Simulated weathering of dinosaur tracks and the implications for their characterization

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Abstract: Digital models of the tracks of bipedal theropod and ornithopod dinosaurs, and the quadrupedal tracks of a sauropod, were computationally eroded to investigate the effects of erosion on the shapes, sizes, and diagnostic details of fossil tracks. Narrow and (or) angular details, such as claw marks, interdigital ridges, and internal ridges, are removed early in erosion, creating the potential for misidentification of eroded theropod tracks as those of ornithopods. However, with the erosion models presented here, all tracks retain their basic shapes as indicated by the relative constancy of their interdigital angles and by the relative constancy of their footlength:footwidth ratios. Surface lengths of tracks did not increase significantly with erosion, so that dinosaurian hip height and speed estimates derived from trackways would not be greatly in error if based on eroded surface tracks. Synthetic undertracks from the surface tracks were also produced using information from published physical models of track formation. The differences between a weathered surface track and a freshly exposed, simulated undertrack are sufficient so that the two model tracks would not be confused. Large, rounded tracks are much better at retaining their characteristics than small, angular tracks, with the implication that large tracks may be over-represented in the fossil record, but they may be more reliably attributed to the appropriate trackmaker. This would bias estimates of dinosaur taxonomic diversity and body size ranges based on trackway evidence.

Résumé : Des modèles numériques d'empreintes de pas de dinosaures bipèdes (théropode et ornithopode) et quadrupèdes (sauropode) ont été soumis à des simulations informatiques du processus d'érosion afin d'étudier les effets de l'érosion sur la forme, la taille, et les détails diagnostiques des empreintes fossilisées. Les modèles érodés démontrent que les détails étroits et (ou) angulaires, tels que les traces de griffes et les arêtes interdigitales et internes, sont rapidement éliminés par l'érosion, menant à la possibilité de confondre des traces érodées de théropodes pour celles d'ornithopodes. D'après les modèles d'érosion présentés ici, toutes les empreintes préservent leur forme essentielle, telle qu'indiquée par la constance des angles interdigitaux et la constance du rapport entre la longeur et la largeur de la trace. La longueur des traces n'est pas affectée de façon significative par l'érosion, de sorte que l'évaluation de la hauteur de hanche et de la vitesse de locomotion des dinosaures ne serait pas grandement affectée si basée sur des traces érodées. Des sous-traces synthétiques pour les traces de surface ont été crées selon des données publiées sur le mode de formation des traces. Une trace de surface érodée est suffisemment distincte d'une sous-trace récemment exposées de sorte que les deux ne peuvent être confondues. Les empreintes grandes et arrondies préservent mieux leurs formes que celles qui sont petites et angulaires, menant à la possibilité que les grandes traces fossiles puissent être sur-représentées. Ceci affecterait l'évaluation de la diversité des dinosaures ainsi que du spectre de taille menée à partir de traces fossiles.

Introduction

A great many tracks and trackways of dinosaurs have been discovered, described, and named (Thulborn 1990), and trackways provide an important source of information about these animals that cannot be retrieved from skeletons. In particular, dinosaur tracks often document the occurrences of dinosaurs in regions that are not known from any skeletal material (e.g., Currie 1989); the range of sizes of animals that lived in a habitat can often be deduced (e.g., dinosaur stampede, Thulborn and Wade 1989); estimates of the speeds of locomotion can be made (Alexander 1976); and lastly examples of different kinds of behaviours can be revealed with tracks and trackways, such as animals shifting from a walking to a running gait (Day et al. 2002), moving as a group (Bird 1941), or possible stalking and hunting (Thomas and Farlow 1997). Tracks and trackways can also aid in the interpretation of the physical environment in which they were made (Currie 1989; Pittman 1989). The robustness of all these inferences and interpretations will depend on what was originally preserved when the tracks were formed and on what erosion has left us with in terms of the detail and quality of the tracks and trackways.

The tracks of dinosaurs are geological objects that have the potential to be subject to erosion both after their initial

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formation and during subsequent exposure as trace fossils. With the aim of investigating the effects of erosion on the identification and characterization of dinosaur tracks, a series of three-dimensional (3-D), digital models of some well-known track types were created. These models were then acted upon by simple transformation rules which replicated the gradual, and sometimes selective, effects of erosion removing rock. This computational technique was chosen as a way to overcome the long times that would be needed to effect the erosion of actual physical models of tracks. Using 2- and 3-D visualizations of different stages of erosion, the changing forms of the simulated tracks were analyzed. It was hypothesized that erosion would substantially affect all aspects of tracks, leading to large uncertainties in many of the aspects of the biology and occurrences of dinosaurs commonly inferred from track and trackway evidence (see in preceding text).

The often overwhelming complexity resulting from the simultaneous action of the different geological processes associated with erosion necessitated making some simplifying assumptions to model erosion. The erosion rate was assumed to be constant, independent of temperature and water chemistry, and that the erosional surfaces were horizontal. In all cases, it was assumed that the simulated tracks were immediately buried and preserved after their formation, and that erosion acted on lithified sediment only. Soft sediment deformation of tracks involves plastic flow, which is subject to the highly variable fluid mechanical properties of sediment (Gatesy et al. 1999; Manning 2004), and these complicating factors were avoided by considering only lithified tracks. Fluid dynamics calculations for even simple shapes are extremely complex (Trefil 1975), and any to attempt to simulate the removal of unlithified sediment from a footprint via entrainment by flowing water or air was rejected as being impractical.

Related to the effects of erosive processes on tracks is whether or not some less-than-pristine dinosaur tracks are the eroded remains of tracks that were originally formed at the surface with clear details or whether they are merely the exhumed instances of tracks that formed at some depth below the true track (undertracks), resulting in a loss of details because of the attenuation of the force of footfall impact with depth (Lockley 1991: 27–32; Thulborn 1990: 26). With the 3-D digital track models of this study, and the results of physical models of track formation (Allen 1997) applied to the digital ones, the characteristics of undertracks and their formation were also investigated.

Materials

Pes tracks of seven habitually or facultatively bipedal dinosaurs, and the pes and manus tracks of one quadrupedal dinosaur, were selected from the line drawings of various tracks in the comprehensive review of Thulborn (1990) (Table 1). These illustrations were chosen for their clarity and consistent style to enable fair comparisons among eroded forms of the different tracks, with the knowledge that they were all initially constructed or redrawn from other sources with the same biases of a single author. Track images were scanned and imported into the general purpose graphics program Canvas, the principal outlines of the tracks digitally traced, and the resulting contours scaled to match the dimensions quoted in Thulborn (1990). The contours are in the form of sets of (*X*, *Y*) coordinate pairs collected in sequence so they that define oriented contours with a right-hand sense of curl (O'Neil 1983). This property of consistent contour orientation was used when generating the footprint impressions (see later in the text). Some tracks are represented by just a single contour (e.g., *Grallator*), whereas others, such as those of the Mexican iguanodontid, are composed of multiple contours: the external contour that defines the limits of the track and a set of internal contours that marks the boundaries of sub-digital pads.

Table 1. Track illustration sources.

	Thulborn (1990) Fig. No.	Reference
Grallator	4.4 (right)	None
Eubrontes	6.4 (e)	Lull (1953)
Moyenosauripus	6.27 (a)	Ellenberger (1974)
Iguanodontid (England)	6.33 (f)	Lockley (1987)
Iguanodontid (Mexico)	6.33 (k)	Ferrusquia-Villafranca et al. (1978)
Hadrosaurid	6.37 (b)	Langston (1960)
Brontopodus	6.15 (a)	Farlow (1987)

As a first approximation, a dinosaur track can be viewed as being composed of both circle-like components, such as the heels and broad toes of a large ornithopod track, and triangular or wedge-like components, such as the heels and the narrow, tapered toes seen in the tracks interpreted to have been made by theropods and small ornithopods (Thulborn 1990). To assist in the investigation of the changes in footprint morphology two simple test shapes (circle and triangle) were used to generate tracks. Erosion of these simple shapes would potentially reveal general principles of weathering that would be applicable to the weathering of the rounded and angular components of dinosaur footprints. To facilitate comparisions among the erosional models of the true tracks and the rounded and angular test cases, the enclosed areas of the circle and triangle tracks were both set to ~0.1 m^2, which is within the range of areas of the true tracks (Table 2).

Methods

Three-dimensional track generation

Square grids of pixels were used to represent sediment surfaces that would receive track impressions, with the resolution for a given track grid ranging between 1 and 3 mm per pixel. Grid dimensions ranged from 103 × 103 pixels for something small like *Grallator*, and up to 189 × 189 pixels for large tracks, such as those of a hadrosaur (Table 2). The grids were made large enough to encompass potential increases in area during erosion. The minimum margin for a track was set to 15% of its maximum linear dimension, and each track was centred in the middle of its grid.

Generation of the track-like depressions in the digital surface made use of the fact that the track outlines were all digitized, consistently with a right hand (positive) sense of curl (O'Neil 1983). Setting the elevation of a grid point required knowing the point's location relative to the track contour(s),

Table 2. Track areas, perimeters, and area changes.

	Original area (m^2)	Eroded area (m^2)	Area change (%)	Perimeter (m)	Perimeter:area ratio
Circle	0.1080	0.1182	9.503	1.157	10.69
Triangle	0.1091	0.1233	13.02	1.500	13.86
Grallator	0.003782	0.006388	68.89	0.4058	106.3
Eubrontes	0.06531	0.08659	32.58	1.701	25.95
Moyenosauripus	0.006486	0.007690	18.56	0.5246	80.61
Iguanodontid (England)	0.1634	0.2118	29.63	2.419	14.80
Iguanodontid (Mexico)	0.05159	0.07002	35.73	1.083	20.90
Hadrosaurid	0.1476	0.1808	22.51	1.747	13.78
Brontopodus (manus)	0.2313	0.2820	21.92	1.965	8.368
Brontopodus (pes)	0.4298	0.4959	15.38	2.640	6.125

Note: Eroded area is measure from erosion stage #24.

either inside or out. For a chosen point on the grid, vectors from it to the nearest two consecutive points on the nearest contour were determined and the cross product of these the two vectors was computed (O'Neil 1983). For contours with a right-hand sense of curl, this cross product will be positive if the chosen point lies inside the nearest contour and negative if it lies outside the contour (Fig. 1). By systematically checking every grid point, the regions of the grid that lie inside the contour(s) can be determined. With the internal track points identified, the next stage is to form the impression.

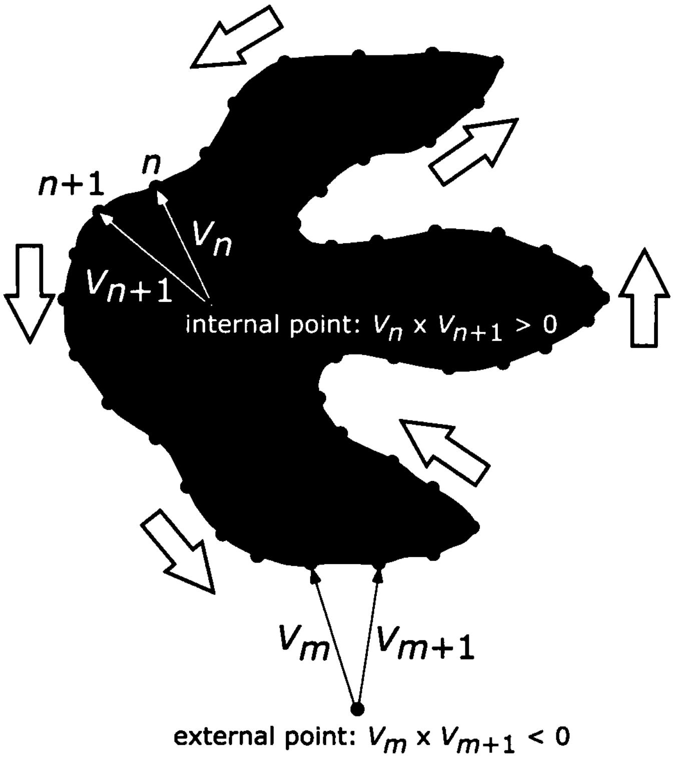
The cross-sectional profiles of deeply impressed dinosaur tracks show steep sides adjacent to the perimeter of the track and then an abrupt flattening towards the centre of the track (Thulborn 1990, pl.10; Milan et al. 2004). The intermediate region between the subvertical sides and the almost flat base will be curved. To create this form a mathematical function was derived that made use of the discrete geometry of the grid. The depth associated with an interior grid point was computed as a non-linear function of its distance from the nearest contour edge point with the following expression:

$$[1] \quad \text{depth} = D_{\max}\left(1 - \frac{\delta}{\text{dist}(P,\ \text{Edge}) + \delta}\right)$$

where $D_{\max}$ is the maximum depth possible for the track, and for all tracks, this was set equal to 10% of the maximum track dimension; dist(P, Edge) is a function that returns the Euclidean distance between a grid point P and the nearest contour edge point; and δ is a small number (typically 10^{-4}) to avoid the problem of division by zero when the a grid point might lie on the edge of a contour. The depth of impression of a real track will depend on a variety of factors, such as the weight of the trackmaker, how fast it was moving, the resistance of the substrate to compaction, etc., so a value of 10% as the depth factor was arbitrarily chosen because it produced realistic looking tracks. This use of a common "relative" depth of impression for all the modeled tracks (expressed as a percentage of footlength) also provides a common baseline for comparing the progress of erosion in different types of tracks when subject to the same erosional processes.

Commonly associated with tracks are raised rims of sediment that were displaced upward and laterally during the

Fig. 1. Schematic view of a closed contour defining a dinosaur track that has been digitized with a right-hand sense of curl (large arrows). When superimposed on a grid, a grid point internal to the contour will be associated with vector cross product that is positive, whereas an external point will be negative. This numerical property was used to rapidly locate internal and external points for the automatic generation of synthetic foot impressions for any given track outline (See "Methods, Three-dimensional track generation").



generation of the track (Allen 1989; Thulborn 1990, p. 20; Manning 2004), and these were also incorporated into the synthetic tracks. An equation was required that would have a rounded shape and a maximum positive value close to the edge of the track and then exponentially decrease to zero with increasing external distance. This equation was obtained by experimenting with summations of various non-linear terms until the cross-sectional profile of the raised rim resembled those produced by the physical modeling of Allen (1997, fig. 1*c*). One possible rim height (h) function is:

$$[2] \qquad h(r) = A\cdot[-(kr)^3 + 4(kr)^2 + 2kr]\cdot e^{-2kx}$$

where r is the radial distance of a point from the edge of a track perimeter, A is the maximum amplitude of the rim (dependent on the size of the track), and k is a parameter also dependent on the track size (e.g., $k = 40$ for a track 30 cm long). The two parameters, A and k, were arrived at by numerically experimenting with different values until a plausible rim shape was produced.

Erosion of tracks

The simulated tracks are assumed to be in a morphological optimal and pristine lithified state when erosion begins. The simulation of track erosion was implemented as a three-step process, with the first step being the removal of a small amount of material from every point of the surface (Erosion Step 1). The amount removed at a given grid point was proportional to the elevation at that point relative to the lowest point on the surface, and was expressed mathematically as

$$[3] \qquad \Delta y_{(i,j)} = k_E \cdot (y_{(i,j)} - y_{min})$$

where $y_{(i,j)}$ is elevation of the grid at row i and column j, y_{min} is lowest point of the track surface, and k_E is a proportionality constant that was set to 0.05 for all simulations of erosion for all tracks, with the exception of the deep sauropod tracks where the value was doubled to 0.1 to make the effects visible. The justification for this expression comes from two observations: (1) the rounding from weathering of formerly sharp edges on stone used in the construction of old buildings and (2) from the large-scale erosion of originally jagged, young mountains, such as the Rocky Mountains of today, that are reduced to low, rounded hills similar to those seen in the present highlands of Scotland. In both these cases, it appears that the higher, sharper edged points are preferentially worn away first. The dependence of the erosion rate on the relative elevation of the surface results in the tracks asymptotically approaching full erasure.

The second erosion step was to apply a smoothing operation to the entire surface and then a partial correction (Erosion Step 2). The initial smoothing involves systematically setting the elevation of each grid point to the average of its neighbours; the neighbours are considered to be all those points that lie within a square patch five pixels on a side and centred on the grid point of interest. The choice of an odd number for the smoothing patch dimension is required so that the grid point in question is centred in the middle of the patch. The value of 5 was a compromise between the longer time required for smoothing when 3 was tried (almost three times longer), and the excessive smoothing obtained when a larger 7 × 7 patch was tried. The smoothing operation lowers a grid point elevation if it is higher than the neighbourhood mean, and raises it if it is lower than this mean. Because the removal of material from the surface was the primary interest, a check was made to ensure that any increase in elevation was negated. The justification for the application of the smoothing function was to have it act as a local, small-scale version of the elevation-dependent erosion, whereas the later correction was based on the idea that wind and flowing water would actively remove material loosened from the surface. Initial simulations of erosion without using the smoothing function did not give results that satisfactorily replicated the appearance of true fossil tracks.

The third and final erosion step was to remove material from a randomly selected set of surface patches (Erosion Step 3). The amount of material removed was set to a fixed thickness of 0.0002 m for all erosion simulations but one; the large size of the sauropod tracks necessitated doubling this factor to make the effect visible. This random process was introduced to match the slightly rough, irregular nature of real trackway surfaces that have been exposed to subaerial erosion. An example of the contrast between exposed and non-exposed surfaces is seen in the trackway collection of the 19th century ichnologist, Edward Hitchcock (Steinbock 1989), where a large, track-bearing slab had been partly immersed in water and partly exposed to the air prior to collection; the air exposed track surface is much rougher than the section that was protected by water (Thulborn 1990, pl. 5). Presumably this increased roughness was associated with subsequent weakening of the rock surface because of thermal stresses associated with freeze–thaw action, and the day–night and winter–summer temperature changes. The direct impact of raindrops on a subaerially exposed surface may have also been important.

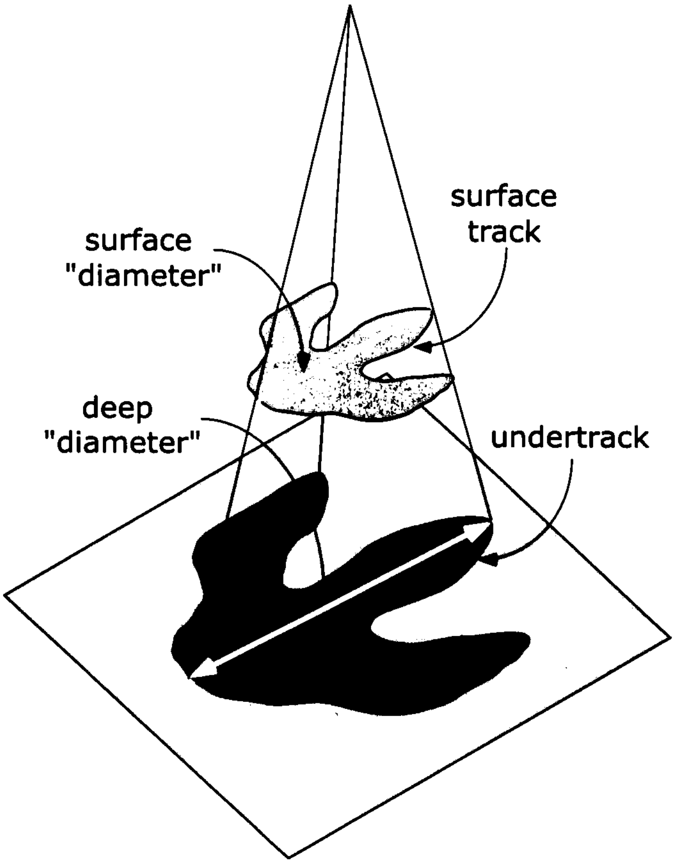
Undertrack generation

The production of undertracks (Lockley et al. 1986) has been observed in the field for both recent and fossil tracks, and in mechanical models of track formation (Allen 1989, 1997; Manning 2004). Undertracks retain the general shape of the initial surface impression, but they are altered with increasing depth. If the original surface track can be thought of as a 3-D waveform, then undertracks represent copies of this waveform whose amplitudes decrease as a function of depth (Thulborn 1990, p. 27). The steady decrease of undertrack amplitudes with depth follows an exponential curve as the deeper sedimentary layers increasingly resist compression (Nadon 2001). Simultaneously, the undertracks become broader — a result of the radially outward pattern of disturbance of the sediment as the foot is impressed into the ground (Allen 1997).

The generation of undertracks was a two-stage process. The first stage was to mimic the lateral spread of a track impression with depth by a horizontal stretching in both the X and Y directions of the initial track surface. The magnitude of the stretching was a function of depth and was based on viewing the perimeter of the track as the broad end of an inverted, non-circular cone (Fig. 2). By projecting the cone perimeter downwards while maintaining the same ratio of cone height to cone "diameter," an increase in the size of the track was produced. The ratio of the cone "diameter" to its height as measured at the surface, multiplied by the depth of an undertrack determines the stretching factor for the given depth.

The second stage was to replicate the decreasing amplitudes of undertracks. This was done with a flattening term that set the amplitude of an undertrack as a constant fraction of the amplitude of the track immediately above it. This flat-

Fig. 2. Schematic view of how an undertrack can be viewed as a downwards conical projection of a surface track. This projection scheme was used to generate a vertical sequence of undertracks for comparison with eroded tracks. The increase in area spanned by real undertracks is not as great as in this hypothetical example (see Fig. 14) (See "Methods, Undertrack generation").



tening term, f, was set to 0.85 because this gave the best match to mechanical simulations of undertracks (Allen 1997), where the amplitude had decreased to almost zero at depths equal to half the longest dimension of the initial surface print. The exponential nature of this process can be seen in the expression for the amplitude of the undertrack at the n^{th} layer, A_n:

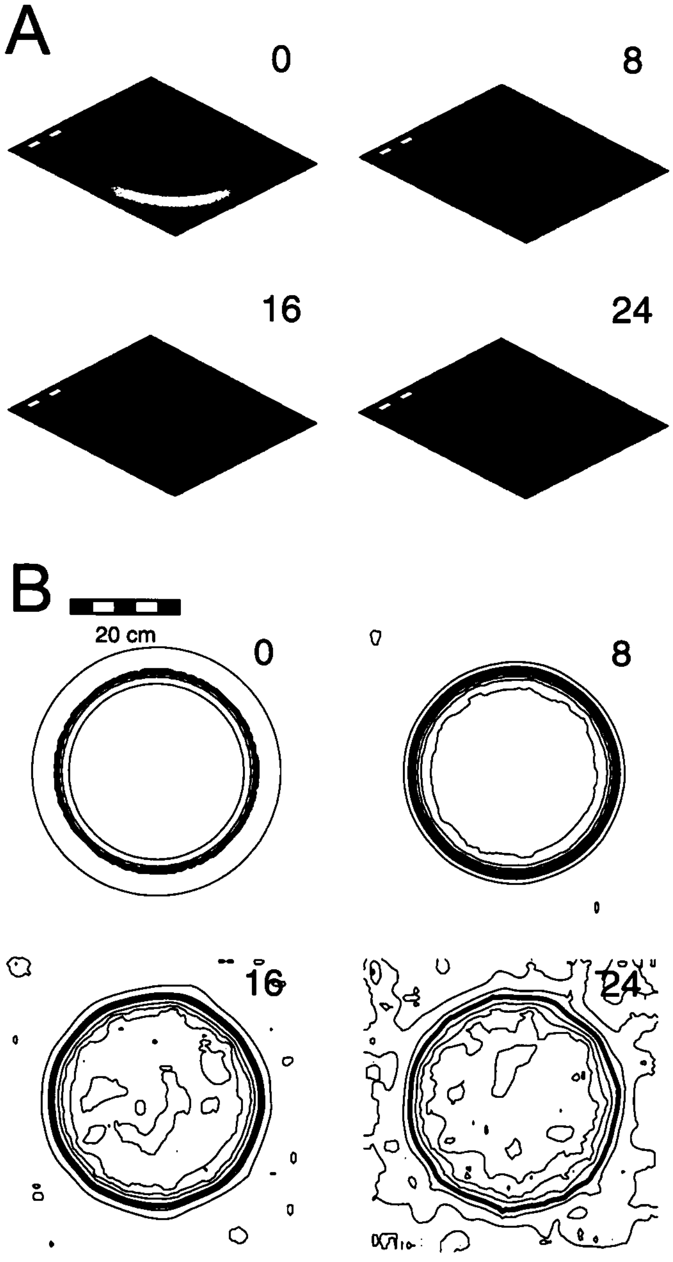
$$[4] \quad A_n = f^n \cdot A_o$$

where A_o is the amplitude of the surface print.

Simulation of erosion

All the erosion sequences were run for 32 cycles each, and the resulting surfaces are presented as both oblique, shaded-relief views, and as contour plots. The surfaces are shown at four different stages which are numbered in the top right hand corner of each type of plot (Fig. 3): 0, the fresh, uneroded surface; 8, the end of the first quarter of the erosion sequence; 16, halfway through; and 24, the end of the third quarter. In the interests of standardizing the erosion process for all the tracks studied, the erosion parameters were set so that all impressions had essentially vanished at the end of the 32 cycles of erosion. The illumination of the

Fig. 3. Simulation of the erosion of a hypothetical track in the form of a circle. The basic circle shape is visible at all stages and only changes size by a small amount (see Table 2). This shape can be considered as an idealized form of the sorts of tracks that could be made by a large sauropod dinosaur with their very rounded manus and pes impressions. (A) Surface plots in oblique view with the light shining from the lower right at an angle 5° below the horizontal. (B) Contour plots of the surfaces in (A). Heavy lines mark the mean elevation for each track surface and are used as the standard for defining all track perimeters. Contour intervals are dynamically rescaled for each plot to span the range from the lowest elevation to the highest. Scale bars on the surface plots are identical to those on the contour plots.



shaded track surfaces was constant for all tracks at all stages and set as coming from the lower right at an angle of 5° below the horizontal. This low angle of illumination highlighted even the shallowest of eroded impressions.

Characterizing shape change

In an attempt to develop an objective measure of the shape and extent of a track, the defining margin of a track at any stage of erosion was defined to be the contour line that marked the mean elevation of the entire track-bearing surface; this level is represented by the heavy line on the contour plots. The mean elevation line is essentially identical with the initial form of all the tracks and is internal to the raised rim bordering tracks. The remaining contour lines on the contour plots were set at eight evenly spaced intervals between the maximum and minimum elevations of a surface in its current state of erosion, so individual contour lines cannot be compared between plots. However, the rescaling of the contour intervals for each plot enables visualization of the full extent of the elevation differences on track surface at all stages, even though total relief becomes less and less with erosion.

Determination of the mean elevation for the track-bearing surface also facilitated identification of grid points that were within the track-defining contour, as their elevations are less than the mean elevation. Computing the area of a track at any stage of the erosion process involved multiplying the number of points internal to the track by the square of the grid resolution. The changes in the areas of tracks with erosion are used as measures of the change in form of tracks.

Results

Erosion of the circle and triangle test cases

Both the circle (Fig. 3) and triangle (Fig. 4) increase in area with advancing erosion, with the increase greater in the triangle. This greater amount of erosion in the triangle is interpreted to result from two factors: (1) the high ratio of perimeter length to enclosed area relative to that of the circle (Table 2), and (2) the presence of the three sharp corners. The erosion model (Erosion Step 2) affects edges, and the relatively higher amount of edge (Table 2, perimeter:area ratio) for the triangle results in more erosion. The corners of the triangle are also sites of increased erosion, as evidenced by blunting of the vertices and departure from the pristine triangular shape. The circle shape, other than developing some random deviations in its perimeter, does not change shape. The deep parts of the circular track are less affected by the general erosion (Erosion Step 1) because it favours high elevation points, so deep portions retain random effects (Erosion Step 3) for longer periods. Apart from their reduction and eventual elimination, the perimeter rims of both the circle and the triangle merely develop a few random deviations while retaining their basic shapes. The uniform increase in area of the circle, and the blunting of the tips of the triangle, are relevant to the interpretation of erosion of both simulated and real tracks.

Erosion of tracks

Figs. 5–11 present the results of eroding the different tracks until they have almost disappeared. All the tracks were assumed to have been emplaced in a massively bedded sediment of uniform composition that lacked any laminae. The erosional processes acting on the track surface never encounter any changes in "sediment" type, and nothing equivalent to an alternation of dominant and recessive weathering or exfoliation will develop. This is similar to the majority of published photographs of tracks which show continuous, unlaminated track surfaces of a uniform composition. This

Fig. 4. Simulation of the erosion of a hypothetical track in the form of a triangle. The triangle shape experiences blunting of its vertices and a greater increase in area relative to the circle owing to its increased perimeter length relative to that of the circle. Both the circle and the triangle are of approximately equal area. This mode of erosion has implications for tracks with sharp corners such as claws.

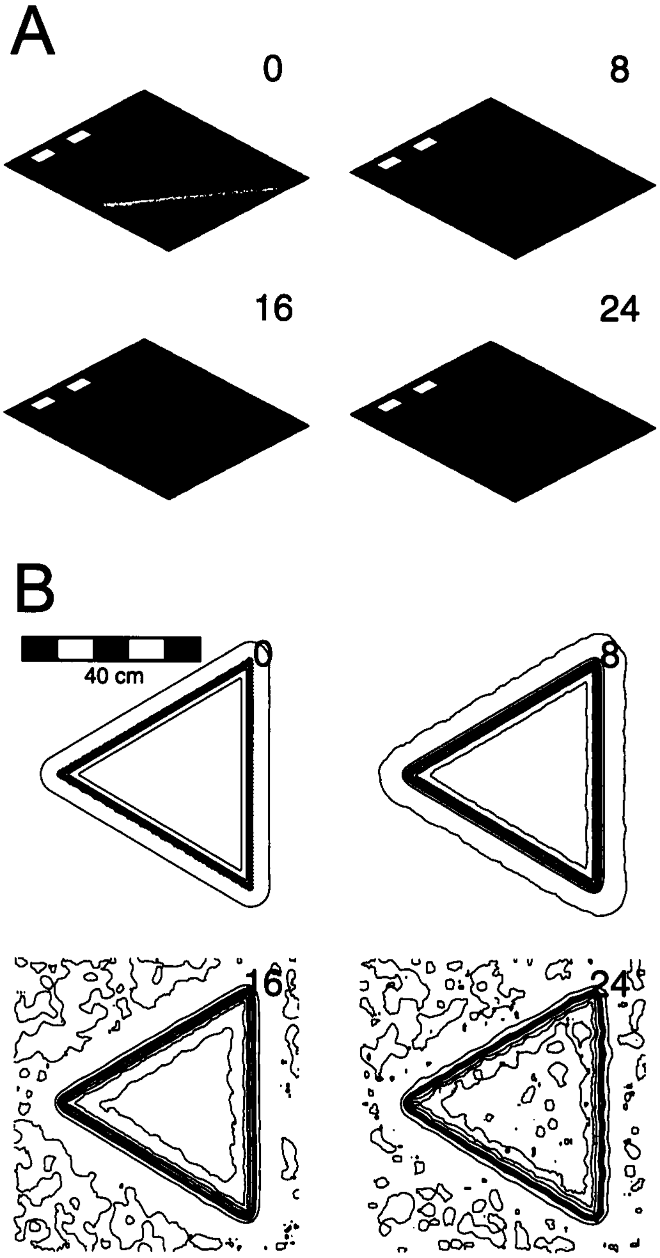
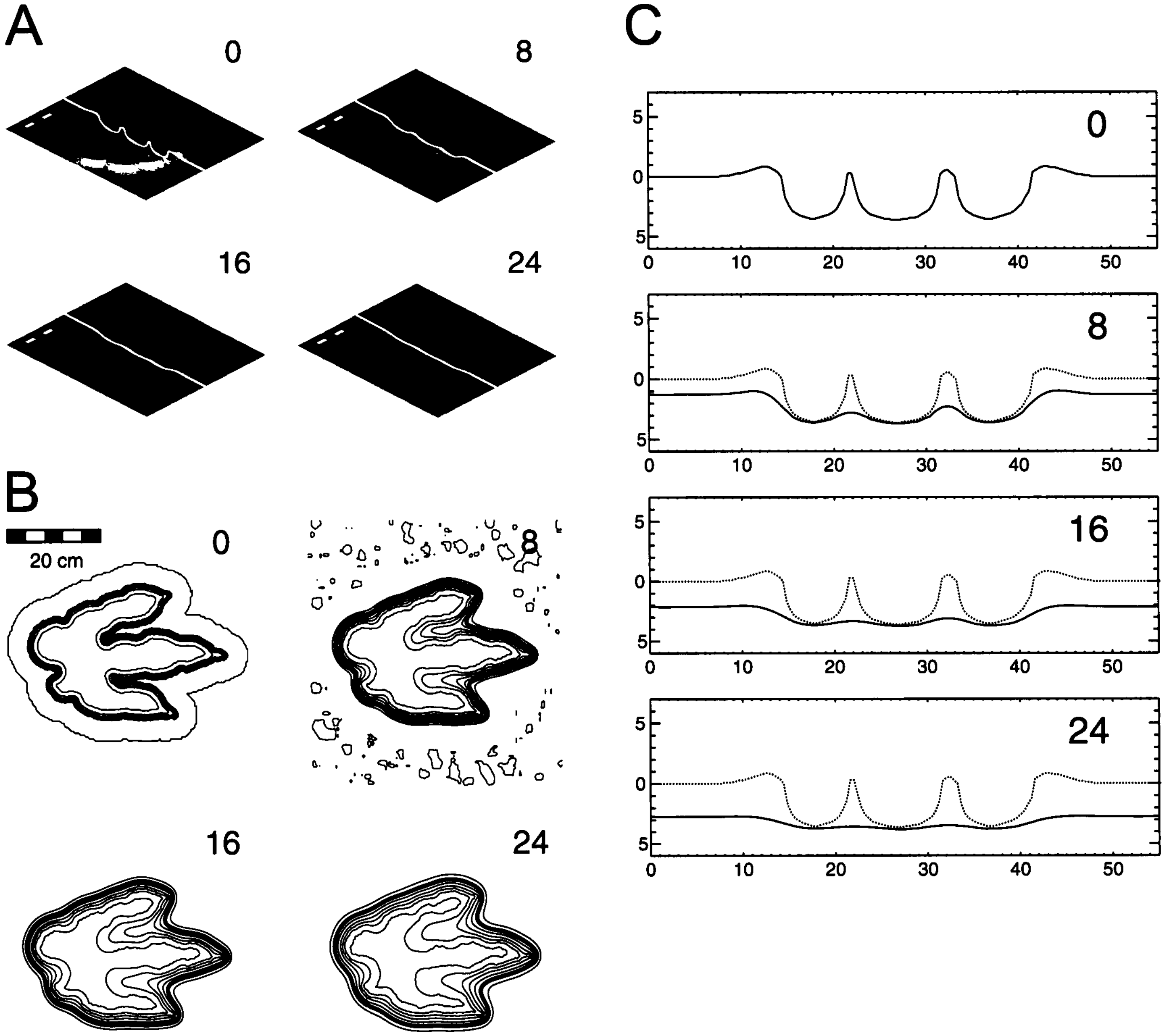


Fig. 5. *Eubrontes* erosion showing the rapid blunting of the claw tips, the rapid removal of interdigital regions, and smoothing of the heel perimeter. The thin white lines traversing the track surfaces in (A) indicate the positions of the transverse profiles. (C) A sequence of transverse profiles (continuous line) demonstrates how the track surface is worn down and how narrow ridges between digit impressions are eroded away early in the erosion sequence. Dotted line is the original track surface. See Fig. 3 for details of figure layout and Table 1 for track image source.



observation has implications for interpretation of eroded tracks as possible undertracks (see "Discussion").

All tracks change form to varying degrees, as measured by their increase in area (Table 2). With one exception, *Moyenosauripus*, the increase in area is positively correlated with the ratio of track perimeter length to enclosed track area, as was seen with the triangle and circle test cases. The amounts of area change for the true tracks are roughly twice that as for the triangle and circle shapes; this is interpreted to be related to the more complex perimeters of the true tracks. A feature of the latter, except for the sauropod tracks, is the presence of narrow ridges between the digits; these ridges quickly become worn down (Fig. 5C), their associated perimeters vanish, and the horizontal space occupied by the former ridges, and external to the fresh track, becomes incorporated into the internal area track. The lone exception of *Moyenosauripus* has very divergent digits and they never coalesce the way the digits of the other tracks do. This results in a relatively small increase in area of this track with erosion, despite its high perimeter:area ratio. The English iguanodontid track (Fig. 8), with its relatively divergent toes, shows a smaller increase in area than that of the Mexi-

Fig. 6. *Grallator* erosion showing the same claw blunting, heel rounding, and interdigital ridge erase as with *Eubrontes* (Fig 5). The small size of this track makes its outline very susceptible to disruption by random erosional effects.

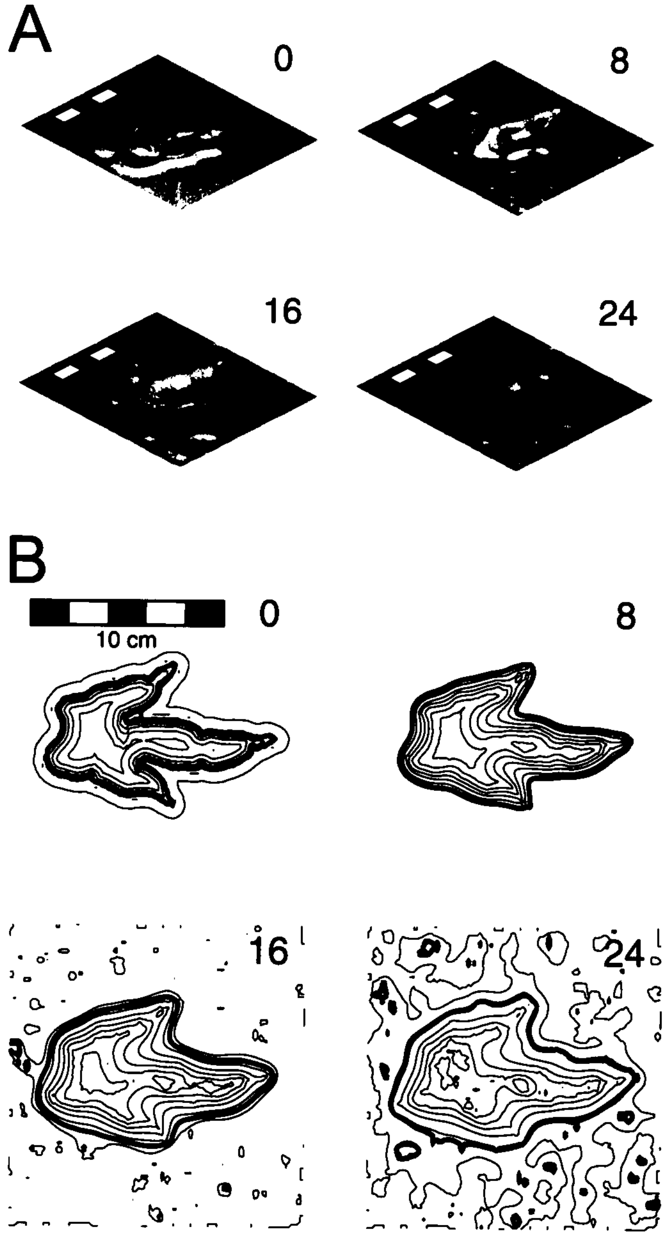
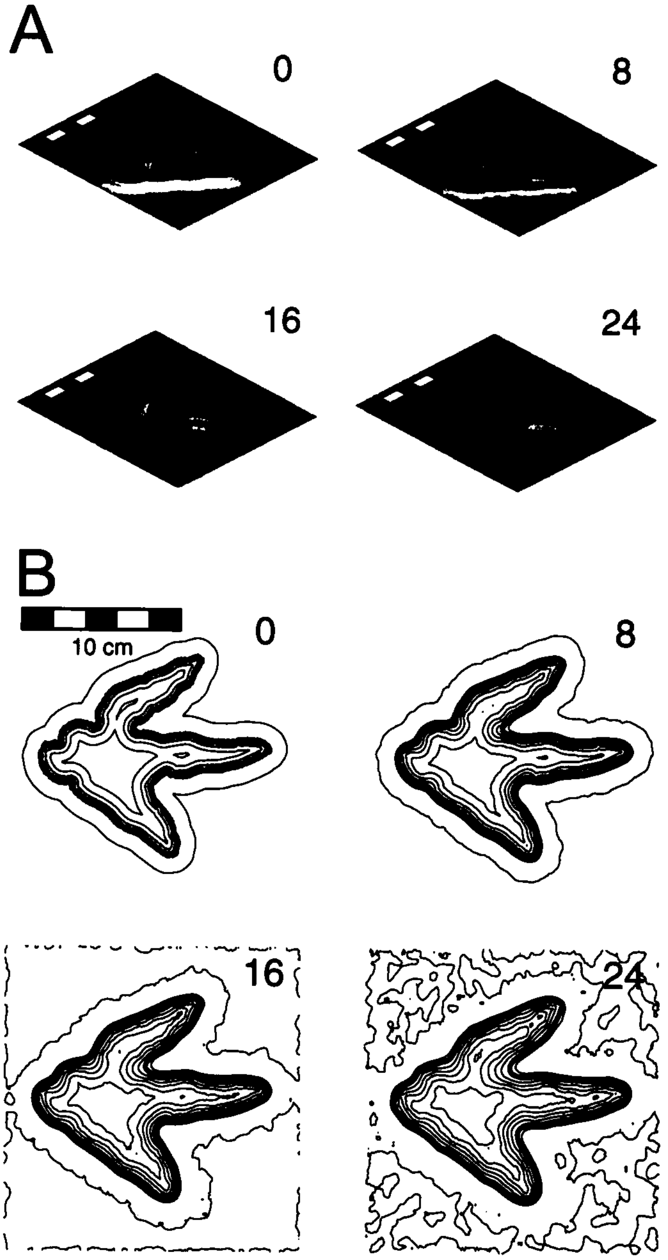


Fig. 7. *Moyenosauripus* erosion that does not show the same degree of claw blunting or heel rounding, nor the removal of the interdigital regions as seen with *Eubrontes* (Fig. 5) and *Grallator* (Fig. 6) The erosion processes result in a form of "straightening" of the upper digit.



can iguanodontid track (Fig. 9), and this is also interpreted to be caused by the persistence of the interdigital ridges on the eroded English form.

A second observation is that with the use of a fixed random patch size and thickness for Erosion Steps 2 and 3 (see "Methods"), the smaller tracks experience a greater disruption of their perimeters because the patch sizes and the depths of random erosion represent a larger fraction of the initial track size, e.g., *Grallator* (Fig. 6) and *Moyenosauripus* (Fig. 7). The same pattern is repeated when the manus and pes impressions of the *Brontopodus* tracks area are compared (Fig. 11). The outline of smaller manus print shows obvious deviations from its original shape, whereas the larger pes print shows only a blunting of the claw impressions (similar to what the triangle shape experienced).

Related to the susceptibility of small tracks to having their outlines perturbed is their more rapid erasure because of the relative shallowness of their impressions. The depth of impression was set to 10% of the longest dimension of the track. With fixed amounts of material being removed from each track at Erosion Step 3, the smaller, shallower tracks will disappear sooner. This is seen with the apparently complete erasure of the *Brontopodus* manus by stage 16 when viewed with the shaded relief surface (Fig. 11A), whereas

Fig. 8. English iguanodontid track erosion showing thickening and straightening of the digits with increasing erosion.

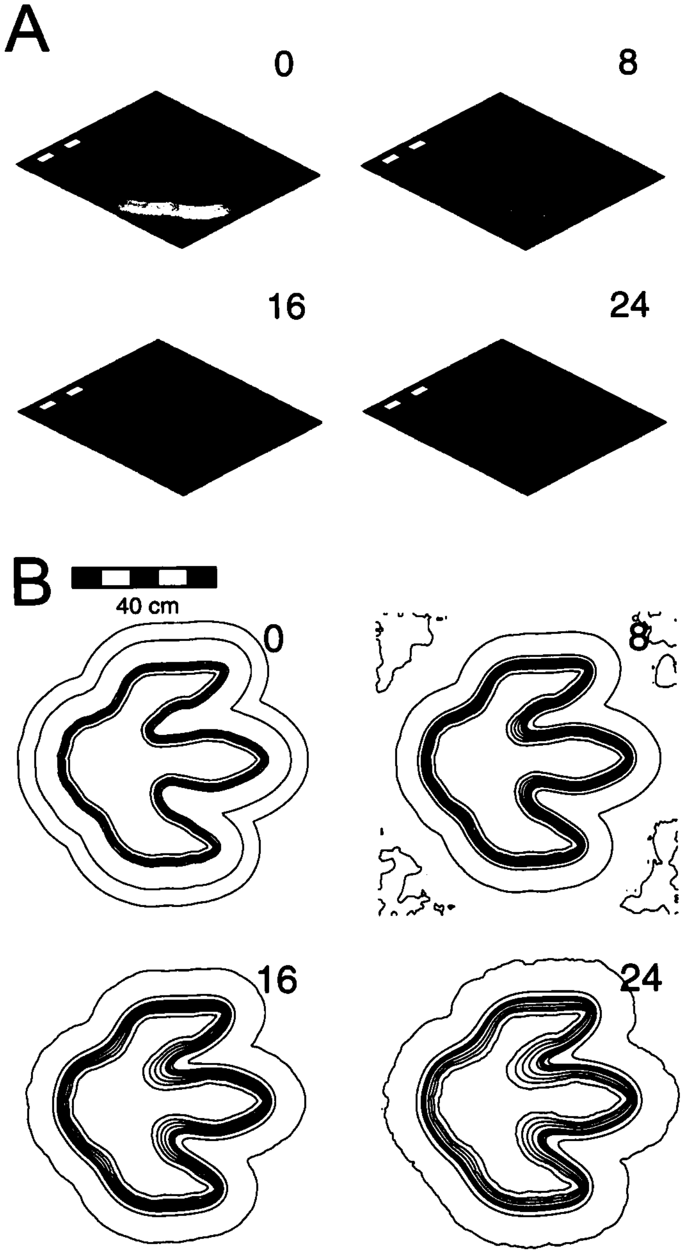
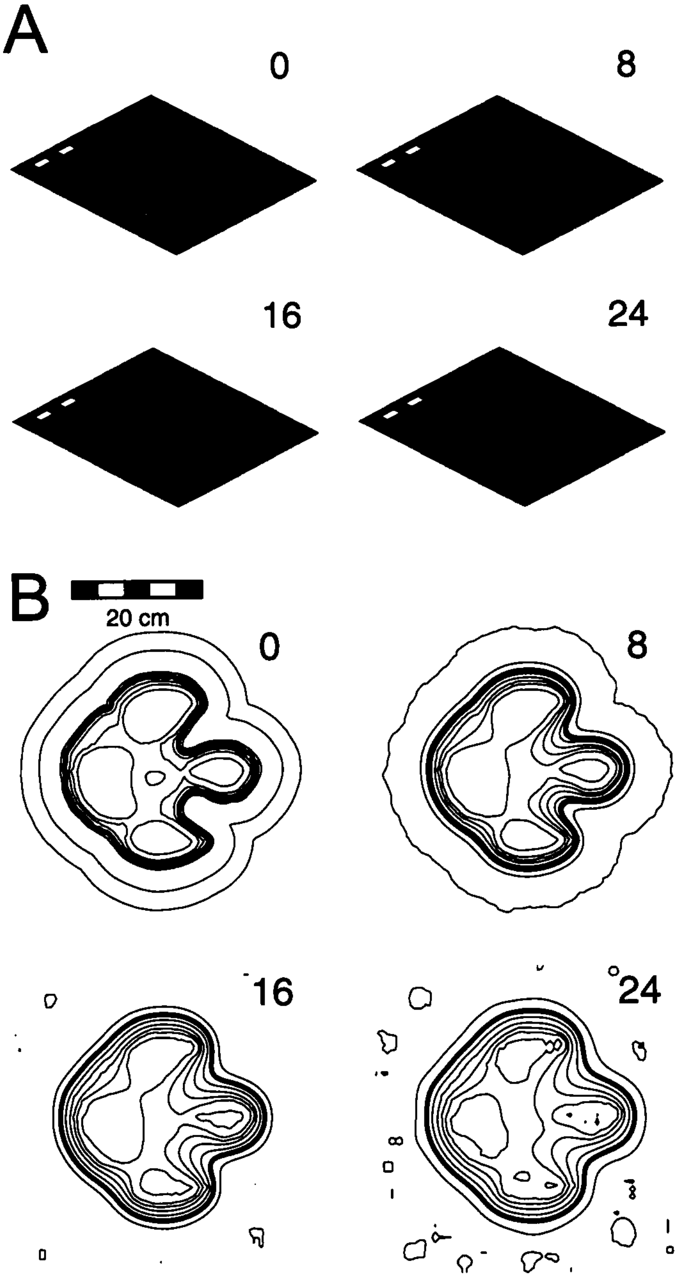


Fig. 9. Mexican iguanodontid track erosion showing removal of the interdigital regions and the flattening of the interior ridges demarking the positions of the sub-digital pads.



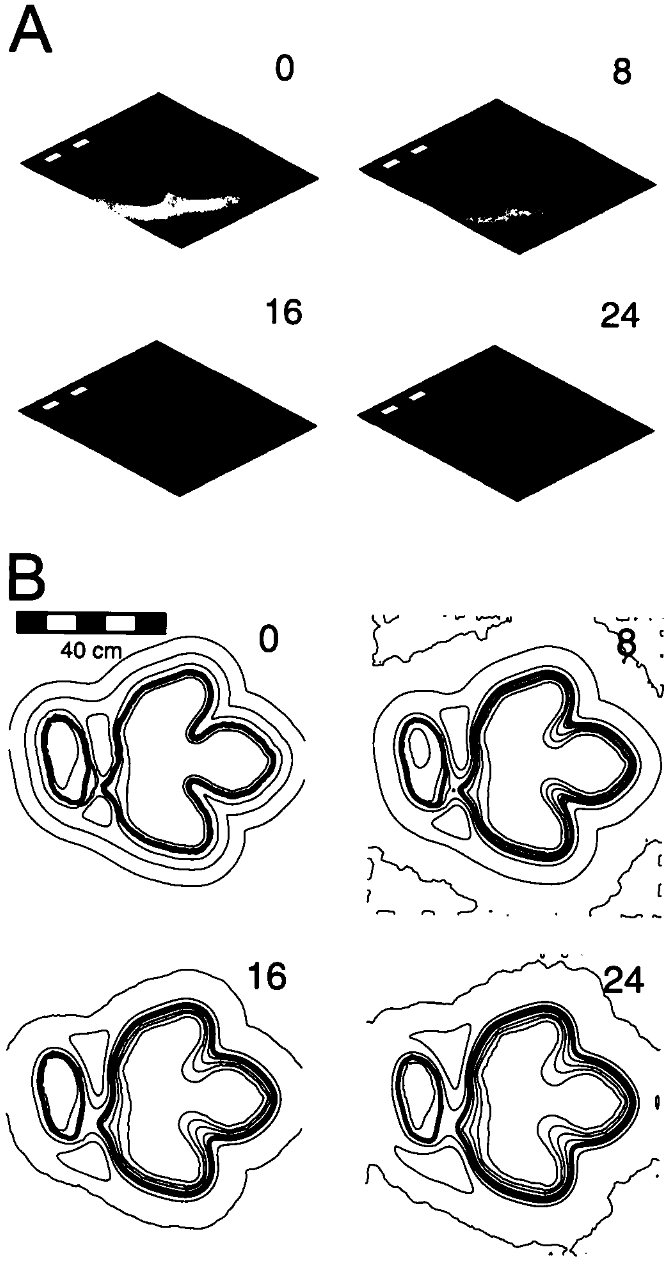
the associated pes impression is still visible (Fig. 11C). Although the *Brontopodus* manus is not visible on the surface plot, the rescaling of the contour plot intervals still manages to discern a manus impression (Fig. 11B). It should be noted that actual *Brontopodus* manus impressions are often better preserved than this model possibly because the original manual prints were more deeply impressed (Lockley 1991). In the present model of *Brontopodus*, both impressions, manual and pedal, were set to the same depth.

A final feature common to all the tracks is that their basic shapes were retained throughout erosion. This is interpreted to be a result of the erosion processes affecting all parts of the track surface equally (Erosion Step 1) or with equal probability (Erosion Steps 2 and 3). The only variation in erosion is in the vertical direction, but this will not affect the horizontal outline of a track. This retention of track form is indicated by two measures: (1) the interdigital angles remain essentially unchanged with erosion (Fig. 12) and (2) the ratios of footlength to footwidth remain virtually constant or changed only by a few percent (Table 3).

Undertracks

Fig. 13 shows two cut-away views of the *Eubrontes* track that present the profiles of the simulated undertracks from a longitudinal slice and a transverse slice. With the alternating colour scheme for different layers used by Allen (1989), the decreasing amplitudes with depth of the impressions and

Fig. 10. Hadrosaurid track erosion showing the removal of the interdigital regions. If it were not for its large size and presence of the heel pad, the highly eroded form of this track could easily be confused with that of the Mexican *Iguanodon* (Fig. 9).



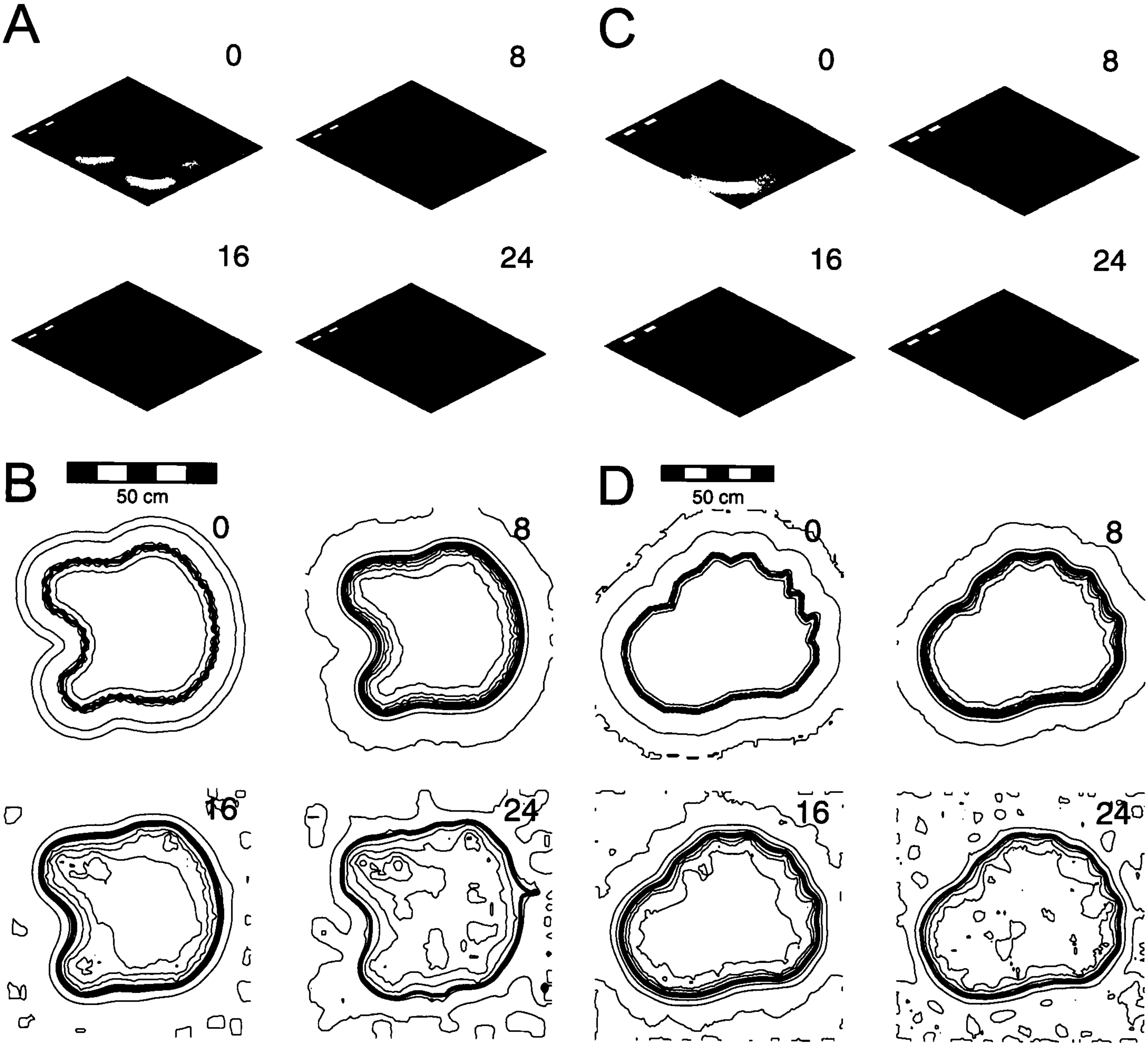
ridges associated with the original print can be clearly seen. The low amplitudes of the deep transverse profiles of this *Eubrontes* track are very similar to the undertracks visible in the polished cross sections of *Grallator* tracks presented by Milan et al. (2004, fig. 6). A noticeable feature of these undertracks is the uniform decrease in amplitude of all parts of the undertrack, and is in contrast to persistence of *relatively* higher marginal rims seen in the eroded surface tracks (Fig. 5C). Fig. 14 shows what the undertracks would look like at four different levels if the overlying laminae could be peeled away. The eroded *Eubrontes* tracks at each of the four stages (Fig. 5) are visibly different from the four undertracks. The latter are much flatter and only in the shallowest of the levels (i.e., <12) are there slight indications of a perimeter rim. There are no differences between the heights of the marginal and interdigital ridges of the undertracks, which is quite unlike the rapid suppression of the interdigital regions and internal ridges seen in the eroded surface tracks. Even the most eroded *Eubrontes* track is visibly different from a deep undertrack with the current models.

Discussion

The initial hypothesis that all aspects of tracks would be severely affected by erosion was not born out. Some key aspects of tracks were severely altered (see later in the text), but others remained relatively intact with only minor implications for the interpretation of trackway evidence. The interdigital angles and length:width ratios of tridactyl tracks were virtually immune to the effects of simulated erosion. For eroded tracks with sufficiently distinct digits, the potential to classify the tracks as either theropod or ornithopod using angles and (or) ratios still remains. Changes in the area of an object are generally thought of as arising from changes in its linear dimensions, but the eroded tracks only increased their linear dimensions by a few percent when measured as the maximum widths and lengths of the mean elevation contours (Table 3). Any large changes in computed track area with erosion are because of the "pushing out" of indentations in the margin of the tracks (i.e., removal of interdigital regions). As the length of a track only increases slightly with erosion, this implies that estimates of dinosaur hip heights and speeds of locomotion based on foot lengths (Alexander 1976) from eroded tracks will be only slightly less accurate than the same measurements from pristine versions of the tracks. With a careful and consistent choice for the defining margins for a set of tracks *from a single, uniformly weathered horizon*, relative sizes and speeds of the trackmakers will not be grossly in error.

Small and (or) shallowly impressed tracks were the most susceptible to the effects of erosion. The smallest track, *Grallator*, shows the greatest disruption in shape owing to random, patch-erosion effects (Erosion Step 3), but even in an advanced stage of erosion, it would be difficult to confuse it with any other track. A possible confusion might arise between it and a small, very eroded *Eubrontes* if the latter had the medial and lateral toes heavily abraded. However, the generally larger size of the *Eubrontes* track would probably prevent it from being mistaken for a *Grallator* track. Ignoring for the moment variations in substrate type, small dinosaurs would be expected to leave shallower impressions on account of their lower body mass. Typically, the forelimbs of habitually quadrupedal and faculatively quadrupedal dinosaurs (sauropods and large ornithopods, respectively) carried a lower fraction of the total body weight (Alexander 1985; Henderson 2004). The mani of these animals would have left shallower impressions as evidenced by lightly impressed, sporadic traces seen in an iguanodontid trackway (Wright 1996) and in the trackway of a possible Triassic theropod (Courel and Demathieu 2000). Erosion would be expected to rapidly remove evidence of shallow impressions formed by small dinosaurs and the lightly loaded forelimbs of quadrupeds. A population survey of dinosaurs in a region based on

Fig. 11. *Brontopodus* manus tracks as (A) surface and (B) contour plots. *Brontopodus* pes tracks as (C) surface and (D) contour plots. A higher rate of erosion was used on these sauropod tracks than was used on other tracks to more completely erode the deep pes impressions. The shallower manus impressions received the same erosion rates and are removed early on. The smaller manus outlines experience greater disruption of their outlines than do the very large pes impressions. The only noticeable erosion feature on the pes tracks is the removal of the claw impressions.



eroded trackways would miss, or under-represent, the occurrences of small dinosaurs as well as the quadrupedal nature of the posture and gait of larger ornithopods.

All those tracks that have sharp "corners" in the form of distinct claw impressions follow the trend seen in the triangle test case of having these "corners" rapidly blunted early in erosion. This is significant in that the presence or not of claw impressions on a track is often used to distinguish theropod from ornithopod (Thulborn 1990, pp. 220–221). This is especially noticeable in the tracks attributed to theropods, *Eubrontes* (Fig. 5) and *Grallator* (Fig. 6), as well as the claw impression of the *Brontopodus* pes (Fig. 11). The enhanced corner erosion progressively degrades small, possibly diagnostic, details of these tracks, reducing them, in the case of the late-stage *Eubrontes*, to little more than "tridactyl dinosaur tracks" in the most general and undiagnostic sense. A similar effect is seen with the "indentations" that define the gaps (interdigital ridges or regions) between the toes. These features become blunted, and in advanced cases almost vanish, when the mean elevation is used as the definition of the track perimeter. This latter effect is seen in both theropod tracks, *Eubrontes* and *Grallator*, the large hadro-

Fig. 12. Relative constancy of the interdigital angles of tracks demonstrating how the erosion model does not alter basic shapes. (A) *Eubrontes*. (B) *Iguanodon* (English). Both figures show the angles from the fresh track on the left-hand side and the angles from the eroded track at stage 24 on the right-hand side.

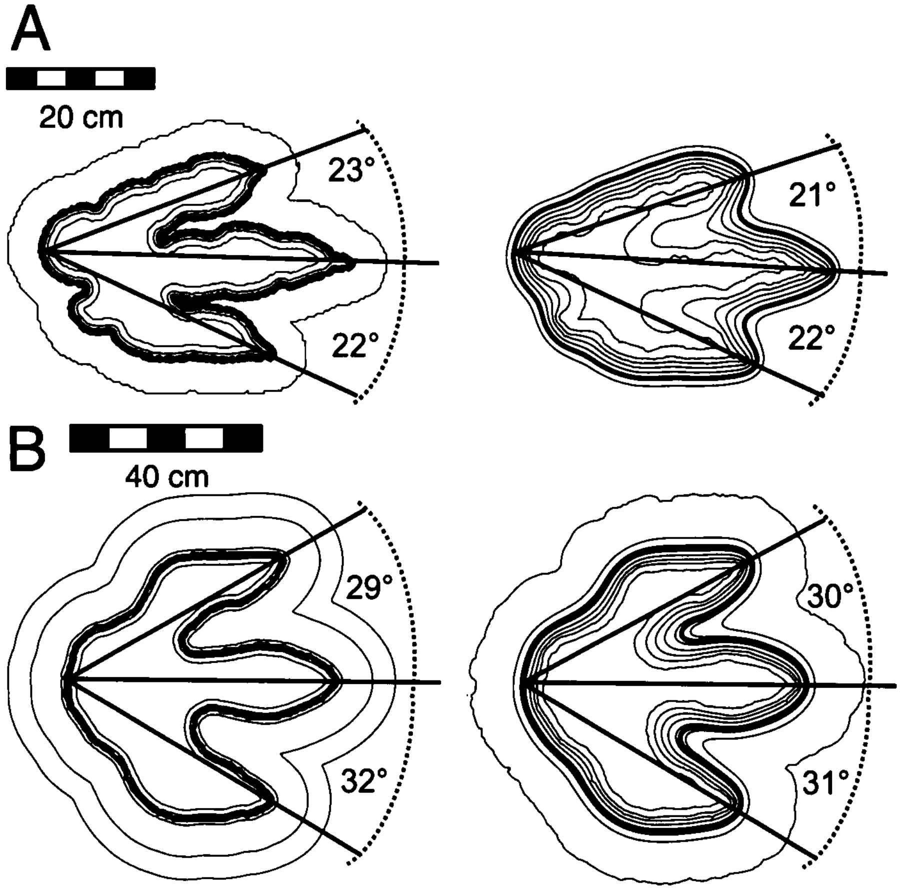


Table 3. Changes in foot length to foot width ratio with erosion.

	Uneroded track			Eroded track (stage 24)			
	Length (cm)	Width (cm)	Ratio	Length (cm)	Width (cm)	Ratio	Ratio change (%)
Grallator	12.1	7.44	1.62	12.8	8.21	1.56	-3.59
Eubrontes	32.0	21.3	1.50	32.7	23.3	1.40	-6.67
Moyenosauripus	14.4	12.6	1.14	14.7	12.6	1.16	2.04
Iguanodontid (England)	56.6	56.6	1	59.3	60.7	0.977	-2.27
Iguanodontid (Mexico)	29.6	30.0	0.988	31.9	32.6	0.977	-1.05
Hadrosaurid[a]	46.7	49.3	0.946	48.0	52.0	0.923	-2.42
Brontopodus	54.7	53.3	1.03	61.3	58.7	1.05	2.00

[a]Heel pad not included.

saurid track (Fig. 10), and both iguanodontid tracks (Figs. 8, 9). This tendency for angular features of tracks to become rounded may confound attempts to distinguish theropod tracks from ornithopod ones because theropod tracks typically have narrower, more angular heels (Thulborn 1990, p. 223), but this detail could be lost on an eroded track. Again, formerly distinctive tracks become reduced to generic "tri-dactyl dinosaur tracks." On a rougher surface with a less uniform degree of erosion, the potential to confuse a highly eroded theropod track with an eroded track of a large ornithopod certainly exists.

The ability of the erosion processes to rapidly remove internal ridges (Fig. 5C), even within a track such as that of the Mexican iguanodontid (Fig. 9), suggests that using the presence or not of sub-digital pad impressions (and associated ridges) as diagnostic features may not be 100% reliable when applied to eroded tracks.

Along with the elimination of corners and indentations, on tracks where the digits are highly divergent (e.g., *Moyenosauripus*, *Grallator*, and the English iguanodontid) there is a tendency for the digits to become relatively wider because the increase in the width of digital impressions is greater

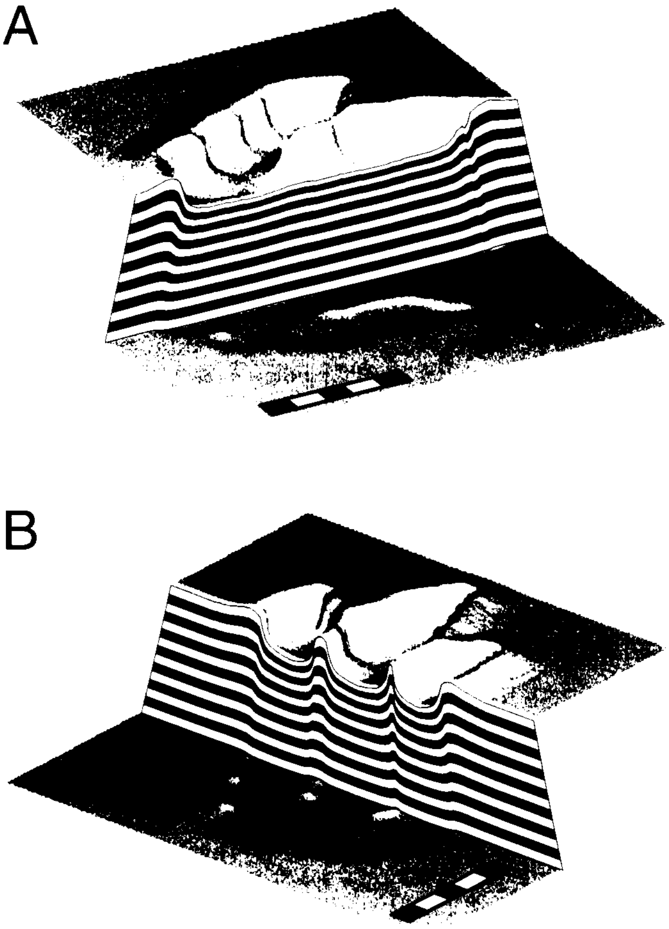


Fig. 13. Visualization of undertracks of *Eubrontes* in (A) longitudinal section, and (B) in transverse section. The areas of the undertracks increase linearly according to the expanding cone model of Fig. 2, whereas amplitude of the undertracks decay according to a power rule. (See "Methods, Undertrack generation").

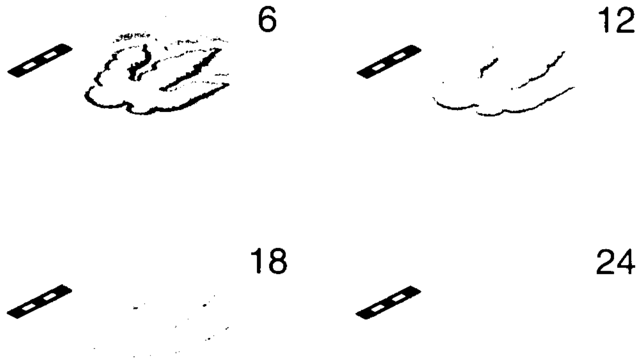


Fig. 14. Presentations of *Eubrontes* undertracks at four different levels after removing overlying layers. The undertracks are distinctly different from the eroded tracks that started with the same initial surface form.

than the increase in length of the digits where they are undergoing "corner" erosional effects. This is especially noticeable on the English iguanodontid track. Corner erosion in the models has the tendency to remove the corner rather than to migrate it distally relative to the centre of the track. The propensity of the erosional processes to remove curved sections and thicken digits has the effect of straightening curved digits, as can be seen on those tracks with divergent digits such as *Grallator*, *Moyenosauripus*, and the English iguanodontid track. This may have implications for the characterization of different types of dinosaur tracks as either theropod or ornithopod (Thulborn 1990, p. 221).

The modeled undertracks appear distinctly different from any of the eroded tracks, and one might assume that it would be always be easy to distinguish the two. The distinctiveness of the two track types results from their different modes of formation. The basic erosion process (Erosion Step 1) preferentially acts on high elevation points, and leaves the low and central regions undisturbed. In contrast, the flattening of the undertrack amplitudes affects the full vertical extent of an undertrack surface giving it the relatively uniform relief surface. However, the effects of erosion on undertracks would soon blur the distinction between the two types, especially if it was erosion acting on relatively shallow undertracks that retain substantial fractions of the topography of the original. In spite of this confounding effect, it may be most parsimonious to assume that lacking any evidence for a given track being preserved in a laminated sedimentary rock, any very flat tracks are unlikely to be undertracks. It is more probable that they are merely the eroded remains of surface tracks. The fissile nature of a finely laminated sediment hosting any undertracks, and the ease with which meteoric waters could penentrate the layers and accelerate erosion, suggests that the exposure lifetime for such tracks must be very short, making them exceptionally rare and thus reducing the chance of their discovery.

One important deficiency in the modeling process presented here is its assumption of a uniform loading of the foot to make the original track. This results in both the modeled surface track and the associated undertracks having the same depth at all points of the impression. Mechanical modeling studies (Manning 2004, fig. 12) of dinosaur track formation demonstrate that foot emplacement is a multiphase process with the foot contacting the substrate at different angles during the stance phase and applying different loads to different parts of the track and the enclosing sediment. The result is an uneven track surface with the distal portions of the track (the distal parts of the toes) being more deeply impressed. This is confirmed by field studies of actual dinosaur tracks (Manning 2004, figs. 19, 21). The greater the degree of differential compaction of the impression, the more the present models would be in error for a given track type. This differential compaction and warping of the sediments also produces slightly different lengths for a given footprint when the surface measured length is compared with a length from an undertrack. Highlighting the complexity of track formation, and in part justifying some of the simplifying assumptions in the model, it was found that the rheology of the sediments hosting tracks, which is a function of grain size and moisture content, exerted a strong influence of the resulting tracks produced by a single indenter (Manning 2004).

The results of this modeling study indicate that tracks emplaced in a sufficiently deep sediment of uniform composition and subject to conditions of uniform erosion will retain their basic shapes and dimensions. However, small, possibly diagnostic details, such as claw impressions and the ridges between digits or between digital pads, are removed early in erosion. The generation of synthetic undertracks resulted in tracks with little difference in elevation between internal and marginal ridges, unlike the situation for weathered surface tracks where the marginal rims persisted whereas the internal ones were removed. It should not be forgotten that the shape of a track is just part of the evidence used to deduce its identity and infer its maker. Size, pace angulation, degree of footprint rotation (positive or negative), geologic age, etc. will all contribute to the evidence supporting a particular diagnosis. Lastly, it would have been very easy to produce an erosion model that would rapidly obliterate a track and make it unrecognizable as such. The more subtle erosion scheme implemented here demonstrates how small-scale erosion can potentially affect the identity and character of fossil tracks.

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