Tetrapod tracks deeply set in unsuitable substrates: Recent musk oxen in fluid earth (East Greenland) and Pleistocene caprines in aeolian sand (Mallorca)

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A plea is made for greater attention to be paid to the ugly traces produced by tetrapods in excessively soft sediments. These rather formless structures are difficult to describe, but they have the potential for providing much information on depositional environments. Two examples are given. (1) The death-march of a musk ox (*Ovibos moscatus*) that blundered into soil liquified by solifluction in Jameson Land, East Greenland; and (2) Pleistocene trackways made by the extinct ruminant goat *Myotragus balearicus* in aeolianites on Mallorca, Balearic Islands. Ichnological evidence shows both to be examples of animals struggling through unsuitable, hazardous substrates. Parallels are drawn with escape structures made by buried invertebrate trace-makers.

Key words: Trace fossil, musk ox, *Ovibos moscatus*, *Myotragus balearicus*, aeolian sand, hazardous substrate, escape trace, East Greenland, Mallorca, Pleistocene.

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One of the most important factors controlling the morphology of tetrapod tracks is the consistency of the substrate (Laporte & Behrensmeyer 1980; Scrivner & Bottjer 1986). A gradient of consistency may be envisaged, passing from fully rigid to highly fluid substrates. The form of a track produced by any one track-making animal in these substrates will show widely different features at different points on the gradient.

At the rigid end member of the series, no track will be produced. However, next along the series, the firmground consistency zone will carry traces, the morphology of which will depend on the water content and firmness of the sediment. Indeed, firm substrates commonly preserve fine detail of the sole of the track-making limb such as hairs, scales, pads, claws. Such tracks are attractive to the ichnologist (Fig. 1) and have received much attention. Furthermore, firmground tracks have a better potential for preservation than tracks in more fluid or loose sediments. With increasing fluidity and softness (reduced shear strength) of the substrate, the impression of the limb causes greater sediment flow and disruption. These disruptions may be considered as micro- and nannotectonics, at a centimetre and a millimetre scale respectively. As a result, the track bears less informa-

Fig. 1. Trackway of a musk ox on firm, damp mud. The tracks are about 10 cm wide. Jameson Land, East Greenland.

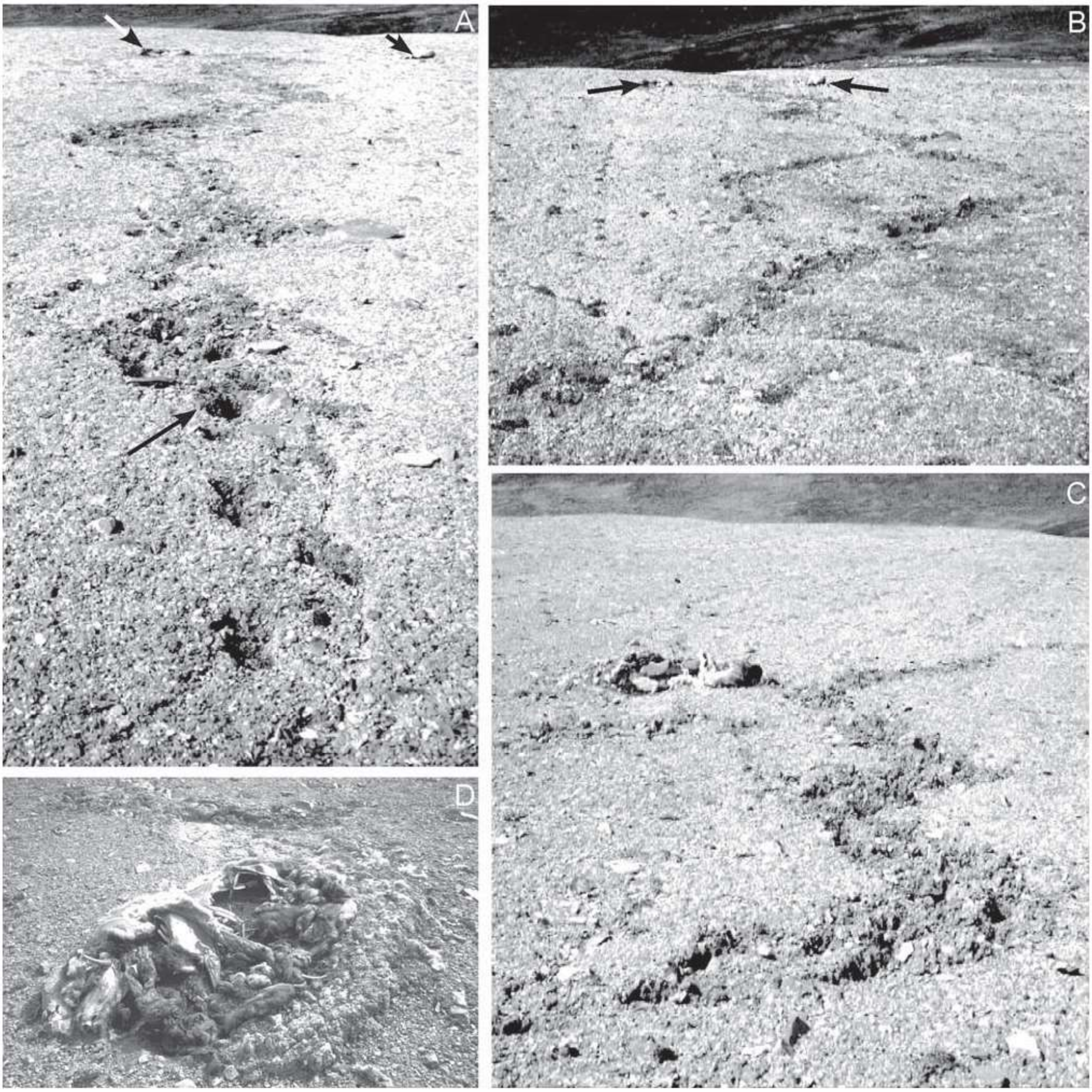


Fig. 2. Flounder trace of a musk ox in fluid mud, Jameson Land, cf. Figure 3. A. In the foreground a few tracks of the mud-wading musk ox are seen, the last one arrowed. Beyond this point the trackway suddenly changes to a broad, zig-zag trail. The corpse of the trace-maker is arrowed at upper left, a rucksack at upper right. B. A more general view of the trackways. The corpse and rucksack are arrowed as in A. The second trackway can be seen leading toward the left-hand arrow. C. View of the corpse and the lower part of the broad trail. D. The dead musk ox. The trail ends at the top of the picture and the corpse has slumped post-mortally down-slope a few metres.

tion on the shape of the limb and thus taxonomy of the track-maker than does its firmground equivalent.

At the fluid end of the consistency gradient, microtectonic disruption dominates the morphology of the track, which may carry little evidence of the nature of the track-maker, yet will provide much environmental information, such as the shear strength and pore-water content of the sediment at the moment of tracking.

Extremely fluid sediments (e.g., quick-sands) normally will be avoided by passing animals as "unsuitable substrates". Heavy animals would sink deeply into the sediment and this would lead to poor control of progress, a large expenditure of energy, and even trauma and limb breakage. Commonly, however, firmness increases rapidly beneath the surface of the sediment, i.e., a soupground may overlie a hidden firmground.

A group of domestic emus were observed to wade through a 30 cm layer of fluid mud in a farmyard without change of speed or gait, because firm mud underlay the fluid zone (unpublished observations, J. Milan Nielsen and the author, 2001). Such tracks in very soft mud by animals that nevertheless have been supported by a firmer underlayer, were called "squelch" tracks by Tucker & Burchette (1977). A nice study of Triassic dinosaur tracks in such a medium was made by Gatesy et al. (1999).

However, examples exist of animals that blunder onto deeply soft substrates that are not suitable to walk on, and the trackways they produce are of great significance for palaeoenvironmental interpretation. Two examples of such "floundering trackways" are described here.

Trackway of a musk ox in fluid earth

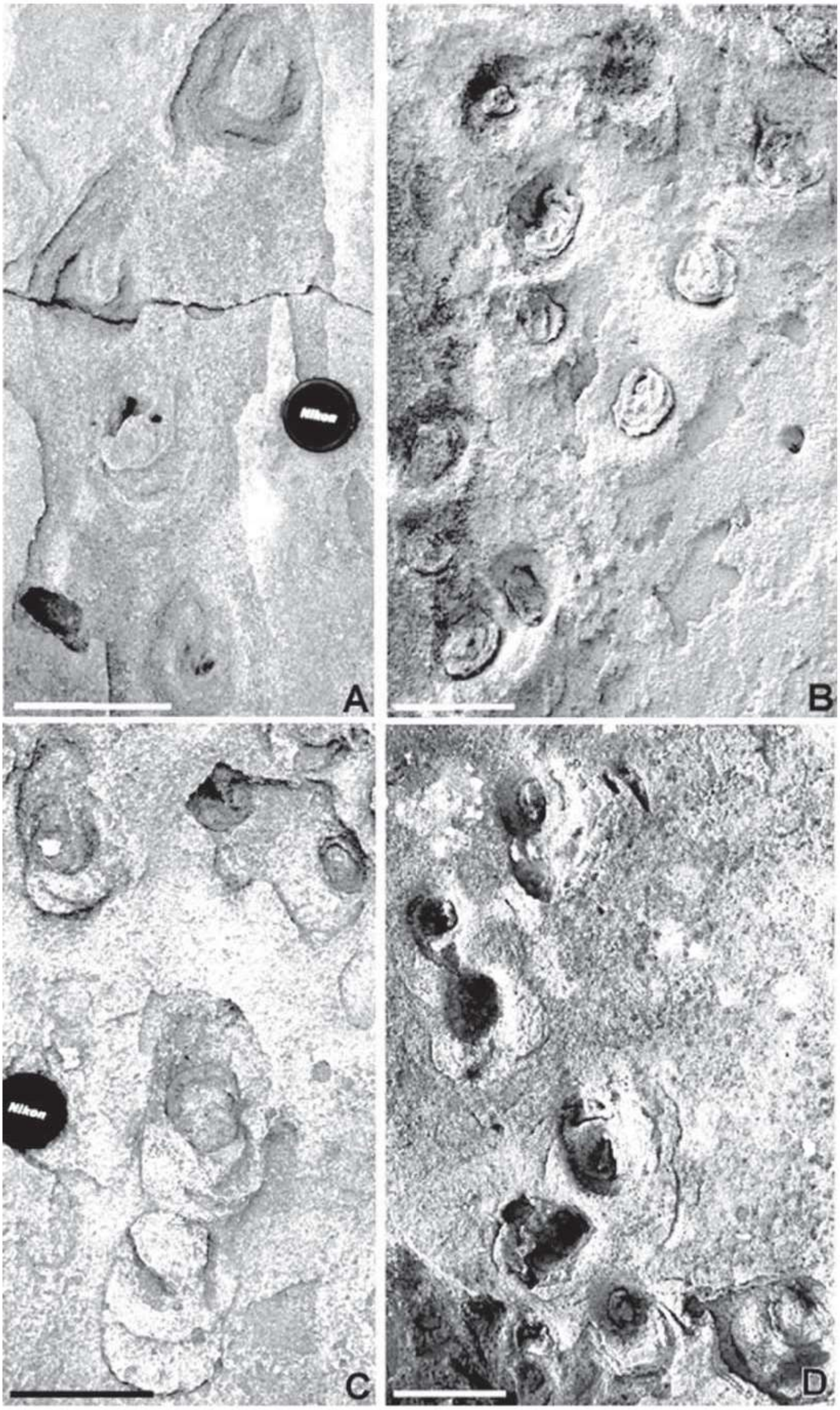
During the Arctic spring, when the winter snows melt, such large amounts of water are released in areas of primitive drainage that soils are temporarily saturated with water to depths of over a metre, and become highly liquidified by solifluction. In Jameson Land, East Greenland, a trackway of a doomed musk ox (*Ovibos moscatus*) was studied in such an environment. Observations were made in July 1970 on one of the Scoresby Sund Expeditions led by Oscar.

Tracks indicated that two individuals had passed over the area while the soil was fluid. In the featureless landscape the two trails followed more or less the same course, indicating that the animals accompanied each other (Figs 2, 3). As they walked, they had sunk deeply into the sediment. At the time of study the sediment had dried out and become hard, and no details of the tracks beneath the surface were available, but the irregularity of the trackways indicated poor motor control under the difficult conditions. The presence of crude drag or scuff traces between successive footprints demonstrated that the animals had sunk so deeply into the substrate that they could not withdraw their feet completely from the sediment as they walked.

One of the trackways showed a sudden and dramatic change in style at one point (Fig. 3). From here on, the animal had floundered deeply through the sediment, creating a broad, zig-zag furrow. Approximately 26 m down the slight gradient, at the end of the trackway, lay the corpse of a female musk ox (Fig. 2D). Unfortunately, the corpse had continued to flow down-slope a few more metres in the fluid soil, and the skeleton had thereby become very disturbed. The cause of death was not immediately obvious. It is surmised, however, that at the sudden change in character of the trackway the animal had broken or fatally damaged a limb by falling clumsily, its legs deeply held in the sediment. There were no signs of human interference.

Fig. 3. Sketch map of the two musk ox trackways, based on a number of ground-level photographs. 1: A sudden change in direction by the doomed musk ox. 2: A corresponding change in direction, indicating that the two animals travelled together. 3: The last normal track. 4: The broad, zig-zag trail. 5: The dead musk ox. 6: direction of view of Figure 2B. 7: Direction of view of Figure 2A. 8: Direction of view of figure 2C.

The other musk ox continued its struggle through the slurry without deviating to check the trauma of its partner, as clearly shown by its trackway.



A
B
C
D

Trackways of mountain goats in aeolian sand

In the Pleistocene and Holocene aeolianites of Mallorca, there are abundant trackways (Fig. 4) produced by a small, extinct caprine bovid, *Myotragus balearicus* (Fornós & Pons-Moyà 1982). The animal was a ruminant goat or goat antilope, related to the tribe of mountain-dwellers that include the chamois (*Rupicapra pyrenaica*) of Europe and the takin (*Ammotragus lervia*) of China (Lalueza-Fox et al. 2000). However, confinement to some of the Balearic Islands since the Miocene had provoked a bizarre island evolution (e.g., Andrews 1915; Bover & Alcover 1999). Anatomical details of numerous skeletons found in caves show the limbs to have been modified through shortening and bone-fusion to become highly proficient for slow progress over hard and rocky substrates. In no respect do the feet show any adaptation to walking on loose or fluid sand. Quite the contrary, the closely bound, narrow feet would seem very poorly adapted for walking on soft sand. But the tracks have been found solely in aeolianitic sandstone – a twist of taphonomy.

The trackways of *M. balearicus* are described in detail by Fornós et al. (in press). These authors concluded that the tracks were made in moist to wet sand, probably during the winter when the dunes were inactive. As in the case of the musk oxen, the evidence that the track-makers were not in their normal environment, and were progressing under great stress, is the extreme irregularity of their trackways and the depth of penetration of the limbs into the substrate (Figs 5, 6). Even the most regular trackways, following the flat crests of the dunes, show signs of staggering, variable length of stride, and great variability in track morphology (Clemmensen et al., 2001, this volume, fig. 4). On the steep flanks of the dunes, however, the irregularity of all parametres increases. In rare cases where the actual tracking surface is preserved, drag traces are seen between consecutive tracks (Fig. 6A, B). Clearly, the track-makers expended a great deal of energy as they floundered through the substrate.

Fig. 4. Contrasting styles of *Myotragus balearicus* trackways, south coast of Mallorca near Punta des Bauç. Scale bars 10 cm. A–C. Horizontal sections parallel with the tracking surface, on sloping flanks of dunes. The length of stride indicates animals moving down-slope. Up-slope is toward top of pictures. A. Four tracks showing much deformation of the surrounding sediment, indicating that this was soft and wet. B. Two trackways side by side, showing irregular stride lengths. There is less sediment disturbance than in A, indicating a less wet substrate. C. Sharp microtectonics associated with tracks indicate a damp substrate. D. Tracks on the flat crest of a dune at S'Estret des Temps near Cala Figuera. The tracking surface is exposed, the pairs of tracks are fore- and hind-foot prints, each surrounded by a marginal ridge. The crisp, arcuate microfaults outside this indicate damp sand.

Conclusions

Tetrapods that blunder into over-soft sediments, where walking is difficult and dangerous, produce recognizable structures that are preservable as trace fossils. Characteristic features are: irregularity of stride and course, caused by the difficulty of passage; deep penetration by the limbs as they sink far into the sediment; development of drag or scuff traces caused by the limbs failing to be lifted clear of the sediment between steps; and in extreme conditions, the loss of preservational detail of the trackway, which becomes a continuous disturbance zone in the sediment, lacking individual tracks.

These ugly scenes of struggle by animals crossing unsuitable substrates are not attractive research material. They may be compared, in invertebrate ichnology, with the irregular escape traces of animals plunging upward through suddenly deposited sediment. These structures have rarely been studied in detail and most escape traces remain unnamed. But like tetrapod floundering traces, these fringe trace fossils contain much information on the depositional environment, and they deserve more attention than they have received.

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Dansk sammendrag

Der opfordres til at være mere opmærksom på "grimme" spor lavet af tetrapoder i ekstremt blødt sediment. Disse ret formløse strukturer er vanskelige at beskrive; men de har muligheder for at give megen information om aflejringsmiljøerne. To eksempler

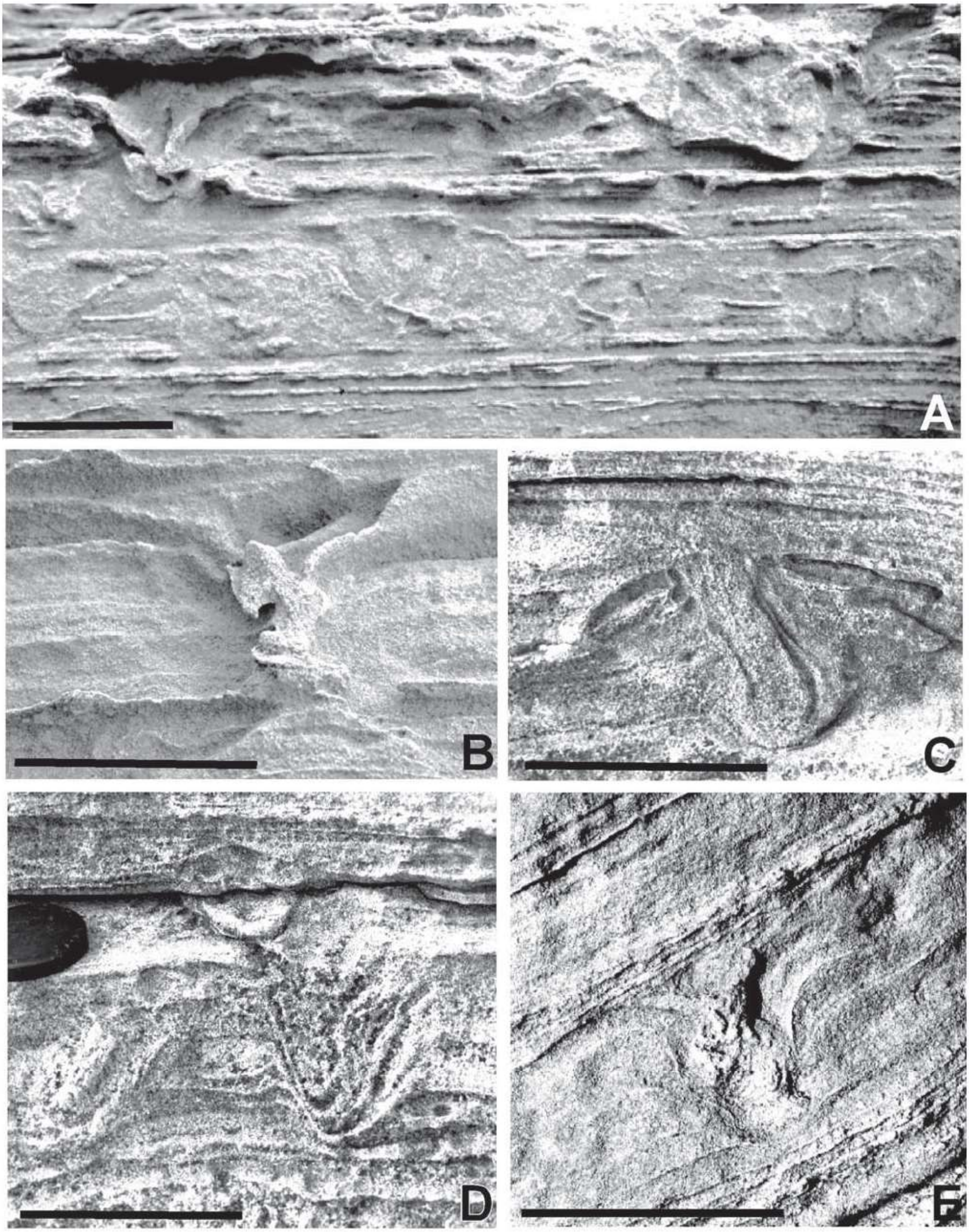

Fig. 5. Vertical sections through *Myotragus balearicus* tracks, S'Estret des Temps. Scale bars 10 cm. The limbs have penetrated the substrate to depths of 8 to 10 cm. These are minimal figures as the tops of the tracks have been truncated by wind erosion before deposition of the next lamina.

gives: (1) en moskusokses dødsmarch. Oksen vandrede ind på et jordflydende område på en skråning på Jameson Land, Øst Grønland. (2) Pleistocæne sporserier dannet af den uddøde, drøvtyggende ged *Myotragus balearicus* i flyvesand på Mallorca. Ichnologiske vidnesbyrd viser i begge eksempler dyr, der kæmper sig vej gennem farlige underlag. Paralleller trækkes til flugtstrukturer dannet af gravende invertebrater.

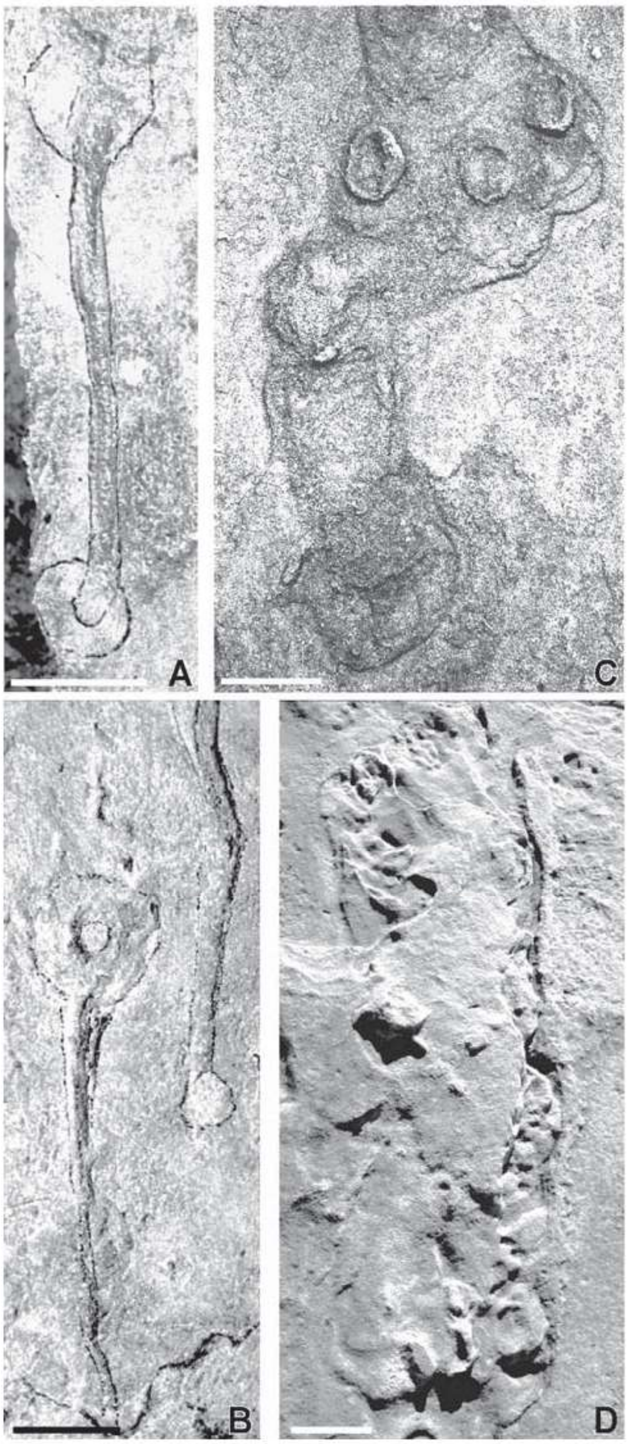

Fig. 6. *Myotragus balearicus* trackways. Scale bars 10 cm. A, B. Drag traces running between consecutive tracks. The limbs have sunk so deeply into the sediment that the animal was unable to lift its legs free of the sediment between steps. The long stride indicates progress down-slope. Up-slope toward top of pictures. C. Part of a trackway showing structures produced by an up-slope struggle of a *M. balearicus*. Some individual tracks and the outer margin of the structures are sharp, indicating a substrate of damp or wet sand. D. Part of a long trackway from bottom to top of a steep dune flank. The substrate was so fluid that individual tracks have not been preserved. The sand was apparently very wet.

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