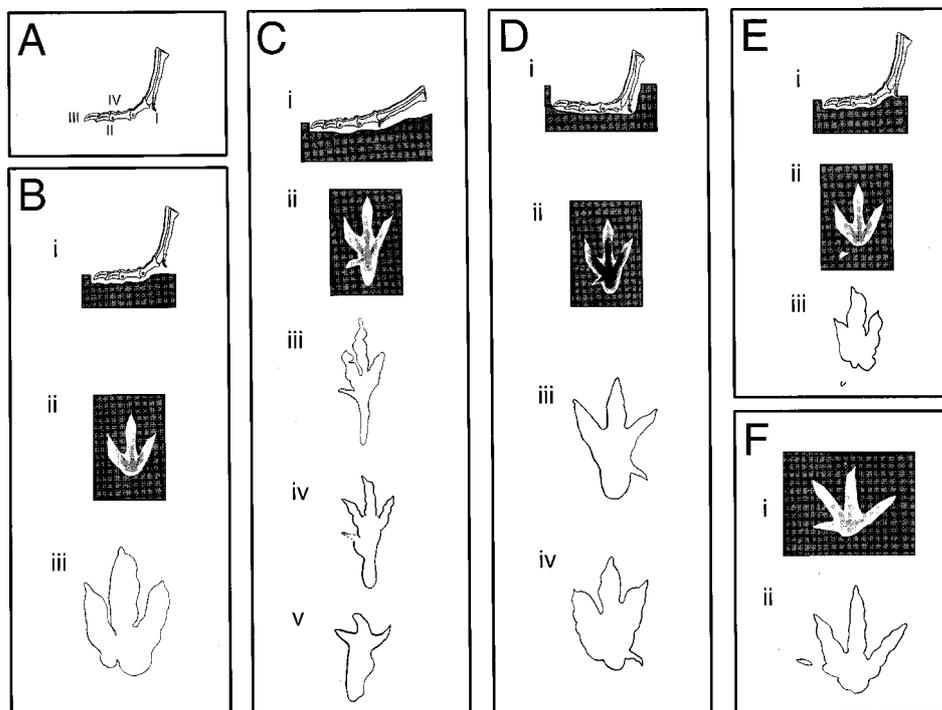
Figure 7. A, Skeletal reconstruction of typical, 3-toed theropod foot, with reduced hallux (digit I). B, (i) Cross-sectional view of track made by typical theropod foot in normal, digitigrade posture. (ii) Overview of track in (i). Note the uniform depth of the impression and the small size of the heel impression. (iii) Example of print made by a theropod in typical, digitigrade posture: *Eubrontes giganteus* (after Lull, 1953). C, (i) Cross-section of track made by typical theropod foot in atypical, plantigrade posture. (ii) Overview of track in (i). Note the uniformity of depth and the greatly elongate heel impression, including the hallux impression. (iii–v) Examples of prints made by a dinosaur in atypical, plantigrade posture: (iii) *Jialingpus yuechiensis* (ornithopod?) (after Zhen et al., 1983). (iv) *Anomoepus* sp. (ornithopod?), in this case, from an animal progressing quadrupedally (after Lull, 1953). (v) *Eubrontes glenrosensis*, a tridactyl theropod track. Note the lack of a hallux print; this may be an artifact of the sticky mud in which the track was made pulling back upon withdrawal of the foot, thus obliterating the hallux impression (traced from Kuban, 1989). D, (i) Cross-section of track made by typical theropod foot in normal, digitigrade posture in a matrix soft enough to allow the foot to sink deeply. (ii) Overview of track in (i). Note the great depth of the heel region of the track, and the resultant hallux impression but without the long metatarsal impression of B(ii). This track is hypothetical because such a soft matrix would likely infill upon withdrawal of the foot. (iii–iv) Examples of prints made by a theropod progressing in normal, digitigrade posture in a water-saturated substrate: (iii) *Bückeburgichnus maximus*, possibly a result of this scenario (no track depth data given) (after Haubold, 1971). (iv) *Gigandipus caudatus*, possibly a result of this scenario (no track depth data given) (after Haubold, 1971). E, (i) Cross-section of track made by typical theropod foot in normal, digitigrade posture possessing a primitive, nonreduced digit I. (ii) Overview of track in (i). Note the small, shallow, and unconnected impression left by the hallux at the rear of the track. (iii) Example of a print made by a typical theropod foot in normal, digitigrade posture possessing a primitive, nonreduced digit I: *Anchisauropus tuberosus* (after Haubold, 1971). F, (i) Track of *Exallopus*. Note that the hallux is impressed despite the lack of track depth. (ii) Print of *Anomoepus intermedius*. Note the similar morphology; however, many prints of this ichnogenus also possess a long metatarsal impression—see C(iv) (after Lull, 1953).

is not a typical theropod reduced and elevated hallux that emanates from an elevated point on the metatarsals. If the *Exallopus* track maker were functionally tridactyl with an elevated hallux, then the only situation in which the footprint could be as markedly tetradactyl, as the *Exallopus* prints, are would be if the

substrate were very wet, allowing the foot to sink in deeply enough to provide digit I full contact with the substrate (Fig. 7d i, ii). If this were the instance with the *Exallopus* prints, then the tracks would be extremely deep. The prints, however, demonstrate none of the signs of having been made in a deep, moist substrate, so this clearly cannot be the case. The size of digit I and its functionality in the foot of the *Exallopus* track maker may indicate a reversion from the 'normal' theropod condition consisting of a reduced and elevated hallux. It is probably not a retention of a primitive character state, as no theropod since the Late Triassic is known to have retained four large, functional pedal digits.

Known Late Cretaceous theropods include both large 'carnosaurian' forms, as well as the more gracile 'coelurosaurs' (the terms 'carnosaur' and 'coelurosaur' are used here in a non-cladistic sense). *Exallopus* tracks are too gracile to have been made by a typical Late Cretaceous 'carnosaur,' such as a member of the Tyrannosauridae. The narrowness of the digits is more indicative of a 'coelurosaurian' origin (Thulborn, 1990).

Ornithomimosaurs are large coelurosaurian theropods, in the correct size range to have possibly made the tracks. Ornithomimosaur feet have a greatly reduced digit I; some forms have either lost this digit entirely or their feet are incompletely known (Barsbold & Osmólska, 1990). Similarly, oviraptorosaurs also possess a greatly reduced pedal digit I (Barsbold *et al.*, 1990). The poorly known group of exclusively Late Cretaceous theropods known as elmisaurids possess a tetradactyl foot, but here again digit I is greatly reduced (Currie, 1990).

Troödontids and dromaeosaurids share both a greatly reduced digit I and a specialized digit II. The second pedal digit in these forms is believed to have been held retracted and off the ground in normal locomotion, holding the 'sickle' claw clear from wear. One would expect footprints from either of these groups to be didactyl. Such prints are known, although extremely rare (*Deinonychosaurichnus*, Zhen *et al.*, 1987, as cited in Zhen *et al.*, 1989; undescribed DMNH specimens).

The three *Exallopus* tracks that display possible interdigital webbing are, perhaps not coincidentally, also the tracks with the greatest interdigital angles. If the track maker did indeed possess webbed toes, then one would expect the webbing to have made the greatest impression when stretched taut, providing the greatest resistance to the substrate, and thus creating an impression. The remaining *Exallopus* tracks, which have much smaller interdigital angles, lack the webbing impressions since the digits are not spread to their maximum angles. The webbing was hence more apt to deform against the substrate, and not leave an impression.

The possible presence of interdigital webbing in the *Exallopus* tracks is an unexpected trait for the track of a theropod . However, many tracks attributed to Mesozoic birds also possess webbing (Mehl, 1931; Currie, 1981; Lockley *et al.*, 1992). The lack of an extended metatarsal impression and the high degree of relief of a semicircular metapodial print in the *Exallopus* tracks is also a feature considered characteristic of birds (Currie, 1981; J. Farlow, written commun., 1993). Thulborn (1990) makes particular note of the extreme similarity in the morphology of theropod and bird footprints, to the point where positive attribution of a track to either taxon is extraordinarily difficult. Although it is negative evidence, we agree with Thulborn (1990) that skeletal remains must play an important role in the process of linking footprints to specific animal groups. A bird large enough to make the *Exallopus* tracks would rival the moas (Order Dinornithiformes) in size, and no such birds are known until the

Paleocene diatrymas (Feduccia, 1980). Of the ratites, many of which have attained large size, those that retain a hallux display the reduced and elevated condition for that digit. In fact, we can find no reference to any bird, living or fossil, which possesses an unreversed, functional, weight-bearing hallux; thus, it is unlikely that any neornithine bird was responsible for the *Exallopus* tracks. Similarly, the unusual Late Cretaceous enantiornithiform birds are characterized by metatarsals which are fused only proximally (Walker, 1981; Martin, 1987), and so are not likely as *Exallopus* track makers. It seems more parsimonious that a theropod, not a bird, was the track maker.

8. Conclusions

Exallopus tracks are highly unusual in possessing a tetradactyl morphology, semicircular metapodial impressions, and interdigital webbing. The length and narrowness of the digits as well as the claw impressions indicate a theropod origin. *Exallopus* tracks were made by a theropod dinosaur which is not currently known from body fossils. Nevertheless, it is quite possible that bones of the type of animal responsible for the tracks will be found: the Harebell Formation and the Pinyon Conglomerate have also yielded dinosaur bones (Love, 1973). Except for a few specimens of the ceratopsians, tyrannosaurids, and questionable fragments of camptosaurids and nodosaurids (Love, 1973; McKenna, 1980), the fauna of the region remains poorly sampled. New expeditions in these Upper Cretaceous rocks could determine the nature of the *Exallopus* track maker.

Many authors (e.g., Russell, 1975; Clemens, 1982; Sloan *et al.*, 1986) have described, based on body fossils from western North America, an apparent decline in dinosaurian diversity towards the end of the Cretaceous. Some authors have interpreted these data to suggest that the extinction of the dinosaurs was a gradual event, spread out over the final 10 million years of the Cretaceous (Sloan *et al.*, 1986). *Exallopus* tracks indicate the existence of a latest Cretaceous dinosaur as yet unknown from the body fossils. This discovery cautions against making judgments about dinosaurian diversity and decline on the basis of the patchy record of body fossils.

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