

# Biomats, biofilms, and biogluce as preservational agents for arthropod trackways

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## ABSTRACT

Due to divergent taphonomic selection, corresponding body and trace fossils are rarely found in the same rocks. In addition to this general rule, arthropod trackways are preferentially preserved in particular settings: (1) lithographic limestones, where toxic bottom waters account for the exceptional preservation of body fossils at the end of their “mortichnial” trackways; (2) estuarine and lacustrine biolaminites that yield blurred surface tracks as well as the sharper undertracks; and (3) Cambrian intertidal sands before the Precambrian/Cambrian substrate revolution had reached this environment. In all these ichnotopes, the original presence of protective microbial films can be inferred from sedimentary structures. By analogy, it is hypothesised that microbes (“biogluce”) may have been involved in the preservation of trackways in eolian dune sands. The absence of arthropod tracks in Ediacaran sands and silts means either that arthropods had not yet evolved or that they were as yet too tiny to pierce the tougher biomats of the time.

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## 1. Introduction

Thirty five years ago, we published a paper on the preservation of arthropod trackways (Goldring and Seilacher, 1971), which emphasised the importance of undertracks and the variation of track patterns at different undertrack levels. This concept became very useful in the analysis of fossil trackways made by both arthropods and vertebrates. It was also noted that arthropod trackways are often found in environments, which do not correspond to the usual habitats of the trace makers. The same applies to the swimming tracks of fishes (*Undichna*). The present paper highlights this paradox and outlines firstly the conditions necessary for trackways to be preserved, and then discusses representative ichnotopes.

## 2. Preservational conditions

Everybody knows the delicate patterns that arthropod locomotion leaves on the dry sand of a dune, on the mud of a rain puddle, or on a rippled tidal flat. They can be photographed in tangent sunlight or can be cast with plaster. Why shouldn't they fossilise as readily when covered by new sediment as a natural casting process? The following conditions are relevant for their fossilisation.

- (1) The casting material must either, as in casting modern traces, be different from the original substrate, or the two media must be separated by a film that does not allow them to amalgamate. In

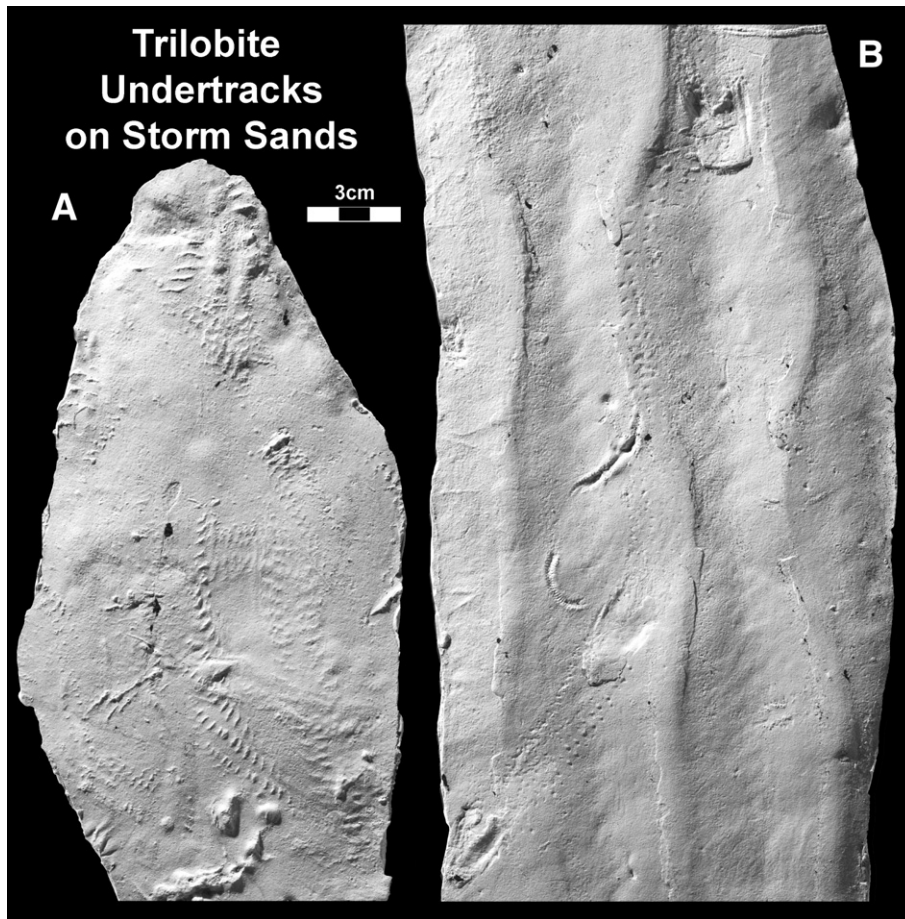
nature, the first condition is met when sand covers mud (or vice versa). Subsequently the mud coating weathers off or can be removed from the now harder sand surface with a metal brush. Alternatively, a mucous biofilm or *biomat* may separate two layers of similar lithology and serve as a plane of splitting.

- (2) The soles of event beds are ideal for the preservation of burrows, but not of *surface tracks*: they are almost invariably wiped out in the erosional phase of sedimentational events and survive only if the substrate was protected by a mucous film of microbes, and if the event was gentle enough not to destroy it.
- (3) In aquatic environments, epichnial surface tracks may be preserved without involvement of a biofilm during the *waning* stage of a storm, flood, or turbidity current. After turbulence has ceased, suspended clay particles can settle on top of the coarser fraction of the same event bed and thereby cast surface traces. This mode of preservation, however, is limited by the *time interval* available for trace production between the deposition of sand and mud. In many cases, however, the tracks observed are actually undertracks that were pierced through the initial mud veneer of the graded event bed (Fig. 1).
- (4) Undertracks (Goldring and Seilacher, 1971) have the highest fossilisation potential. They are mostly produced by aquatic arthropods, because their legs pierce the sediment rather than stamping like snow shoes. But, again, they can form only if buried interfaces or biofilms are within reach.

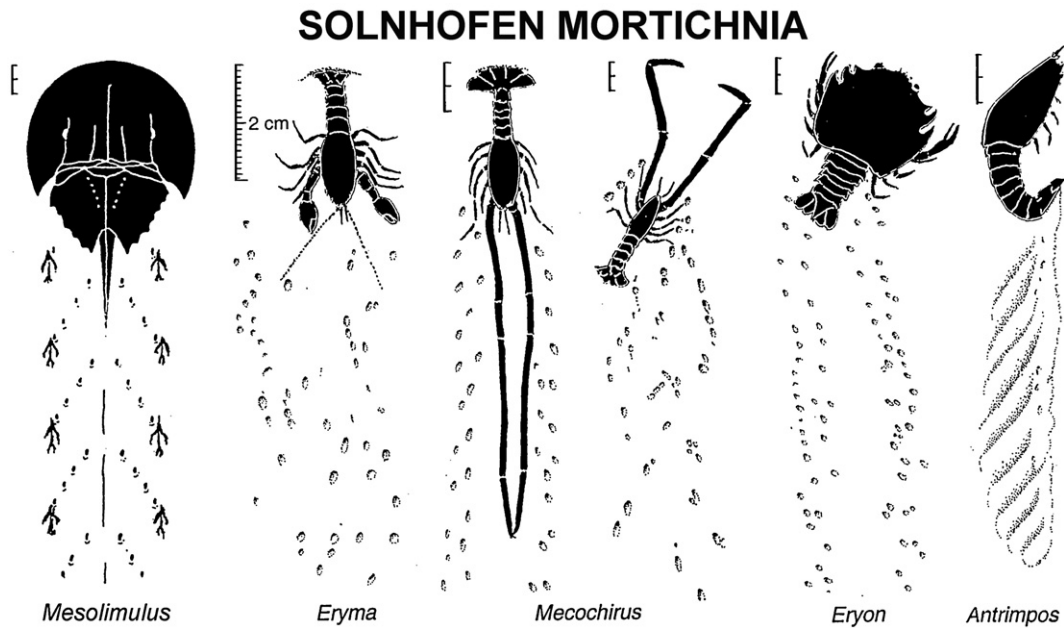
These limitations are the reason why fossil arthropod trackways can be expected only in particular types of lithotopes, as illustrated by the following examples.

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**Fig. 1.** Trilobite trackways from a centimetre-thick storm sand in the Upper Silurian (Sharawa Fm.) of Saudi Arabia were probably made as undertracks. On the lower surface (A) this is indicated by their apparent discontinuity, variation in the number of prints, and by the overprinting of erosional structures. In (B), a trilobite came from the lower left and stopped three times for feeding. Before the third stop, it slid down the slope of a spillover ripple. Note that the shallow rusophyciform burrows show lateral grooves made by the edges of tergites, as well as heaps of flushed-out sand on the posterior side of the burrow. Their steep rear edges indicate that the sand was already covered by a veneer of tempestitic mud (Geologisches Institute Tübingen, Nr. GPIT 1907/1-2).



**Fig. 2.** In the centre of Solnhofen-type basins (U. Jurassic, Germany) the animals' carcasses are preserved at the ends of tracks. Having been swept into the toxic zone by turbidity currents, they survived long enough to produce a last trackway. It is preserved as a shallow undertrack on the mat, while the trace maker itself became embedded into the veneer of turbiditic mud on top (from specimens in Tübingen, Solnhofen and Stuttgart museums).



### 3. Ichnotopes preserving arthropod trackways

#### 3.1. Solnhofen *mortichnia*

Trackways of limulids and various crustaceans (Fig. 2) are known from the Upper Jurassic lithographic limestones of Solnhofen, Germany (Barthel, 1990). They were formed by fully marine organisms, but show an additional anomaly: in the centre of the *Plattenkalk* basin, the trace maker is invariably preserved at the end of its trackway. They represent “death marches” (*mortichnia*, Seilacher, 2007) of animals swept into the anoxic (and hypersaline) zone by muddy turbidity currents. The lengths of the trackways reflect the varying ability of different species to withstand asphyxiation by the toxic bottom waters. Small bivalves (*Solemya*) continued for only a few centimetres, crustaceans for decimetres, and limulids for metres after having landed alive on the sea bottom. Another anomaly is that this lithotope also favoured the preservation of carcasses, providing one of the rare cases, in which body and trace fossil of the same animal co-occur.

In Solnhofen there is unequivocal evidence that the calcareous mud was covered by a *microbial film*. It is documented by sedimentary structures resembling elephant skin and by situations in which the film was locally peeled off, behaving as a coherent and pliable sheet (Fig. 3). These films later caused the platy parting. The trace makers themselves became embedded in the veneer of new turbiditic mud, which must be removed in preparation from below.

Limulid trackways from a locality closer to the basin margin (Pfalzpaint) are not associated with carcasses. They also include long tracks of individuals larger than those found in *mortichnia*. Apparently this track-site was near the limulids' oxygenated habitat, from where only the smaller individuals, were occasionally carried downslope by turbidity currents. Nevertheless the host rock is still platy due to the presence of a non-bioturbated microbial film. So, all Solnhofen trackways are, strictly speaking, undertracks. Nevertheless they are blurred because the pushers dragged the sticky film when closing their blades. As a result, their impressions resemble trifold bird tracks and were at times referred to *Archaeopteryx* hopping in the opposite direction (Walther, 1904.)



Fig. 3. Ruptures caused by turbidity currents illustrate the textile-like consistency of Solnhofen biomats (courtesy of H. Tischlinger).

### Limulid Undertracks (U. Carboniferous, Nova Scotia)

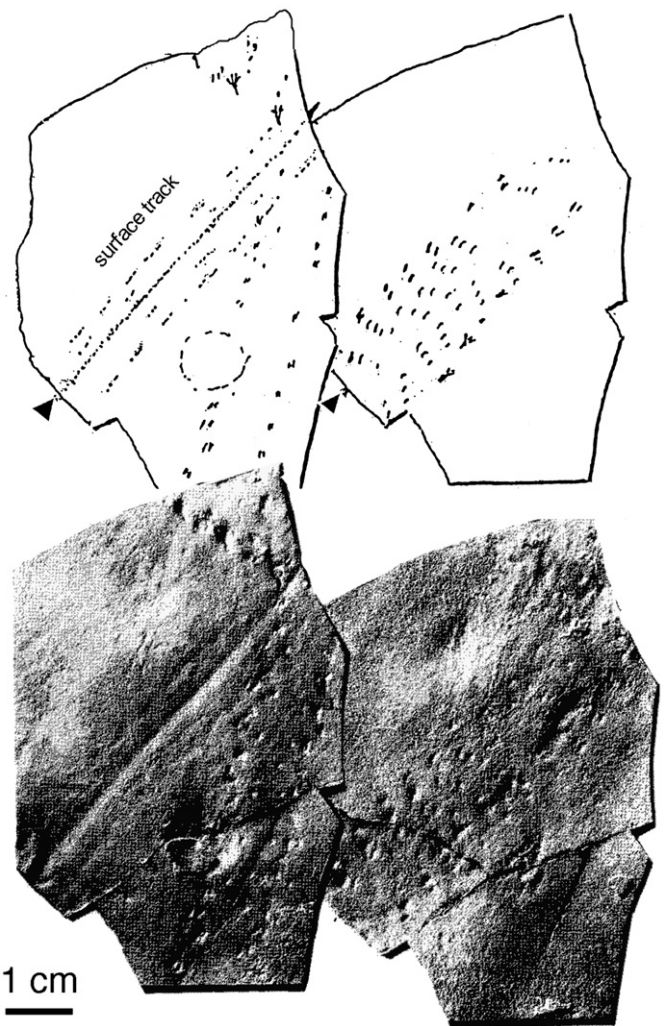
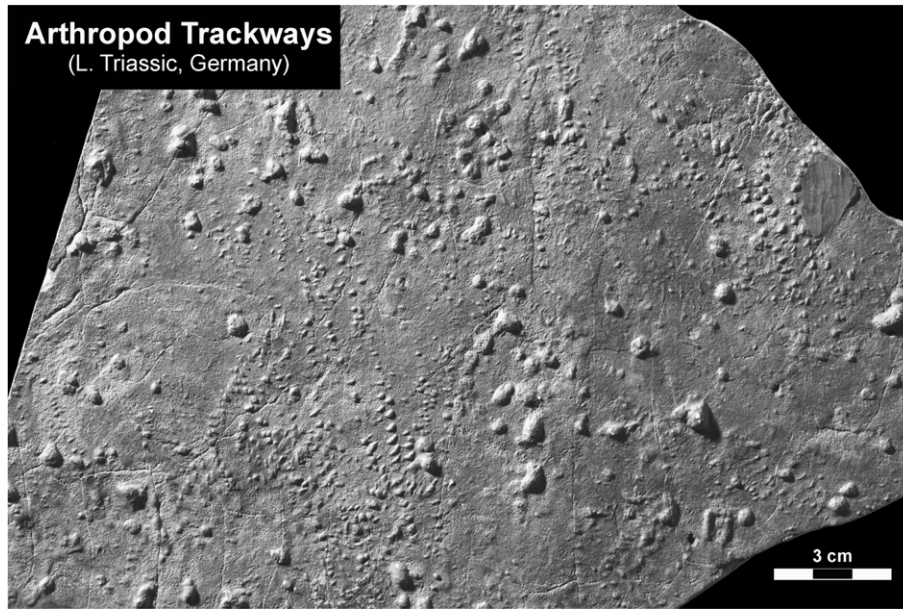


Fig. 4. The blurring of surface tracks and their association with sharper undertracks pierced through from a higher level suggest that all laminae correspond to former biofilms in these paralic Carboniferous siltstones (from Goldring and Seilacher, 1971).

#### 3.2. Estuarine and lacustrine tracksites

In contrast to lithographic limestones, fissile shales and silts deposited in the quiet waters of estuaries allow the study of surface tracks together with undertracks of small limulids on subsequent millimetric laminae (Fig. 4). The *surface tracks* are blurred and have very low relief, whereas the corresponding *undertracks* are much more distinct. Both kinds commonly co-occur on the same surface. So, all partings between successive laminae presumably correspond to former biofilms. Because sedimentation rates were so low, the pointed tips of the limulid legs could pierce several laminae at a time; but as penetration depths differed between the telson, legs of different sizes, and pushers, the shallowest undertracks show the most complete track pattern. This model (Goldring and Seilacher, 1971) can also be applied to freshwater or hypersaline *lake deposits* (e.g. Fig. 5), where traces of aquatic insects and insect larvae are commonly more dominant. The tracksite in Lower Permian red beds of Nierstein, Germany (Schmitgen, 1927) is a representative example. There may, however, be a bio-historical bias: most described examples (Buatois and Mangano, 2004) come from the Palaeozoic. Possibly, bioturbation by meiofauna (that



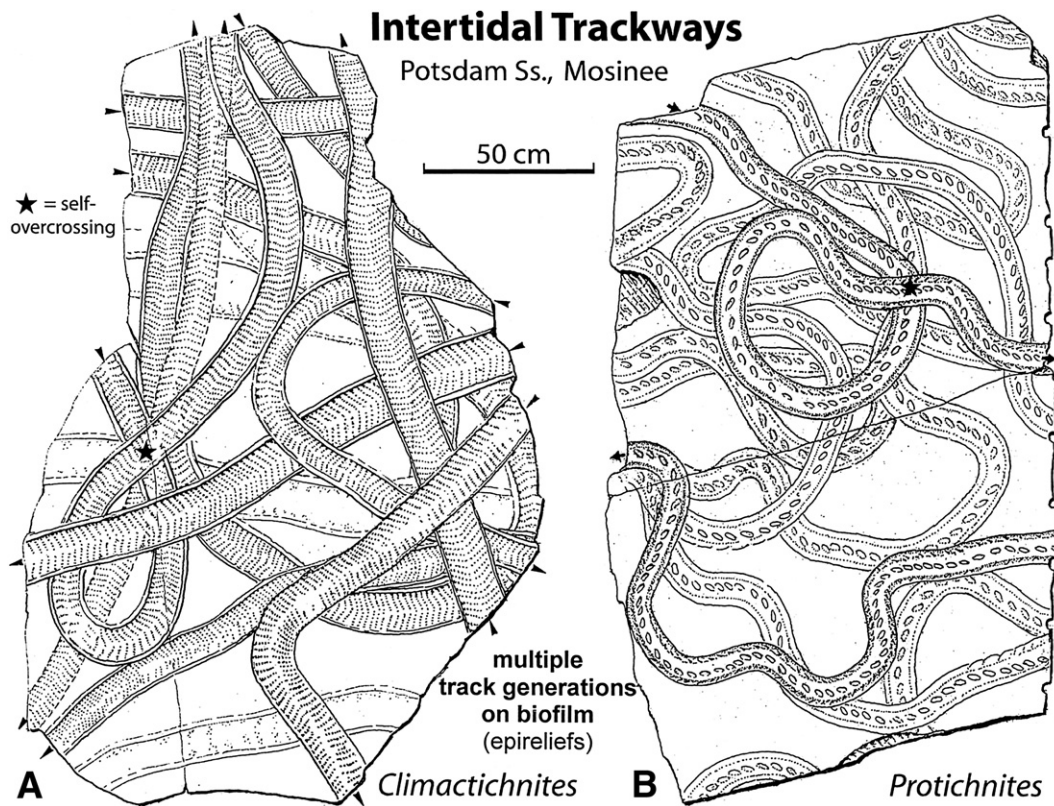


**Fig. 5.** The hypichnial trackways consist of oblique series of up to 8 footprints; but because they come from fluvial Lower Triassic red beds of Germany, their producers were probably crustaceans rather than trilobites. As there are no erosional features other than faint drag marks, the underlying mud was probably protected by a microbial mat when cast by sand in a flood event (Yale Peabody Museum 218366). See Machalski and Machalska, 1994, for a similar specimen from Poland.

left no recognizable traces) increasingly precluded the formation of coherent biofilms, an analogue to what had happened in the marine realm during the Cambrian Substrate Revolution (Seilacher and Pflüger, 1994; Bottjer et al., 2000). Muddy rain puddles may serve as an analogue even today; but they are too short-lived to develop a biolaminated substrate and for benthic animals to complete a whole life cycle. Insect larvae are therefore the dominant trace makers.

### 3.3. Cambrian intertidal ichnotopes

A truly anactulistic ichnotope is represented by littoral sandstones of Cambrian age that have been best studied in Wisconsin, USA (Hagadorn et al., 2002), where wave-rippled surfaces are covered with multiple generations of continuous trackways made by giant molluscs (*Climactichnites*; Yochelson and Fedonkin, 1993) and arthropods



**Fig. 6.** Various tracks of the Upper Cambrian Potsdam Sandstone of Wisconsin owe their preservation to the persistence of biomats on intertidal sands beyond the Cambrian Substrate Revolution. Meandering courses indicate that the unknown large track makers left the water for grazing on these mats. (A) Mollusc tracks (*Climactichnites*) after cast in “Fossil Art” (Seilacher, 2001). (B) Arthropod tracks (*Protichnites*; Yale Peabody Museum 204961).

(*Protichnites*). The depth of the impressions suggests that these traces were made on wet sand while it was exposed during low tide, rather than under water. Also unique are the impressions of stranded jellyfish (Hagadorn et al., 2002). The preservation of all these features is due to microbes that covered the sand with a protective veneer. Obviously the Cambrian Substrate Revolution (Bottjer et al., 2000) had not yet reached the intertidal zone, so that a taphonomic window remained open for a limited time in Earth history. Through this window we get a glimpse of the first animals leaving the water at low tide. Their winding courses (Fig. 6) indicate that they grazed on microbial films, which soon regenerated. Thereby multiple track generations, distinguished by differential blurring, survived on the same bedding planes. Possibly these creatures came out only at night in order to avoid sun and ultraviolet radiation. Other protective features were large body sizes in order to reduce surface to volume ratio.

Whereas the biofilm allowed continuous surface tracks to be preserved, it also tended to smoothen minor relief. This effect is expressed in the blurring of ripple crests, of earlier trackways, and of smaller footprints.

### 3.4. Precambrian matgrounds

Previous to the Precambrian/Cambrian substrate revolution, the sea-bed was covered by microbial mats at all depths. As in lake deposits (see above), signatures of every storm are thus preserved, even in arenaceous tempestites, while they tend to become amalgamated in Phanerozoic times. In contrast to the even lamination of lake deposits, however, the boundaries between storm layers are marked by oscillation ripples. During the succeeding event, the ripples of the previous one remained either intact and became replicated by the new sand layer. In other events, the old microbial crust became abraded on ripple crests, resulting in a pattern of concave washouts (“palimpsest ripples”, Seilacher, 1997).

Precambrian *biomats* grew much tougher than lacustrine and intertidal biofilms. Large erect organisms such as the Vendobionta (Seilacher et al., 2003) could be anchored to them by attachment discs, just as modern filter feeders attach to hard substrates. Centrimetric stem molluscs (*Kimberella*) also failed to leave a trail when crawling over the mat. On the other hand, these microbial veneers were soft enough to be penetrated by radular teeth of the same animals, so that scratch patterns (*Radulichnus*; Seilacher et al., 2003) appear as undertracks on the lower, elephant-skinned faces of the mats.

It may thus be assumed that in Precambrian seas the microbes were able not only to form mucous veneers, but also to impregnate the upper millimetres of the silty or sandy substrate. In addition, early microbial mineralization (mainly pyrite and its precursor phases) appears to have hardened not only the “death masks” of soft-bodied organisms (Gehling, 1999), but also the mats themselves, so that partings developed unaccompanied by any change in lithology.

As the pointed legs of marine arthropods penetrate into the sediment, their tracks should have been preserved as readily as the undertrack scratches of *Radulichnus*. Nevertheless no such tracks have ever been found. Not even the resting and furrowing traces of trilobites (*Cruziana*) are known from Ediacaran ichnotopes. It thus appears that arthropods of adequate size did not yet exist. In any case they did not burrow for food or protection.

### 3.5. Dune ichnotopes

Very delicate tracks of small rodents, lizards, snakes and terrestrial arthropods can be observed on the smooth slopes of modern dunes. So the occurrence of similar trackways on fossil dunes is not surprising. Prominent examples are the trackways of large arthropods (*Protichnites*; Seilacher, 2001; MacNaughton et al., 2002) in the eolian facies of the Upper Cambrian Potsdam Sandstone, or of scorpions (*Octopodichnus*; Brady, 1947, 1961) in the Permian Coconino Sandstone (Fig. 7).

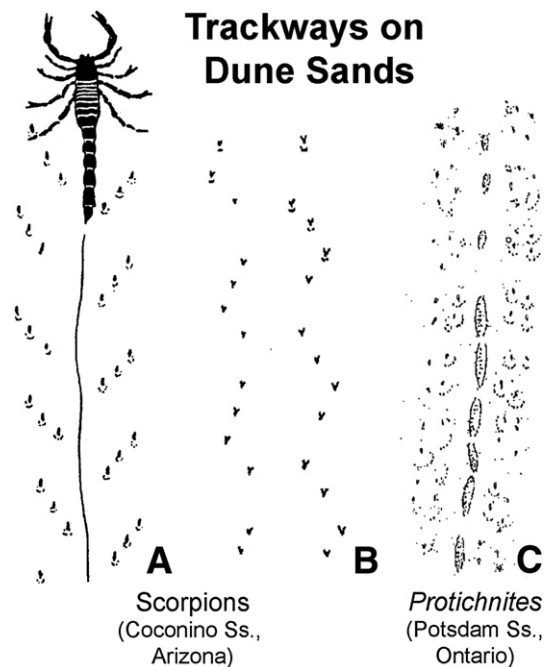


Fig. 7. Arthropod tracks preserved on parting surfaces of ancient eolianites raise the question, whether moist dune surfaces may be stabilized by the “bioglu” of microbial grain envelopes. (A,B) Scorpion tracks in the Permian Coconino Sandstone of Arizona (after Brady, 1947). C. *Protichnites* in an eolian facies of the U. Cambrian Potsdam Sandstone of Ontario (field photo).

Yet, the preservation of surface tracks is as improbable on land as it is under water: in dunes they should become obliterated during deposition of the next sand lamina. What separating agent protected them? Two anecdotal observations are pertinent:

1. Some years ago, a building in the holy town of Mecca collapsed, probably because the dune sand used for making the concrete had not been cleaned to remove biological constituents (personal communication by Frei Otto, 2006).
2. Field geologists know that dunes should be crossed in the early morning, when dew makes the sand surface more resistant than during the day. But dew alone hardly suffices for the development of partings in the lithified sandstones. One possibility would be interlayering with finer particles from a dust storm; another could be microbial envelopes that make surficial grains stick to each other in moist sand.

These ideas need to be tested by thin sections through fossil eolianites and by SEM study of samples taken in the morning from surfaces of modern dunes. Microbial participation in the form of *bioglu* (new term) remains an interesting possibility.

## 4. Conclusions

The preservation of arthropod trackways in the fossil record is a problem. It is favoured in particular ichnotopes (trace fossil *Lagerstätten*) that do not necessarily coincide with the normal distribution of the trace makers. In general, undertracks are more distinct than surface tracks and have much higher fossilisation potential (Goldring and Seilacher, 1971); they do, however, become visible only on mud/sand interfaces or if the sediment contained suitable and closely-spaced films that developed into partings upon lithification.

Marine storm sands are commonly too thick for post-event undertracks to reach the base of the bed. Their rippled tops, however, favoured the preservation of surface tracks or shallow undertracks, because they became coated shortly afterwards by the mud veneer settling from suspension.



Laminated silts deposited in the quieter waters of lakes and estuaries are ideal for the preservation of *multiple* undertracks, because the laminae are thin and planar. In addition, they appear to have been separated by biofilms, the diagenesis of which tends to induce partings. Blurred surface tracks also imply the original presence of such films.

The importance of mucous biofilms for track preservation is epitomized by the death marches (*mortichnia*) of arthropods swept into the toxic zone of the Upper Jurassic Solnhofen basins and their less dramatic equivalents in shallower facies.

Because the Cambrian Substrate Revolution had not yet reached them, wet *intertidal* sands of Late Cambrian age represent a non-actualistic preservational window for continuous trackways; but this window remained open only for a limited geologic time and preserves only surface tracks blurred by the smoothing effect of regenerating biofilms.

*Precambrian* biomats comprised the upper few millimetres of the sediment and were therefore much tougher. These mats did not deform when heavy, slug-like animals crawled over them; but they were pierced by their radular teeth. Thus they would as likely have been penetrated by the pointed legs of adequately sized arthropods if they existed. The preservation of continuous arthropod trackways on the partings of *dune sands* (Fig. 7) remains enigmatic. It is suggested herein that surficial grains may be coated by microbes that acted as a *bioglue* when moistened. It also induced the formation of partings during diagenesis.

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