The neoichnology of terrestrial arthropods

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Abstract

A comprehensive systematic neoichnological study was conducted to investigate the affect of substrate conditions on the morphology and survivorship of terrestrial arthropod trackways. Experiments utilized five different extant arthropods, representing a range of body forms and higher taxa: discoid cockroaches (*Blaberus discoidalis*), emperor scorpions (*Pandinus imperator*), Chilean rose tarantulas (*Grammostola rosea*), African giant black millipedes (*Archispirostreptus gigas*), and common woodlice (*Oniscus asellus*). Trackways were produced on substrates of various grain size and moisture content, in protocols simulating subaerial and transitional subaqueous–subaerial depositional settings. The results are illustrated systematically to provide a comprehensive record of the morphological variation that can occur in arthropod trackways under different substrate conditions. General morphological trends, of increased definition of individual tracks and loss of tracks within series, are highlighted as "dry to dampground" and "soft to firmground" surface moisture taphoseries in the subaerial and transitional subaqueous–subaerial protocols respectively. Heavier arthropods produced trackways across a broader moisture and grain size range, whilst different arthropods can produce similar trackways under certain conditions. Undertrack fallout was investigated using discoid cockroaches, and the resultant undertrack taphoseries mimics the surface moisture taphoseries. Previous hypotheses on the factors that influence trackway survivorship were also investigated. Increasing concentrations of clay minerals exponentially increases the survivorship of trackways subjected to an air current, whereas increasing surface moisture has a linear affect, and a combination of the two provides excellent conditions for trackway survivorship. The results of this study are fundamental to the study of fossil arthropod trackways and can be used to aid ichnotaxonomic revisions, whilst also facilitating the identification of trace fossil producers and highlighting potential biases in palaeoecological reconstructions based on trace fossils.
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1. Introduction

Trace fossils have a wealth of potential applications. They represent the direct evidence for animal behaviour in the fossil record and, unlike body fossils, are gen-erally preserved *in situ*, so are therefore of tremendous utility in palaeoecological and palaeoenvironmental reconstructions. The body fossil record of arthropods is relatively incomplete (Wills, 2001) and so their trace fossil record is particularly important, often pre-dating the oldest body fossils and providing evidence for their earliest activity on land (Johnson et al., 1994; Mac-Naughton et al., 2002), as well as enabling reconstructions of their locomotory techniques (Minter and Braddy, 2006).

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Producers are rarely found at the end of their trace fossils (e.g. Abel, 1935) and so the majority of producer identifications are interpretations, albeit informed. Neoichnology is the study of traces of modern animals, including the affects and rate of bioturbation, and is therefore a particularly useful approach for attributing producers to particular trace fossils, sometimes with unexpected results (Martin and Rindsberg, 2006), and consequently facilitating palaeoecological reconstructions. Neoichnology also provides a useful tool for investigating the processes that result in morphological variation in trace fossils, such as variations in behaviour and substrate conditions at the time of formation, and preservational factors such as undertrack fallout and survivorship. Such observations can be used to assist in rationalizing existing, and diagnosing new, ichnotaxa.

Given the utility of neoichnological investigations, it is perhaps surprising that such studies are not more prevalent. Most neoichnological studies have focussed on vertebrates, particularly salamanders (Peabody, 1959; Brand, 1979; Brand and Tang, 1991; Brand, 1996), as well as larger vertebrates (Padian and Olsen, 1984; Farlow and Pianka, 2000; Milàn, 2006; Milàn and Bromley, 2006). Neoichnological experiments involving arthropods have received comparably little attention and have tended to focus on burrows (e.g. Chamberlain, 1975; Elders, 1975; Frey et al., 1984). Studies of modern arthropod trackways have generally been as an aside to aid interpretation within more descriptive papers, particularly with respect to arachnids (Brady, 1947; Alf, 1968; Sadler, 1993), crustaceans (Margerard, 2000; Walker et al., 2003; Gaillard et al., 2005) and myriapods (Johnson et al., 1994). Trackways of modern hexapods have been documented, but as a means to deducing locomotory techniques (Manton, 1972), or thanks to opportunistic observations (Metz, 1987). A notable exception is the recent paper by Uchman and Pervesler (2006), which experimentally investigated the influence of substrate consistency on the behaviour and surface trace morphology of modern amphipods and isopods.

2. Aims

The principal aim of this study is to present the first comprehensive systematic neoichnological investigation on the trackways produced by a range of modern terrestrial arthropods. Experiments were carried out to investigate the influence of substrate moisture content and grain size on trackway morphology in protocols designed to simulate subaerial (aeolian) and transitional subaqueous–subaerial (tidal flat and floodplain) depositional settings. The results illustrated herein are intended as a

record of the morphological variation resulting from systematic variations in substrate conditions for a range of terrestrial arthropod trackways. The documentation of poorly preserved trackways, as well as the conditions under which no trackways were formed, was considered equally as important as that of well preserved trackways. The vast majority of fossil arthropod trackways are poorly preserved or incomplete and so it is hoped that this study will provide a basis for other researchers to understand the processes that result in morphological variation in trackways, which will assist in ichnotaxonomic assignments, palaeoenvironmental analysis of substrate
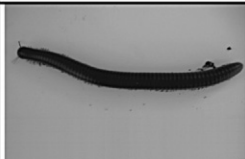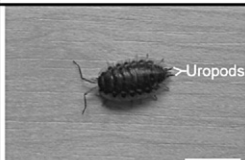

Arthropod	Mean length (mm)	Mean mass (g)
Discoid cockroach (*Blaberus discoidalis*)	64.8	3.7
Emperor scorpion (*Pandinus imperator*)	58.9	15.4
Chilean rose tarantula (*Grammostola rosea*) Spinnerets	59.3	17.6
African giant black millipede (*Archispirostreptus gigas*)	287.5	84.1
Common woodlouse (*Oniscus asellus*) Uropods	13.3	0.1

Fig. 1. Arthropods used in neoichnology experiments. Note that arthropod lengths do not include antennae or tails. Scale bars 10 mm.

conditions, identification of producers, and palaeoecological reconstructions. The implications of undertrack fallout on resultant trackway morphology were also investigated and previous hypotheses of factors influencing trackway survivorship (McKee, 1947; Loope, 1986; Metz, 1987; McKeever, 1991; Sadler, 1993) were tested.

3. Materials and methods

3.1. Experimental animals

Five different extant arthropod species, representing a range on body forms and higher taxa, were utilized during these experiments: discoid cockroaches (*Blaberus discoidalis*), emperor scorpions (*Pandinus imperator*), Chilean rose tarantulas (*Grammostola rosea*), African giant black millipedes (*Archispirostreptus gigas*), and common woodlice (*Oniscus asellus*). See Fig. 1 for details of their morphology. These species were selected to represent a range of body forms and higher taxa. They are also the most commonly attributed producers of terrestrial arthropod trackways (e.g. Schmidtgen, 1927; Brady, 1947; Sadler, 1993; Johnson et al., 1994) and therefore enable these interpretations to be tested. Arthropods were kept in small plastic containers under a light for a few minutes prior to each experiment and then encouraged to walk across prepared substrates.

3.2. Substrates

Sediments were obtained from WBB Minerals (Sandbach, UK). Three different grain sizes of sediment,

corresponding to fine-, medium- and coarse-grained sand, were utilized in both protocols. See Table 1 for full technical specifications. Natural systems are complex, and rather than attempting to replicate all of these parameters the following protocols were designed to be repeatable with parameters that could be held constant whilst one was systematically varied. The grain size ranges of the sediments were therefore intended to represent standards of fine-, medium- and coarse-grained sand, rather than attempting to mimic those of natural sediments found in different depositional environments.

3.2.1. Subaerial protocol

The subaerial protocol was designed to simulate an aeolian depositional setting whereby the substrate surface is moistened following rain or dew. Plastic trays measuring $30 \times 26 \times 5$ cm (or $37 \times 31 \times 5$ cm for the African giant black millipedes) were filled with sediment, and the surface levelled off but without compaction. Some silt grade material (0.2%) was present in the fine-grained sand, although this was uniformly distributed throughout the prepared substrates and is unlikely to have affected the results. These trays were then placed in a larger Perspex tank measuring $80 \times 40 \times 19$ cm. Non-uniform building sand was placed around the outside of the plastic tray, providing a level surface for arthropods to move across at either end of the larger tank. A black cardboard shelter, mimicking a natural retreat, was constructed at one end of the larger tank and lights situated at the other end (*cf.* Peabody, 1959). Arthropods were positioned at the lighted end and invariably moved towards the shelter, although they occasionally required some additional gentle persuasion with a fine paintbrush. The arthropods were channelled across the substrate using cardboard barriers, which slotted into the non-uniform building sand at either end of the plastic tray, but did not disturb the prepared substrates. Barriers were positioned centrally so that the arthropod could walk across the area that received the most even spray of water (Fig. 2). This experimental design enabled continuous trackways to be produced on the prepared substrate surface because the arthropod would begin walking on the non-uniform building sand and it could then be removed from the shelter without further disturbing the prepared substrate.

The moisture content of the substrate surface was increased by spraying water onto the substrate alternately from each end of the tank at a distance of 30 cm and an angle of 45°. The amounts of sprayed on moisture are quoted in terms of both coverage (ml/cm^2) and volume (ml), and represent the maximum received

Table 1
Technical specifications for the sands used (supplied by WBB Minerals, Sandbach, UK). Sorting was calculated using the equation of Folk and Ward (1957)

|	Leighton Buzzard DA 80F (fine-grained sand)	Leighton Buzzard DA 50 (medium-grained sand)	Leighton Buzzard DA 30 (coarse-grained sand)
Mean grain size (μm)	176	273	468
Interquartile range (μm)	130–206	213–305	369–547
Sorting	Well sorted	Well sorted	Well sorted
Sphericity	Low	Medium	Medium
Roundness	Sub-angular to sub-rounded	Rounded	Rounded
Chemical composition	97.6% SiO_2, 0.57% Fe_2O_3, 0.69% Al_2O_3, 0.38% K_2O, 0.76% LOI	97.54% SiO_2, 0.86% Fe_2O_3, 0.35% Al_2O_3, 0.15% K_2O, 1.1% LOI	92.03% SiO_2, 5.36% Fe_2O_3, 0.54% Al_2O_3, 0.09% K_2O, 1.98% LOI
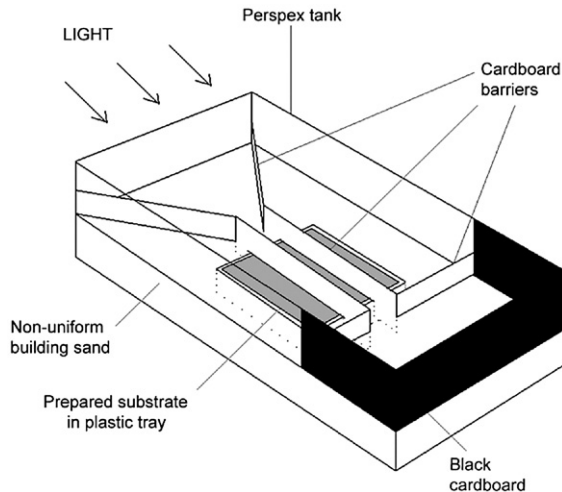
Fig. 2. Experimental apparatus for the subaerial experimental protocol.

under each experimental condition. Up to four moisture levels per substrate were used for each arthropod under investigation, and were chosen, following a preliminary set of experiments, to represent regular intervals along a moisture gradient to the point at which no further morphological change occurred (i.e. the "morphological variation endpoint"). Initial conditions of dry sand (0 ml/cm^2 (0 ml) of sprayed on moisture) were used in each case. A "drygroundto dampground" scale is introduced to describe the moisture gradient in the subaerial protocol. The point along a moisture gradient at which an arthropod can no longer make a trackway is referred to as the "trackway production endpoint," and is not to be confused with the morphological variation endpoint. Three replicates were carried out for each arthropod and substrate condition.

3.2.2. Transitional subaqueous–subaerial protocol

The transitional subaqueous–subaerial protocol was designed to simulate situations where sediment settles out from suspension and is subsequently exposed, such as tidal flats or floodplain sheetflood deposits. Following a series of preliminary experiments, a method was settled upon which produced even substrate surfaces and repeatable results. Sediment was measured into the plastic trays to a depth of 2 cm and then removed. The trays were then filled with water to a depth of 2.5 cm and the sediment reintroduced by sprinkling it lightly and evenly across the water surface. The sediment was allowed to settle overnight. The silt grade material in the fine-grained sand was re-suspended by gently tilting the tray in alternate directions. This re-suspended material was then siphoned off along with the majority of the

water to ensure that the dominant grain size was exposed at the surface. The plastic trays were not transferred to the larger Perspex tank because transport of these trays disturbed the surface.

In this protocol, the moisture level of the substrate equated to the drying time of the substrate following siphoning at room temperature (22–24 °C). As with the subaerial protocol, up to four moisture levels per substrate for each arthropod under investigation were used. These moisture levels were chosen, following a set of preliminary experiments, to represent regular intervals along a moisture gradient until the morphological variation endpoint was reached. Initial conditions of 0 min following siphoning were used in each case. The surface moisture taphoseries for this protocol can be divided into a soft to firmground scale (*cf.* Buatois et al., 1997). The barriers were attached to the sides of the plastic trays in this protocol and the arthropods could be channelled across any part of the substrate as it had a relatively uniform moisture level. At least two replicates were carried out for each arthropod and substrate condition.

3.3. Undertrack fallout

The implications of undertrack fallout on discoid cockroach trackway morphology were investigated following the general methodology of the subaerial protocol. Fine-grained sand was mixed with 4% by dry weight Kaolin 50 (a blended China Clay obtained from WBB Minerals, consisting of 63% Kaolinite, 25% Potash mica, 3% Soda mica and 7% Quartz, and with an unfired modulus of rupture of 1.3 MPa) to enhance the cohesion of the substrate such that a plaster mould could be recovered. Ten different discoid cockroaches were used to produce individual trackways in order to avoid potential biases resulting from using just one individual. Following trackway production, a film of spray paint was carefully applied to form a protective crust over the substrate surface. Once the paint had dried, a mould of the trackway was made by carefully pouring plaster over the surface. Once the plaster had set, the mould was then removed from the substrate and any remaining sand and paint were removed by washing with water and acetone. The "depths" of the individual tracks (i.e. hyporelief of the mould) were measured using Mitutoyo CD-6"CP digital callipers (accurate to 0.01 mm). The mean depths of the tracks of the fore, middle and hindlimbs were obtained for each trackway and standardized against the mass of their producer. The ratios of track depths were calculated in order to determine the hypothetical order of track loss with successive undertrack fallout.

3.4. Trackway survivorship

Previous hypotheses of factors influencing trackway survivorship, such as moisture (McKee, 1947; Sadler, 1993) and the presence of clay minerals (Loope, 1986; Metz, 1987; McKeever, 1991) were tested, again following the general methodology of the subaerial protocol. Trackway survivorship was tested, in a series of simple experiments, by subjecting them to an air current from a Pelonis 12" desk fan (model No. FT30-A4), which was measured in a wind tunnel as producing a wind speed of 5 m/s when placed on the maximum setting. The trackways were raised to the level of the centre of the fan by adding more non-uniform building sand to the Perspex tank and placing the plastic trays in a depression in this sand. The influence of clay minerals was tested by mixing fine-grained sand with Kaolin 50 at levels of 0, 1, 2, 3, and 4% by dry weight; whilst the role of moisture was tested by spraying pure fine-grained sand with 0 ml/cm^2 (0 ml), 0.0051 ml/cm^2 (4 ml), 0.0103 ml/cm^2 (8 ml) and 0.0154 ml/cm^2 (12 ml) of moisture. Trackways were produced as before, but using a single discoid cockroach to avoid any potential biases from different walking techniques and track depth. The time taken for complete trackway degradation was recorded. Five replicates were carried out for each experimental condition.

3.5. Documentation of results

All trackways produced during the course of these experiments were photographed using a digital camera (Fujifilm FinePix A345, 4.1 Megapixels) and were illuminated from the left using low angle, raking light. Some of the photographs appear grainy due to the coarse-grained nature of some of the substrates. The terminology used to describe arthropod trackways follows that of Minter et al. (in press). Tracks are the marks left in the substrate by the limbs, whereas imprints are produced by other anatomical features, and a track row represents all of the tracks on one side of a trackway. The term series refers to the discrete groups of tracks produced on one side of a trackway after each limb on that side has pivoted on the substrate once. The symmetry of a trackway is described as being opposite if the series on either side are in-phase, alternate if they are half out-of-phase, or staggered if they have an intermediate relationship.

4. Results

4.1. Influence of substrate conditions on arthropod trackway morphology

Trends concerning morphological variation in trackways along a dry to dampground and soft to firmground moisture gradient in the subaerial and transitional subaqueous–subaerial protocols respectively (i.e. with increasing firmness of the substrate due to increasing sprayed on moisture or time following siphoning), are similar on fine-, medium- and coarse-grained sand, although they are compressed into a shorter moisture range with increasing grain size. For a particular
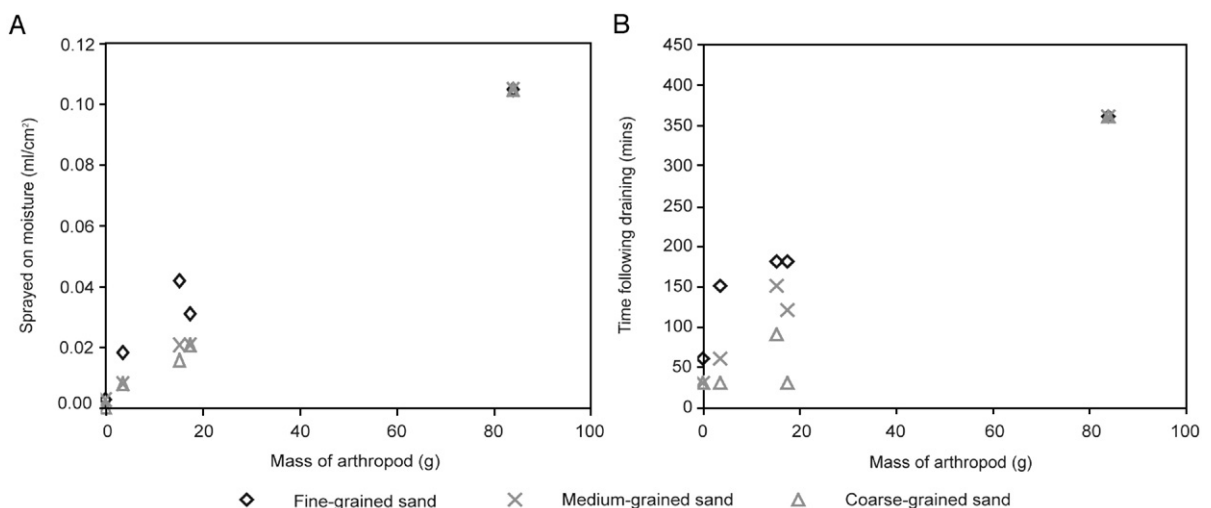

Fig. 3. Trackway production endpoints for arthropods of different mass on different substrates. (A) Subaerial protocol. (B) Transitional subaqueous–subaerial protocol. Note: the African giant black millipede (mass 84.09 g) still produces trackways at 0.1046 ml/cm^2 (120 ml) of sprayed on moisture (subaerial protocol) and 360 min following siphoning (transitional subaqueous–subaerial protocol) but was not tested beyond this point for a true trackway production endpoint.
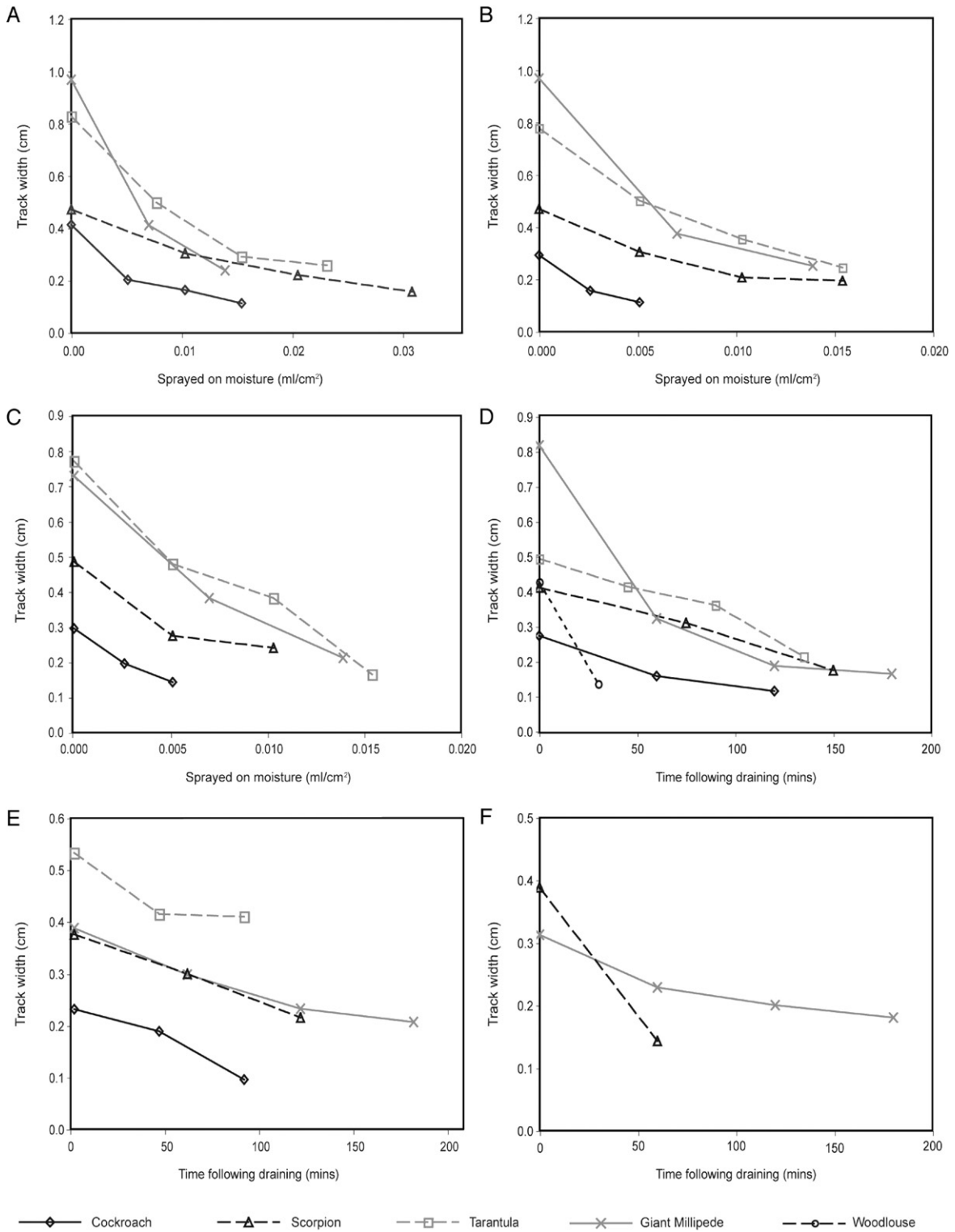
Fig. 4. Arthropod track widths along moisture gradients. (A) Subaerial protocol on fine-grained sand. (B) Subaerial protocol on medium-grained sand. (C) Subaerial protocol on coarse-grained sand. (D) Transitional subaqueous–subaerial protocol on fine-grained sand. (E) Transitional subaqueous–subaerial protocol on medium-grained sand. (F) Transitional subaqueous–subaerial protocol on coarse-grained sand.

arthropod, the trackway production endpoint occurs earlier along these moisture gradients with coarser-grained substrates (Fig. 3). Heavier arthropods can produce trackways across a greater moisture range, although the morphological variation endpoint does not have a simple linear relationship with arthropod mass.

Along the dry to dampground and soft to firmground moisture gradients, in the subaerial and transitional subaqueous–subaerial protocols respectively, there is a trend across all arthropod trackways towards increased definition, measured as the width of individual tracks or track rows (Fig. 4). Overall track morphology also tends to change along these gradients, together with a gradual loss of tracks for those arthropods that produce discrete, recognizable, track series (discoid cockroach, emperor scorpion and Chilean rose tarantula). The loss of individual tracks is difficult to observe in multi-limbed arthropods (African giant black millipede and common woodlouse), but there is a trend from trails, which lack discrete tracks, to trackways. Track orientation and track arrangement within a series can vary considerably within an individual trackway.

4.1.1. Discoid cockroach trackways

All discoid cockroach trackways comprise series of up to three linear tracks with different orientations, and
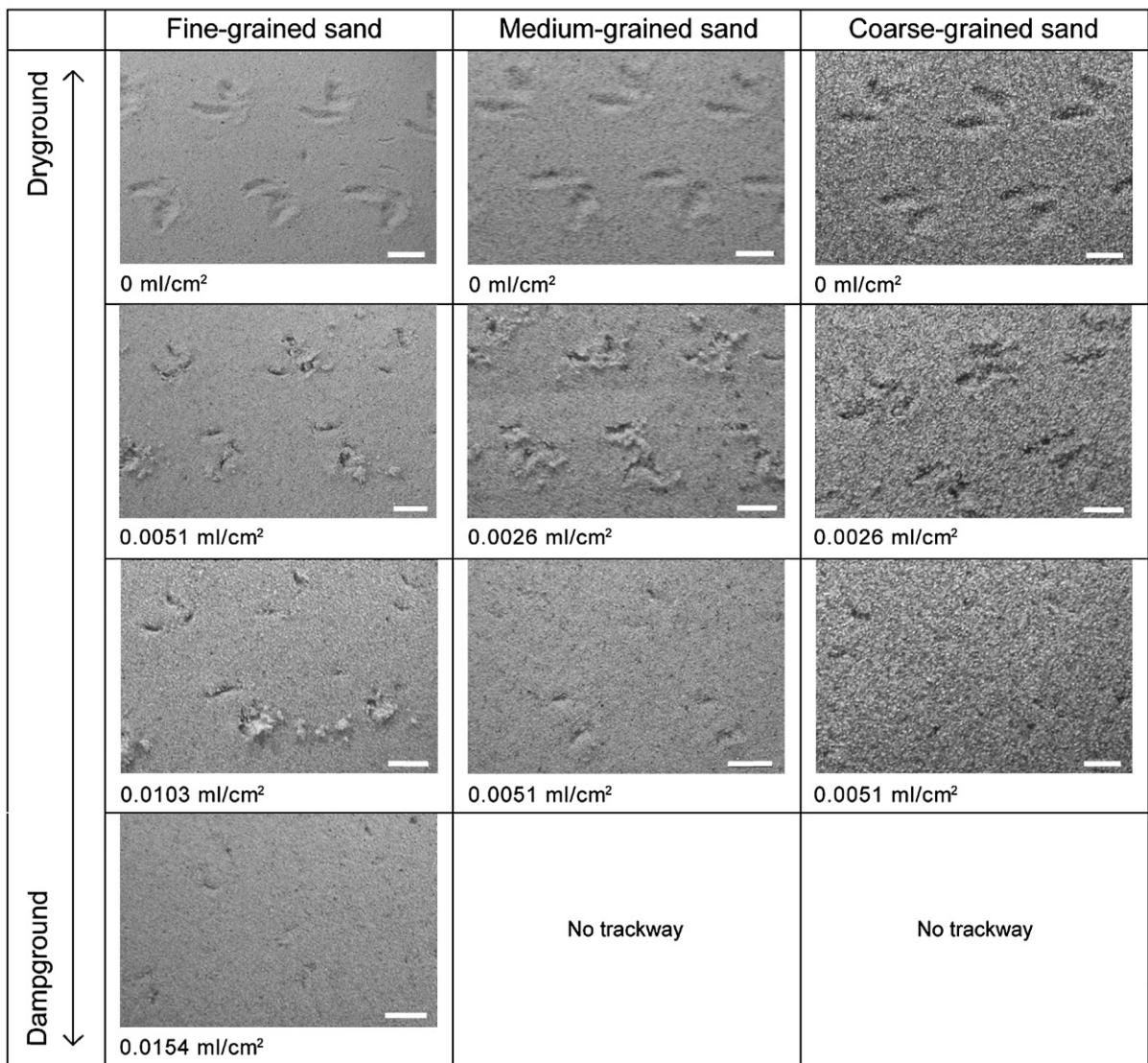

Fig. 5. Subaerial protocol surface moisture taphoseries for the discoid cockroach. The animal was moving from left to right in all cases. Scale bars 10 mm.

have alternate symmetry. In the subaerial protocol with 0 ml/cm^2 (0 ml) of sprayed on moisture, the forelimb and middle-limb tracks commonly merge into one and taper away from the mid-line, and so, together with the elongate hindlimb track, there are often only two discrete tracks. Imprints made by the cerci are also occasionally present. The introduction of sprayed on moisture results in three discrete tracks at first, with gradual loss of the forelimb track along the dry to dampground moisture gradient. The tracks also become shorter, narrower and more elliptical. Cerci imprints are not observed following the introduction of 0.0051 ml/cm^2 (4 ml) of sprayed on moisture (Fig. 5).

In the transitional subaqueous–subaerial protocol on fine-grained sand at 0 min following siphoning, the fore and middle-limb tracks are discrete; whilst they occasionally merge on medium-grained sand at 0 min, but are often discrete. On coarse-grained sand only the middle-limb tracks are visible. There is only a very short time period following siphoning (<30 min) when the cockroaches will make tracks on coarse-grained sand. The loss of tracks on fine- and medium-grained sand

along a moisture gradient generally occurs in the order of forelimb tracks followed by hindlimb tracks. Again, tracks become shorter and narrower along the soft to firmground moisture gradient, and are more elliptical in shape (Fig. 6).

Track orientation within a series depends on the limb responsible and is not affected by grain size, moisture content or depositional regime. The hindlimb track is parallel or backwardly oblique to the mid-line of the trackway, whilst the middle-limb track is backwardly oblique or perpendicular to the mid-line of the trackway, and the forelimb track is perpendicular or forwardly oblique to the mid-line of the trackway. The positions of these different tracks within a series, relative to the mid-line of the trackway, can vary within individual trackways. In particular, the hindlimb track can either be the inner or middle track in a series.

4.1.2. Emperor scorpion trackways

Emperor scorpion trackways comprise series of up to four circular to elliptical tracks with alternate symmetry. In the subaerial protocol with 0 ml/cm^2 (0 ml) of
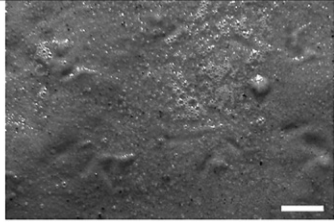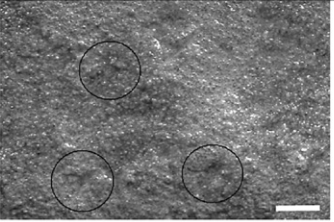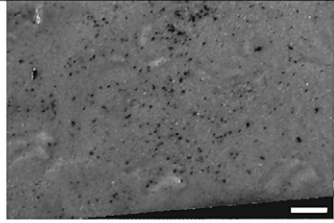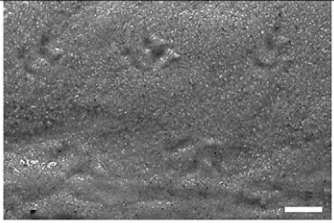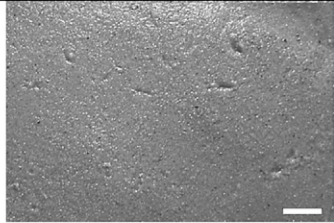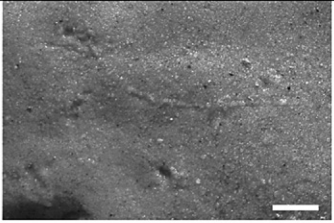

Fig. 6. Transitional subaqueous–subaerial protocol surface moisture taphoseries for the discoid cockroach. The animal was moving from left to right in all cases. Circles highlight tracks. Scale bars 10 mm.

sprayed on moisture, tracks are diffuse, elliptical and in many cases taper forwards. Tapering is more noticeable on fine-grained sand. There is also a slight asymmetry regarding the number of tracks within series, and often three rather than four tracks are visible within a series. Series arrangement can vary within individual track-ways, from three tracks in an oblique linear arrangement to a triangular arrangement (e.g. Fig. 7, coarse-grained sand with 0.0051 ml/cm^2 (4 ml) of sprayed on moisture). With increased surface moisture, the circular tracks become progressively smaller, with one or two being lost per series at successively higher moisture levels (Fig. 7).

In the transitional subaqueous–subaerial protocol at 0 min following siphoning, tracks taper in a similar fashion to those in the dry subaerial regime, again with most noticeable tapering occurring in fine-grained sand. With increased time following siphoning, tracks become smaller and circular. In fine- and medium-grained sand, at 150 min and 120 min following siphoning respectively, the only tracks are double dots or double scratches made by the tarsal claws of the emperor scorpion. This is not observed in coarse-grained sand. Few tracks themselves are visible by the morphological variation endpoints. Due to the generally uncooperative nature of the emperor scorpion during these experiments, and the
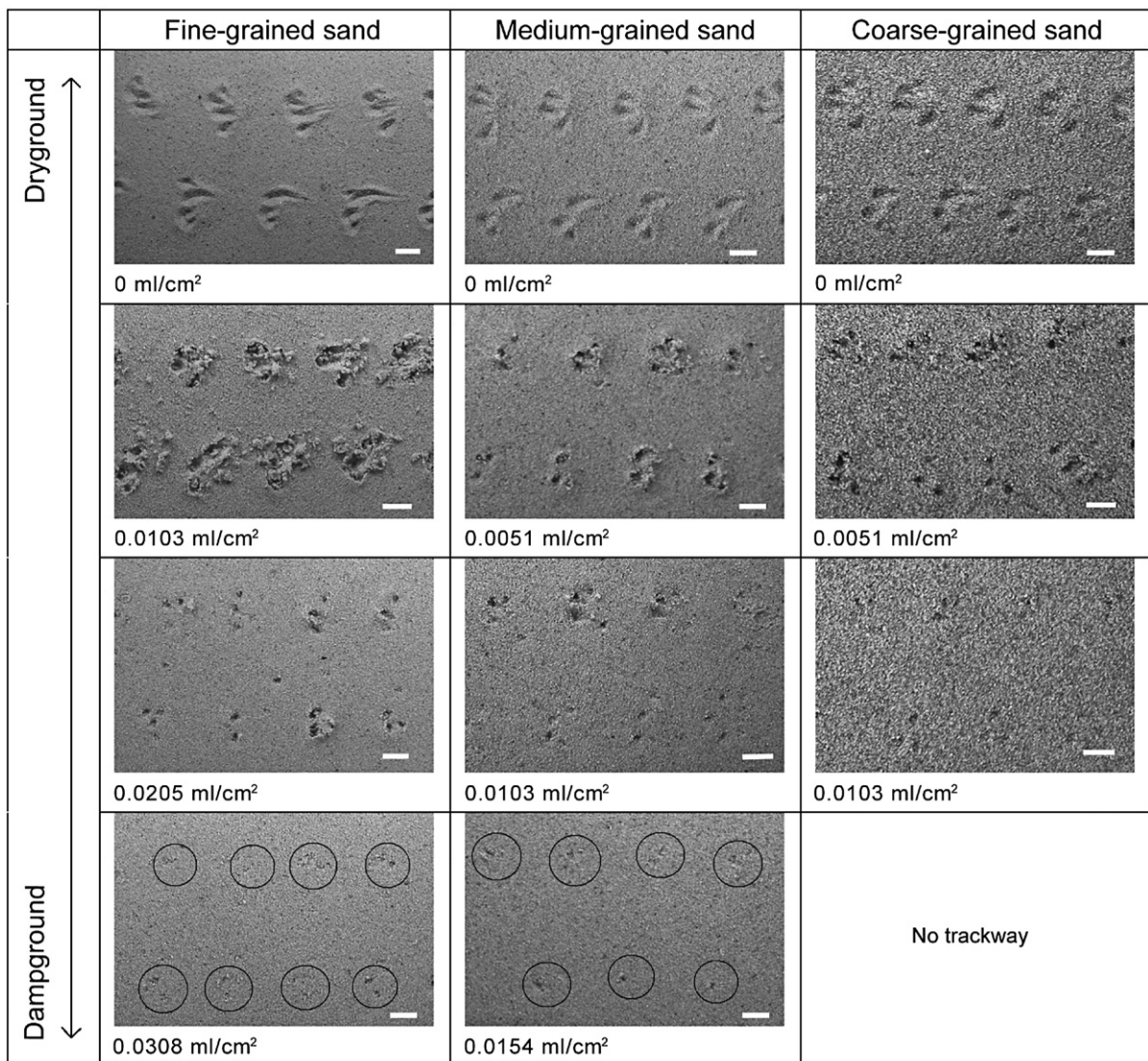

Fig. 7. Subaerial protocol surface moisture taphoseries for the emperor scorpion. The animal was moving from left to right in all cases. Scale bars 10 mm.
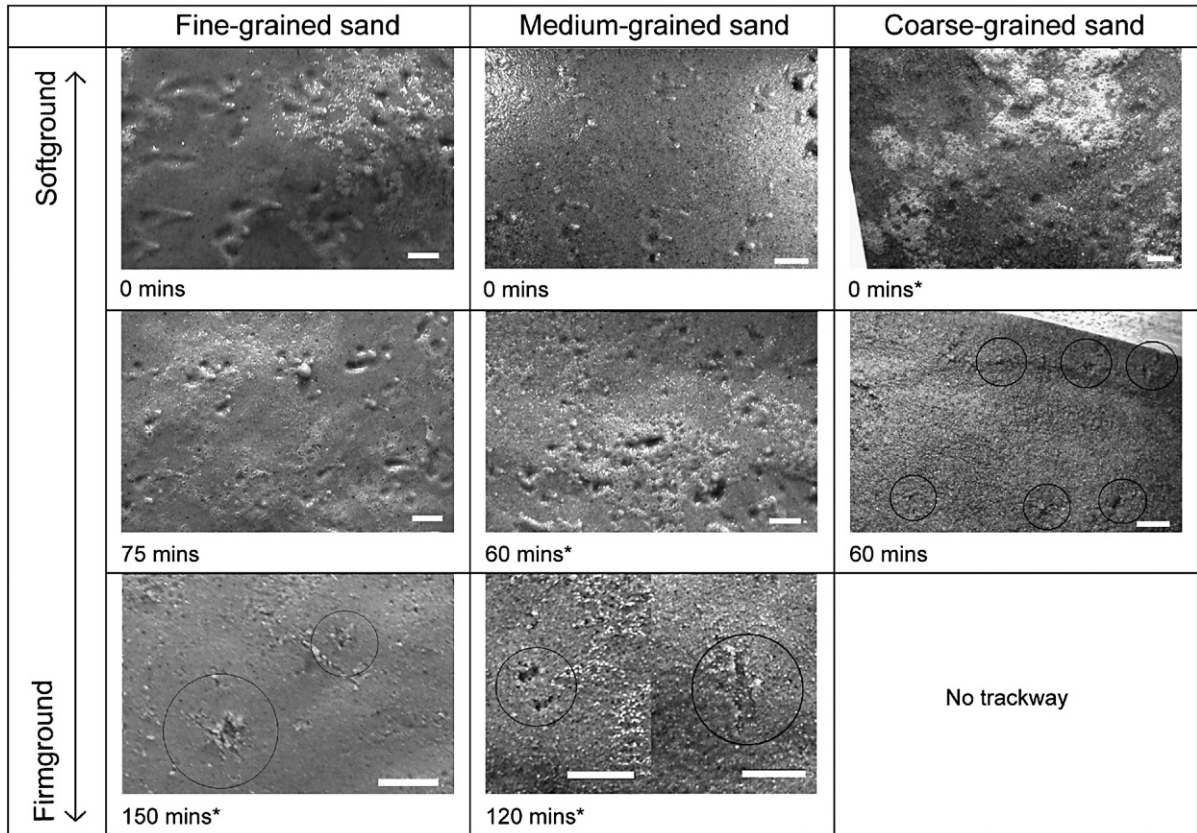
Fig. 8. Transitional subaqueous–subaerial protocol surface moisture taphoseries for the emperor scorpion. The animal was moving from left to right in all cases. Circles highlight tracks. Occasions on which the animal did not cooperate are indicated with *. However, despite failing to obtain a straight trackway, individual track morphologies are evident in these cases. Scale bars 10 mm.

resultant lack of clear trackways, it is difficult to accurately analyse the loss of tracks along the soft to firmground moisture gradient (Fig. 8). On very rare occasions the emperor scorpion produced a medial impression by dragging its postabdomen across the substrate surface, but this was independent of grain size, moisture content or depositional regime.

4.1.3. Chilean rose tarantula trackways

Chilean rose tarantula trackways comprise series of up to four tracks with alternate symmetry. In the subaerial protocol with 0 ml/cm^2 (0 ml) of sprayed on moisture, tracks are circular or elliptical, and often taper in the direction of locomotion in the finer-grained substrates. Series commonly comprise four tracks, but often only three in coarse-grained sand, two of which, produced by the posterior two pairs of limbs, tend to be larger than the others. Regularly spaced, circular imprints with alternating symmetry near the mid-line of the trackway are made by the palps, and crescentic imprints along the mid-line are also occasionally made by the spinnerets (e.g. Fig. 9,

fine-grained sand with 0 ml/cm^2 (0 ml) of sprayed on moisture). Along the dry to dampground moisture gradient, the circular tracks become progressively smaller. Palp imprints are not observed following the introduction of moisture, except for on fine-grained sand where they disappear beyond 0.0077 ml/cm^2 (6 ml) of sprayed on moisture. Spinneret imprints do not form outside of dry conditions. Along the dry to dampground moisture gradient, those tracks produced by the two anterior pairs of limbs are lost first, one after the other and followed by the tracks of the two posterior pairs of limbs (Fig. 9).

In the transitional subaqueous–subaerial protocol at 0 min following siphoning, most tracks are circular, with the occasional track tapering forwards on fine-grained sand and less so on medium-grained sand. There are generally four tracks per series, but this is less common with increased grain size. Palp imprints are observed on fine-grained sand at 0 min following siphoning, but not in other sediments or other stages of drying, and there are no spinneret imprints. Tracks are lost in the same order along the soft to firmground transitional
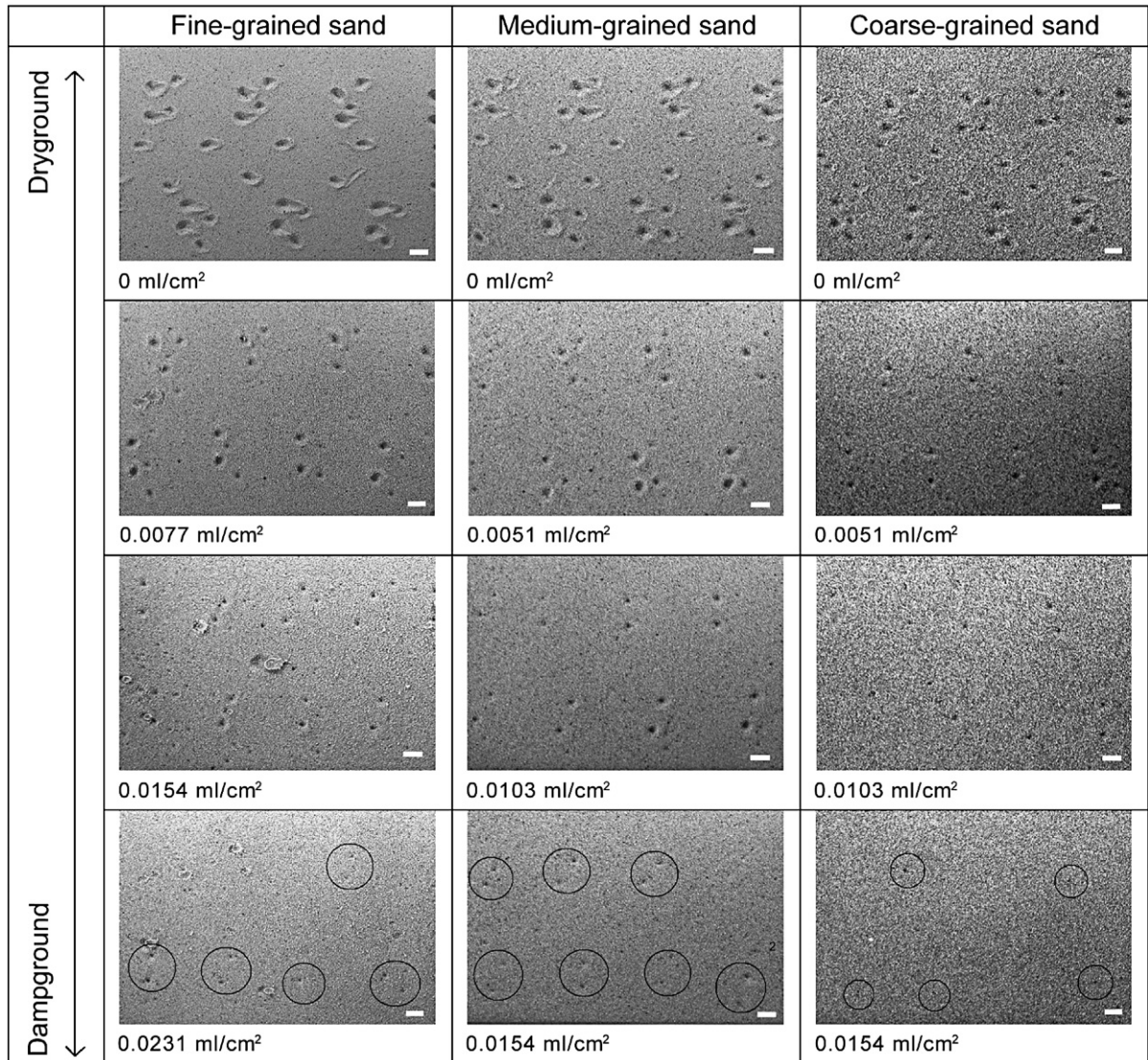
Fig. 9. Subaerial protocol surface moisture taphoseries for the Chilean rose tarantula. The animal was moving from left to right in all cases. Circles highlight tracks. Scale bars 10 mm.

subaqueous–subaerial moisture gradient as in the dry to dampground subaerial moisture gradient. In fine-grained sand after around 135 min following siphoning the only tracks produced are double dots made by the tarsal claws. No tracks are made beyond this point. On medium-grained sand, double dot marks were not observed at the end of the soft to firmground moisture gradient, and on coarse-grained sand the Chilean rose tarantula is only able to make trackways for a very short time following siphoning (<30 min) (Fig. 10).

4.1.4. African giant black millipede trackways

The African giant black millipede produces both track-ways and trails. In the subaerial protocol with 0 ml/cm^2

(0 ml) of sprayed on moisture, individual tracks are hard to discern and two wide parallel grooves form a trail. In fine-grained sand these track rows are wide enough that there is only a small gap (∼ 0.1 mm) between them and they form a "W" shape in cross section, but this is less extreme on medium- and coarse-grained sand. On fine-grained sand, in particular, it is possible to identify distinct chevron marks along the middle of the trail that are produced by the back pair of limbs pinching inwards, which provides a measure of the stride. Along the dry to dampground moisture gradient these trails become track-ways with distinct tracks, although due to the multi-limbed nature of the African giant black millipede, distinct series are not observed due to intense overprinting. At
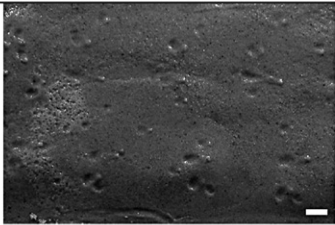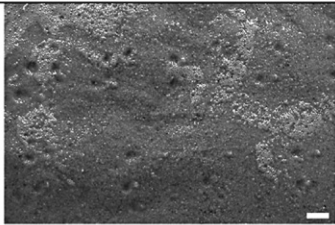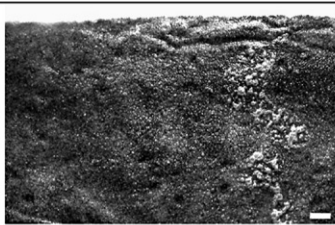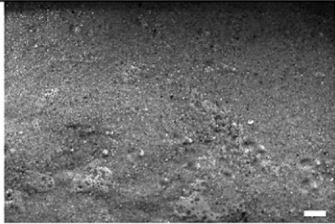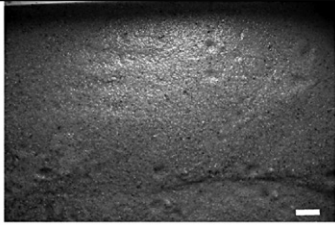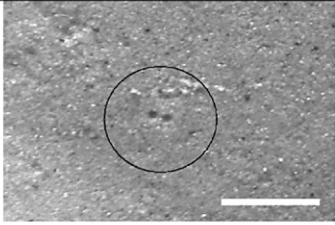
Fig. 10. Transitional subaqueous–subaerial protocol surface moisture taphoseries for the Chilean rose tarantula. The animal was moving from left to right in all cases. Circles highlight tracks. Occasions on which the animal did not cooperate are indicated with *. However, despite failing to obtain a straight trackway, individual track morphologies are evident in these cases. Scale bars 10 mm.

first these tracks are elliptical but grade to being circular (Fig. 11).

In the transitional subaqueous–subaerial protocol, similar morphologies are present at relative stages along a moisture gradient. At 0 min following siphoning, trails form in which individual tracks are unclear. Again, chevron marks along the centre of the trackway are evident giving some indication of the stride of the African giant black millipede. Distinct tracks appear after 60 min following siphoning, and are elliptical at first, but grade into large and then small circles by 180 min following siphoning (Fig. 12). Elliptical tracks

are orientated backwardly oblique or perpendicular to the mid-line of the trackway.

4.1.5. Common woodlouse trackways

The common woodlouse produces both trackways and trails. In the subaerial protocol with 0 ml/cm^2 (0 ml) of sprayed on moisture, the common woodlouse makes trackways on fine- and medium-grained sand, but not on coarse-grained sand. Tracks are elliptical to circular in shape. Trackways comprise two main parallel track rows on either side of the trackway, each of which is composed of an inner and outer line of tracks. The inner

Fig. 11. Subaerial protocol surface moisture taphoseries for the African giant black millipede. The animal was moving from left to right in all cases. Scale bars 10 mm.
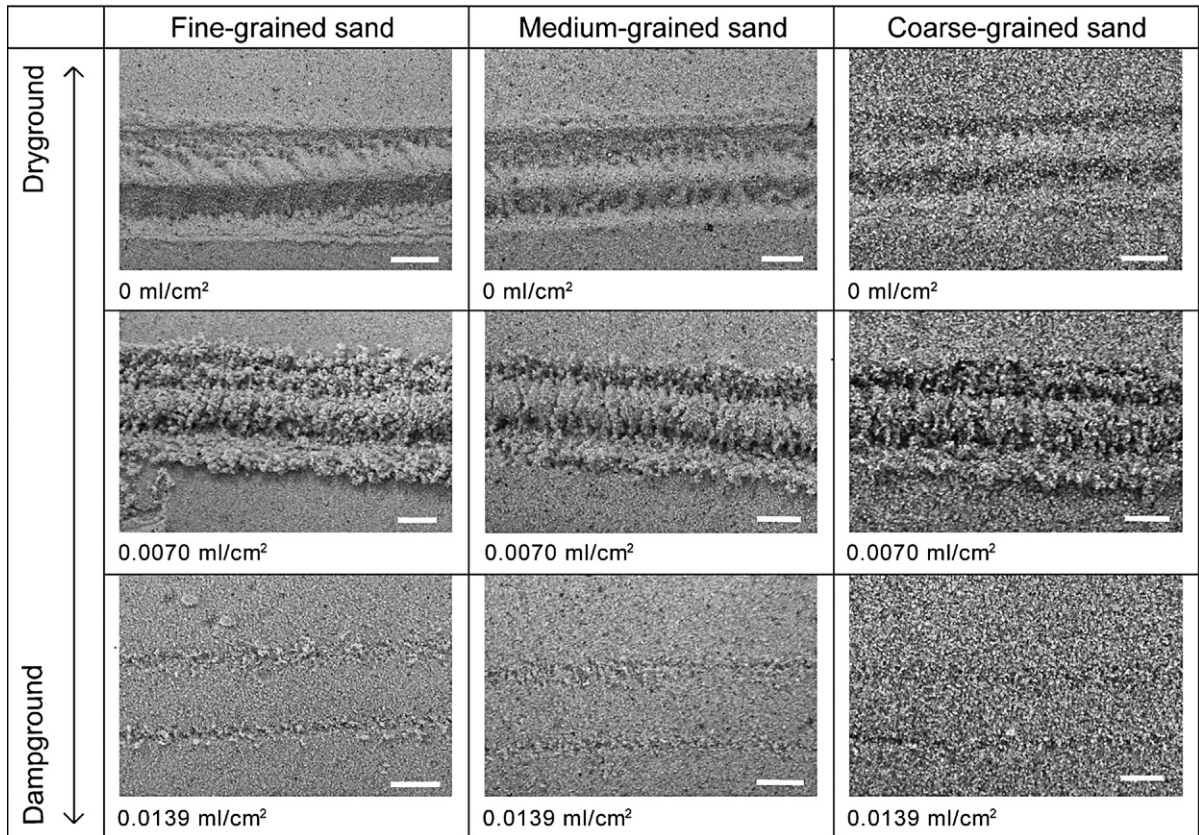
line comprises regularly spaced circular tracks with staggered symmetry. These are made by the posterior pair of limbs and indicate the stride. Between strides, there are three to five tracks in the outer line. The common woodlouse is incapable of producing trackways following the introduction of just 0.0026 ml/cm^2 (2 ml) of sprayed on moisture (Fig. 13).

In the transitional subaqueous–subaerial protocol at 0 min following siphoning a gradation of trackway morphologies is observed across the three grain sizes. In fine-grained sand a continuous broad medial impression produced by the uropods is evident, either side of which are elongate tracks, orientated obliquely backwards. This is less defined on medium-grained sand and the medial impression is narrower. On coarse-grained sand the uropods make a continuous medial impression and tracks are totally absent. At 30 min following siphoning on fine-grained sand, tracks are more elliptical and the two track rows are obviously separated. The uropods no longer make impressions. Tracks are not produced on fine-grained sand beyond 30 min following siphoning, and there is only a very short time period (<30 min)

following siphoning during which the common woodlouse is able to make trackways on medium- and coarse-grained sand (Fig. 14).

4.2. Undertrack fallout

Measurements of moulds from the trackways of 10 individual discoid cockroaches demonstrate that, on average, the deepest track is made by the middle-limb. However, across trackways, there is very little overall difference in the average depths of the hindlimb and forelimb tracks. The overall hindlimb:middle-limb: forelimb track depth ratio is $0.76:1:0.75$ (Fig. 15), although it was noted that within the series of individual trackways, the hindlimb track tended be deeper than the forelimb track or vice versa.

4.3. Trackway survivorship

Increases in sprayed on surface moisture or Kaolin 50 content in fine-grained sand enhanced the survivorship of a trackway when subjected to an air current. The
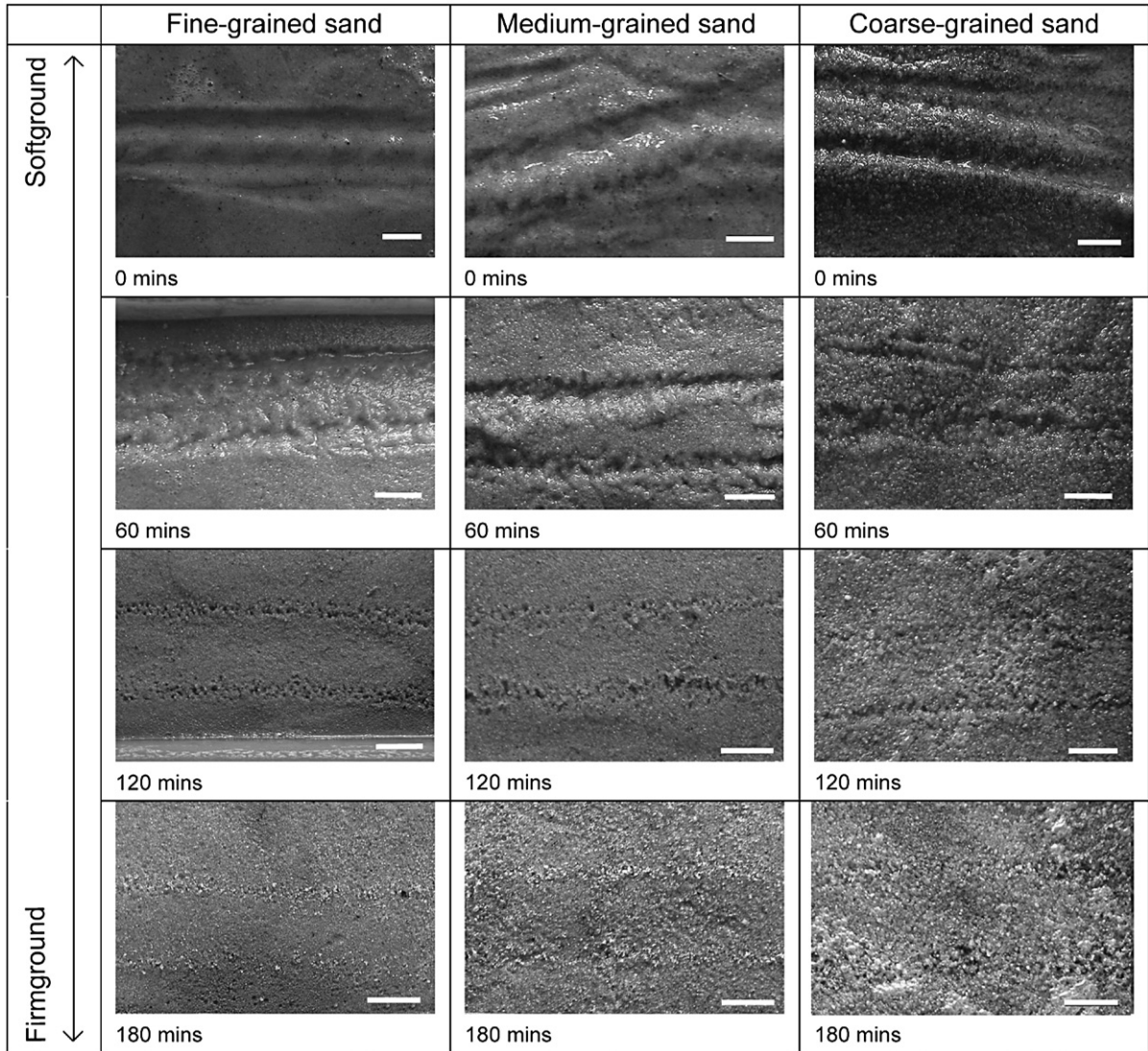
Fig. 12. Transitional subaqueous–subaerial protocol surface moisture taphoseries for the African giant black millipede. The animal was moving from left to right in all cases. Scale bars 10 mm.
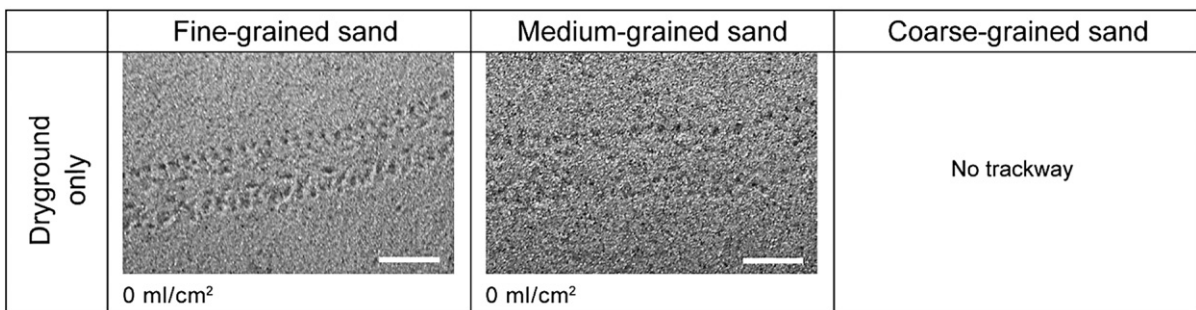

Fig. 13. Subaerial protocol surface moisture taphoseries for the common woodlouse. The animal was moving from left to right in all cases. Scale bars 10 mm.
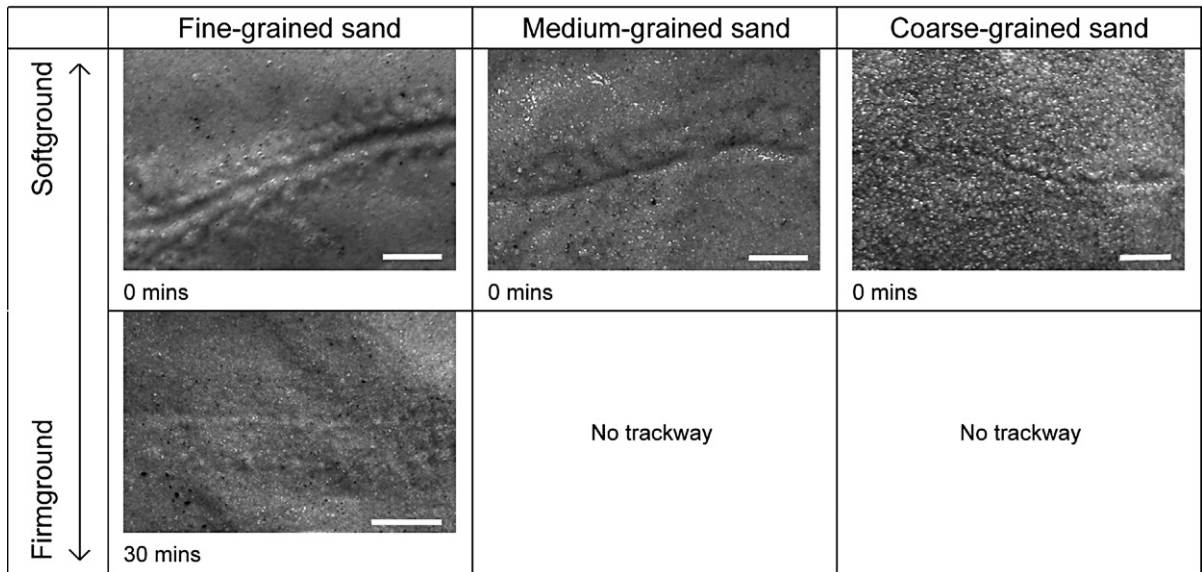
Fig. 14. Transitional subaqueous–subaerial protocol surface moisture taphoseries for the common woodlouse. The animal was moving from left to right in all cases. Scale bars 10 mm.

relationship between the volume of sprayed on surface moisture and the time taken for total trackway degradation is linear (Fig. 16A). Trackways produced in dry fine-grained sand were obliterated after an average of 2 min and 22 s, whilst those produced following spraying of 0.0154 ml/cm^2 (12 ml) of moisture lasted an average of 14 min and 28 s. The relationship between the percentage of Kaolin 50 in the fine-grained sand and the time taken for total trackway degradation is exponential (Fig. 16B). Trackways

Fig. 15. Standardized depths of discoid cockroach tracks. Error bars 95% confidence intervals.

produced in 100% fine-grained sand lasted an average of 2 min and 22 s, but took an average of 1 h, 47 min and 11 s to degrade completely with 4% Kaolin 50 in the substrate. Qualitative observations indicate that, in all cases, the area of the trackway closest to the fan was obliterated first. In cases where moisture had been sprayed on, there was a period of drying before the trackway began to degrade by minimal collapse of the surface at first, followed by the initiation of sand transport. In the experiments with added Kaolin 50, the trackways degraded by the initiation of sand transport. There was no degradation at all after 2 h for trackways produced in fine-grained sand with 0.0051 ml/cm^2 (4 ml) of sprayed on moisture combined with 1% Kaolin 50 in the substrate (i.e. the lowest increments used).

5. Discussion

5.1. Morphological trends in modern arthropod trackways

Similar morphological trends along the dry to dampground and soft to firmground moisture gradients in subaerial and transitional subaqueous–subaerial protocols respectively (i.e. with increasing firmness of the substrate due to sprayed on moisture or time following siphoning), in terms of increased definition of individual tracks and loss of tracks, were observed for all arthropods on all sediment grain sizes. These morphological trends are highlighted herein as "surface
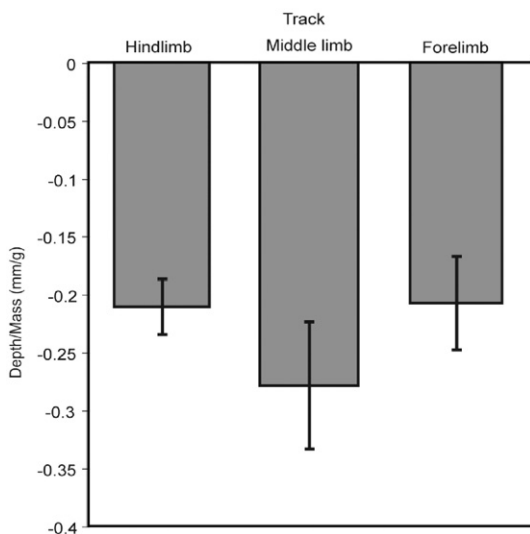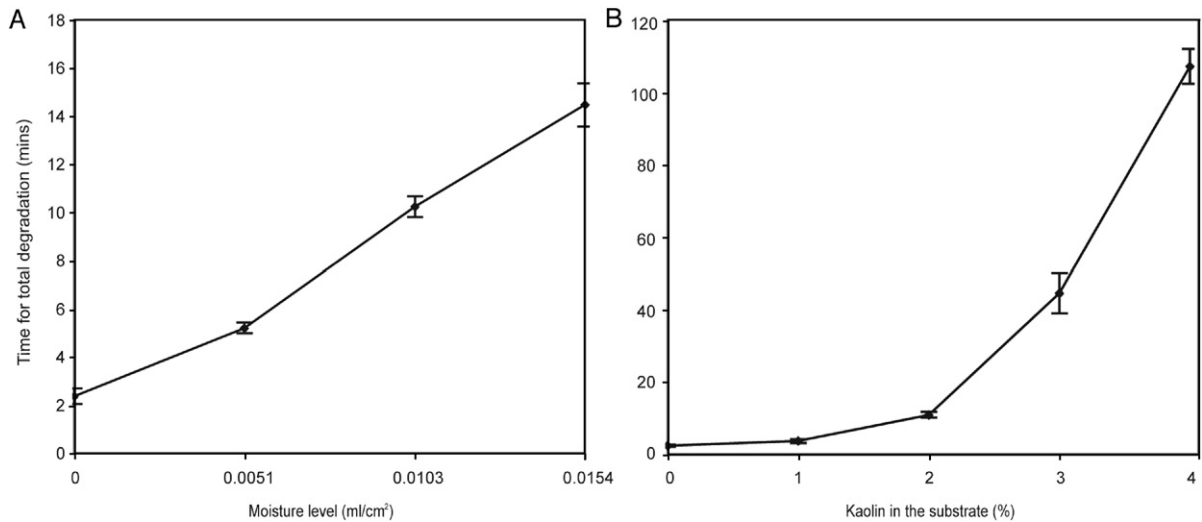
Fig. 16. Factors affecting survivorship of trackways in a fine-grained sand substrate when subjected to a wind speed of 5 m/s. (A) Surface moisture. (B) Kaolin 50 (clay). Error bars 95% confidence intervals.

moisture taphoseries." The concept of taphoseries was first introduced by MacNaughton and Pickerill (1995, 2003) for "theoretical series including ichnotaxa that may potentially be mistaken for each other with increasing taphonomic overprint" (MacNaughton and Pickerill, 1995, p. 160). MacNaughton and Pickerill (1995, 2003) recognized that a range of pre- and post-lithification factors could influence observed trace fossil morphology, and the affect of surface moisture documented herein represents just one of such factors.

These general morphological trends support the work of Sadler (1993), who noted that large, amorphous tracks are produced in dry sand (*cf.* subaerial protocol), whereas tracks become more defined in damp sand. This is quantified herein as a decrease in individual track width (Fig. 4). In the subaerial protocol, the addition of moisture produces a surface crust. Tracks produced by the discoid cockroach and emperor scorpion, with 0.0026–0.0103 ml/cm^2 (2–8 ml) of sprayed on moisture on fine-grained sand, and 0.0026–0.0051 ml/cm^2 (2–4 ml) of sprayed on moisture on medium-grained sand, break through this crust leaving a disrupted surface around the tracks. This is similar to the observations of McKee (1947) and Brand (1979), although beyond these moisture levels the surface is more saturated and sharply defined tracks are formed. The increase in definition with increasing moisture content should not be confused with a scenario whereby the trackway more accurately reflects the anatomy of the producer because increases in sprayed on moisture and time since exposure also lead to loss of tracks, until the trackway production endpoint is eventually reached. For example,

in the subaerial protocol with 0.0051 ml/cm^2 (4 ml) of sprayed on moisture on medium-grained sand, the Chilean rose tarantula produces series of three well-defined circular tracks, but in reality, has four pairs of walking limbs in addition to palps, which all produce larger, poorly-defined tracks and imprints in dry sand (Fig. 9). Similar trends regarding track loss are apparent for the discoid cockroach and emperor scorpion. The same trends are observed in both protocols and with medium- and coarse-grained sand, although they are compressed into a shorter moisture range with increasing grain size.

The order of track loss can be related to the amount of pressure that each limb exerts on the substrate. The observed trackway morphology is therefore a product of both behavioural aspects of arthropod locomotion and the substrate conditions. Cockroaches rest most of their body weight on the middle pair of limbs (Blickhan and Full, 1993). Despite small variations in the angle of pitch of the body as they walk (Ting et al., 1994), individual cockroaches appear to pitch their body more anteriorly or posteriorly (Boggess et al., 2004), resting the majority of the remainder of their weight on either the forelimbs or hindlimbs respectively. This is represented along the dry to dampground and soft to firmground moisture gradients through the initial loss of the tracks made by the forelimb or occasionally the hindlimb (e.g. Fig. 5). Observations of Chilean rose tarantula locomotion identified that the tracks made by the anterior two pairs of limbs are lost first along the dry to dampground and soft to firmground moisture gradients. This is because the tarsi of the posterior two pairs of limbs are twisted into the substrate as it pushes
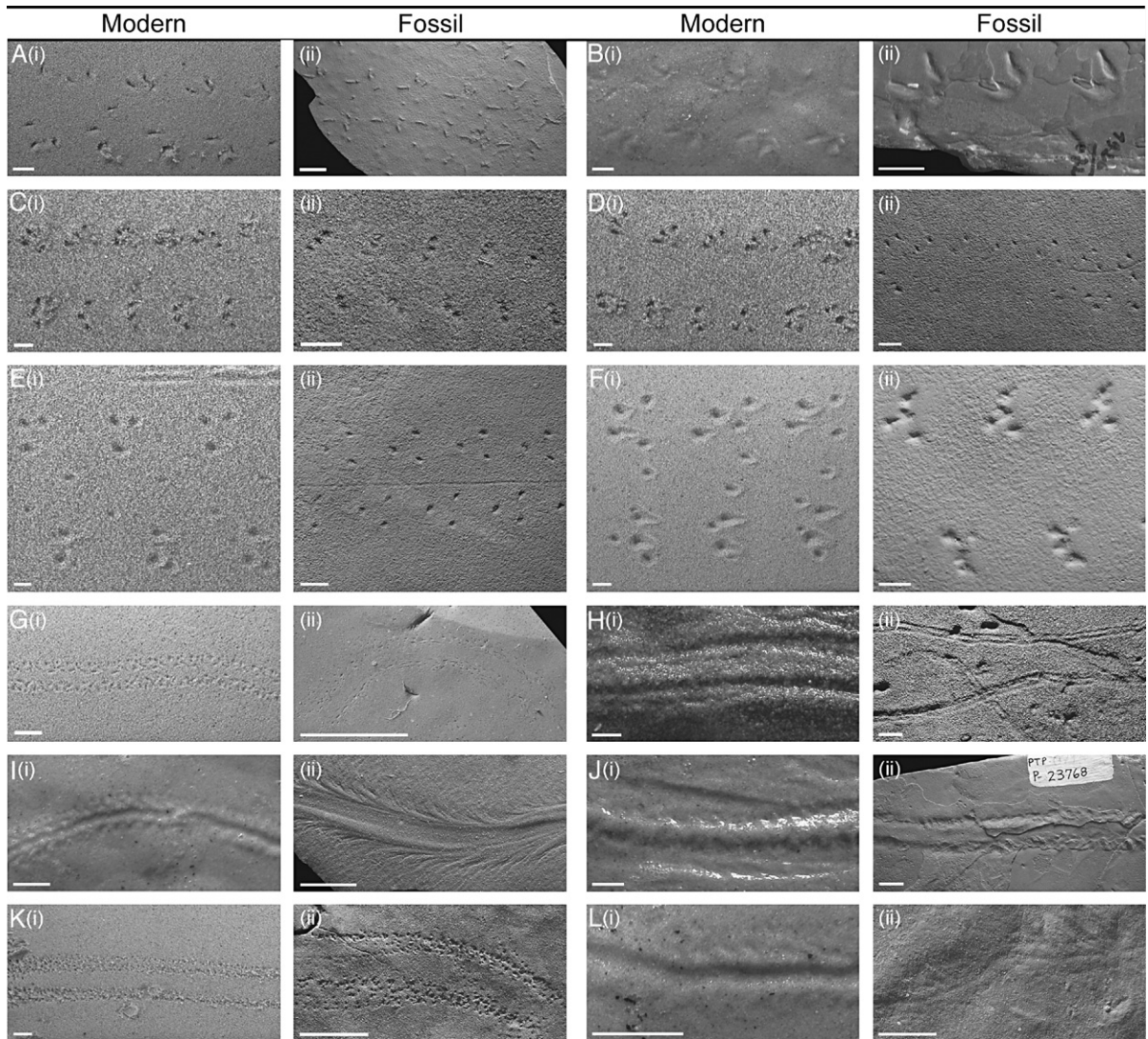
Fig. 17. Comparisons of modern and fossil arthropod trackways and trails. (A) (i) Discoid cockroach trackway on fine-grained sand with 0.0103 ml/cm^2 (8 ml) of sprayed on moisture in the subaerial protocol, (ii) *Lithographus hieroglyphicus* intergrading with '*Hexapodichnus casamiquelai*' (Mainz Naturhistorisches Museum, Germany) MNHM 1926/74. (B) (i) Discoid cockroach trackway on medium-grained sand at 0 min following siphoning in the transitional subaqueous–subaerial protocol, (ii) *L. hieroglyphicus* intergrading with '*Permichnium bidirectum*', MNHM 1926/672. (C) (i) Emperor scorpion trackway on coarse-grained sand with 0.0051 ml/cm^2 (4 ml) of sprayed on moisture in the subaerial protocol, (ii) *Paleohelcura tridactyla* (Museum of Northern Arizona), MNA N3702. (D) (i) Emperor scorpion trackway on medium-grained sand with 0.0051 ml/cm^2 (4 ml) of sprayed on moisture in the subaerial protocol, (ii) *P. tridactyla* intergrading with '*P. dunbari*', MNA N3691. (E) (i) Chilean rose tarantula trackway on coarse-grained sand with 0 ml/cm^2 (0 ml) of sprayed on moisture in the subaerial protocol, (ii) holotype '*P. dunbari*', MNA N3660. (F) (i) Chilean rose tarantula trackway on medium-grained sand with 0 ml/cm^2 (0 ml) of sprayed on moisture in the subaerial protocol, (ii) cast of holotype *Octopodichnus raymondi*, MNA N9391. (G) (i) Common woodlouse trackway of fine-grained sand with 0 ml/cm^2 (0 ml) of sprayed on moisture in the subaerial protocol, (ii) *Diplichnites* isp. (New Mexico Museum of Natural History and Science), NMMNH P46848. (H) (i) African giant black millipede trail on coarse-grained sand at 0 min following siphoning in the transitional subaqueous–subaerial protocol, (ii) holotype *Diplopodichnus biformis*, MNA N3657. (I) (i) Common woodlouse trail on fine-grained sand at 0 min following siphoning in the transitional subaqueous–subaerial protocol, (ii) *Dendroidichnites irregulare* NMMNH P24158. (J) (i) African giant black millipede trail on medium-grained sand at 0 min following siphoning in the transitional subaqueous–subaerial protocol, (ii) *D. biformis* trail intergrading with *Diplichnites* isp. with tracks, NMMNH P23768. (K) (i) African giant black millipede trackway on fine-grained sand with 0.0139 ml/cm^2 (16 ml) of sprayed on moisture in the subaerial protocol, (ii) *Diplichnites* isp., NMMNH P37474. (L) (i) Common woodlouse trail on fine-grained sand at 0 min following siphoning in the transitional subaqueous–subaerial protocol, (ii) *Diplichnites* isp. with a continuous medial impression with tracks to impressions on either side, NMMNH P23324. Scale bars 10 mm.

itself forwards, which results in two large tracks, whereas the tarsi of the anterior two pairs of limbs have a less forceful action on the substrate, producing smaller tracks. Unfortunately, it was more difficult to associate particular tracks with the corresponding limb in the emperor scorpion.

The loss of tracks in multi-limbed arthropod trackways cannot be observed easily due to overprinting and the fact that the majority of limbs place similar amounts of pressure on the substrate. The African giant black millipede places least pressure on the substrate with its anterior few pairs of limbs, which are often used in conjunction with the antennae in a more sensory role and rarely touch the substrate. Similarly, the posterior pair of limbs rarely touches the surface unless it is soft enough such that the animal is dragging itself through the substrate (e.g. Fig. 11, dry subaerial protocol where the posterior pair of limbs produces chevron marks as they pinch inwards). However, the remaining limbs have the same digitigrade stance and place equal pressure on the substrate. The only time a loss of tracks is truly seen is when the trackway production endpoint is reached. This is observed for the common woodlouse, but not the African giant black millipede, which was too heavy, with too much resultant pressure per limb, to stop producing tracks at the maximum moisture range used in this investigation.

5.2. Comparisons with fossil arthropod trackways

Many of the trackways produced in this study bear a strong resemblance to those in the fossil record (Fig. 17). The discoid cockroach produced trackway morphologies resembling examples of *Lithographus hieroglyphicus* Hitchcock, 1858, '*Hexapodichnus casamiquelai*' de Valais et al., 2003 and various ichnospecies of '*Permichnium*' (Guthörl, 1934; Walter, 1983) from the Lower Permian Standenbühl Formation of the Saar-Nahe Basin in Germany (Fig. 17A–B), and it is likely that many pterygote insects would produce similar morphologies, with only slight variation due to differences in their body plans. Intergradations between these morphologies were observed within individual modern trackways and also occur in the fossil trackways (Minter et al., in press).

The emperor scorpion and Chilean rose tarantula both produce trackways resembling *Paleohelcura tridactyla* Gilmore, 1926 and '*P. dunbari*' Brady, 1961 (Fig. 17C–E). The Chilean rose tarantula also produces trackways with series arrangements that sometimes resemble *Octopodichnus raymondi* Sadler, 1993 (Fig. 17F), as can the emperor scorpion (Fig. 17D(i)),

although palp imprints are not present in the fossil specimens of *O. raymondi*. Interestingly, morphologies such as *O. didactylus* Gilmore, 1927 and *O. minor* Brady, 1947 are not produced. These morphologies are therefore unlikely to be a consequence of substrate conditions, and are probably related to the behaviour or body plan of the producer. The neoichnological experiments herein, and those of Brady (1947) and Sadler (1993), demonstrate intergradation between *P. tridactyla* and '*P. dunbari*' within individual trackways; and the same is also observed in some fossil trackways (e.g. Fig. 17D).

The African giant black millipede produces numerous variations on *Diplichnites* Dawson, 1873 (Fig. 17H, J–K). For example, beyond 0.0070 ml/cm^2 (8 ml) of sprayed on moisture in the subaerial protocol, and beyond 60 min following siphoning in the transitional subaqueous–subaerial protocol, there are numerous similar, but slightly differing trackway morphologies, which all show two rows of close, short tracks, diagnostic of *Diplichnites*. The common woodlouse also produces similar trackway morphologies to *Diplichnites*, despite being much smaller. Similar fossil examples occur from the Lower Permian Choza Formation of Texas (Minter et al., 2007; Fig. 17G). In the transitional subaqueous–subaerial protocol at 0 min following siphoning, the African giant black millipede produces trails consisting of two parallel grooves, similar to *Diplopodichnus* Brady, 1947 from the Lower Permian Coconino Sandstone of Arizona (Fig. 17H). Some of these trails in fine- and medium-grained sand also have a chevroned central region similar to *Dendroidichnites* Demathieu et al., 1992 (Fig. 12). At 0 min following siphoning the common woodlouse also produces trails resembling *Dendroidichnites* in fine- and medium-grained sand (Figs. 14, 17I(i)). The African giant black millipede also produces *Dendroidichnites*-like trails in the dry subaerial protocol (Fig. 11). Similar *Dendroidichnites*-like fossil examples occur from the Lower Permian Robledo Mountains Formation of New Mexico (Fig. 17I(ii)). Examples of *Diplopodichnus*-like trails with some tracks are also observed in both the modern and fossil material (Fig. 17J). Whilst moving across the prepared substrate, the African giant black millipede often moved from side to side at its anterior end whilst sensing the environment ahead and this lateral undulation could travel down the length of the body as it progressed. This resulted in some sections of the track rows being wider and comprising many more tracks across their widths at certain points (e.g. subaerial protocol with fine-grained sand and 0.0139 ml/cm^2 (16 ml) of sprayed on moisture), which is very
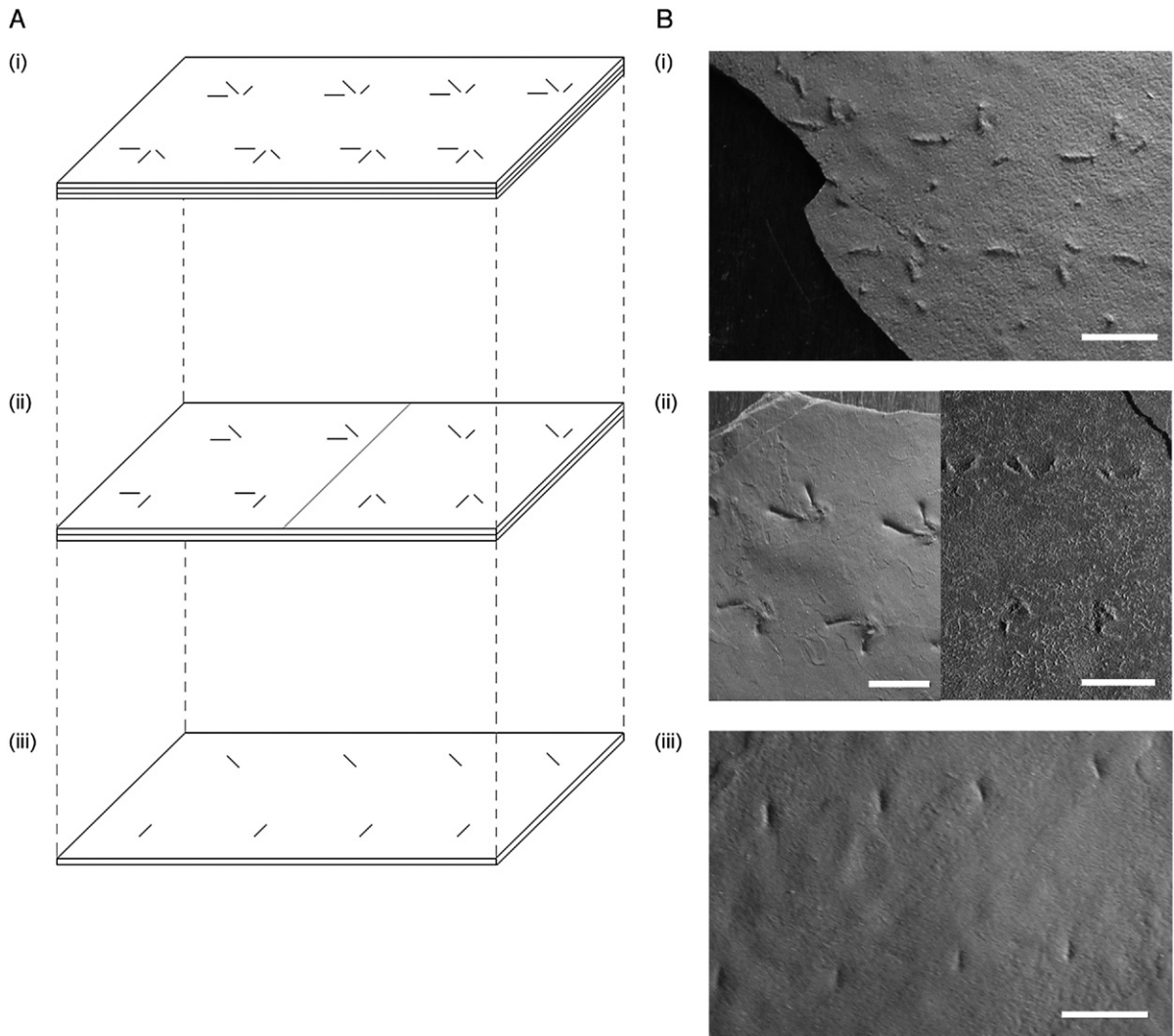
Fig. 18. Undertrack fallout from an insect trackway. (A) A theoretical undertrack taphoseries from a discoid cockroach surface trackway: (i) Surface trackway with fore, middle and hindlimb tracks, (ii) Loss of forelimb (left) or hindlimb (right) tracks, (iii) Loss of fore and hindlimb tracks. (B) Fossil trackways resembling layers of an undertrack taphoseries: (i) *Lithographus hieroglyphicus* intergrading with '*Hexapodichnus casamiquelai*', MNHM 1926/74, (ii) '*Permichnium bidirectum*', MNHM 1945/266 (left) and '*Permichnium völckeri*', SSN 11 N102 (right), (iii) *Diplichnites*-like variant of *Lithographus*, MNHM 1945/1253. Scale bars 10 mm.

similar to a trackway from the Lower Permian Clear Fork Formation of Texas (Fig. 17K). One trail of particular interest is produced by the common woodlouse at 0 min following siphoning on coarse-grained sand in the transitional subaqueous–subaerial protocol (Fig. 14). Here only the uropods make an impression, and the trail looks superficially like invertebrate grazing trails such as *Helminthoidichnites* Fitch, 1850. Some of these modern trails also have faint impressions and tracks on either side of the medial impression and are similar to a trackway from the Lower Permian Robledo Mountains Formation of New Mexico (Fig. 17L).

5.3. Consequences of undertrack fallout

The phenomenon of undertrack fallout (Goldring and Seilacher, 1971) can influence observed trackway morphology, and can be considered as an example of a taphoseries. The loss of tracks in the theoretical undertrack taphoseries, produced by measuring the depths of discoid cockroach tracks, mimics that observed for the surface moisture taphoseries. The order of track loss can be related to the amount of pressure that each limb applies to the substrate, so it is perhaps not surprising that the same trends are observed.

The predicted undertrack morphologies are very similar to some fossil trackways from the Lower Permian of Germany (Fig. 18). Surface trackways, with three tracks per series, strongly resemble *Lithographus hieroglyphicus* and/or '*Hexapodichnus casamiquelai*' (Figs. 18A(i), B(i)). At deeper levels, either forelimb or hindlimb tracks are lost first, resulting in '*Permichnium bidirectum*' Walter, 1983 or '*Permichnium völckeri*' Guthörl, 1934 morphologies respectively (Figs. 18A(ii), B(ii)). At the point where both forelimb and hindlimb tracks are lost, the morphology of the trackway becomes *Diplichnites*-like (Figs. 18A(iii), B(iii)), although there is a large separation between tracks and obvious alternate symmetry, unlike in true *Diplichnites* specimens.

5.4. Factors involved in trackway survivorship

Various hypotheses for factors that enhance trackway survivorship and preservation potential, particularly in aeolian settings, have been proposed. McKee (1947) and Sadler (1993) suggested that moisture contributed to trackway survivorship, stabilizing the trackway surface so that it could be buried; whilst Loope (1986) and McKeever (1991) suggested that clay minerals contributed to trackway survivorship. The results of the experiments carried out herein demonstrate that increasing moisture content has a linear affect (Fig. 16A), whilst increasing the clay mineral content has an exponential affect (Fig. 16B) on the survivorship of a trackway subjected to an air current in a subaerial environment. Trackways produced on substrates with both moisture and clay minerals are highly resistant to any morphological distortion when subjected to a wind speed of 5 m/s.

Surface moisture weakly cements individual sand grains together (Walker and Harms, 1972), maintaining the trackway in its original morphology, but once the moisture has evaporated, the sand becomes loose and is rapidly blown away. Conversely, clay minerals are a more permanent component and make the substrate cohesive due to electrostatic charges (Nichols, 1999). The more clay that is in the substrate, the more cohesive the substrate will become and the more resistant to degradation any trackways made in that substrate will be. Loope (1986) noted that 4% clay was sufficient to maintain the original morphology of mammal tracks without the need for moisture, and the results of this study demonstrate that such concentrations provide resistance to degradation when subjected to a wind speed of 5 m/s for over 100 min. When clay and water are both introduced, even in small amounts, the effect of cohesion is enhanced (Nichols, 1999), and is the likely cause of such prolonged survivorship.

Fossil examples of those trackways produced in the dry subaerial protocol are rare, and are perhaps a consequence of a mist or dew settling onto a "dry" trackway and preserving it long enough for more sand to settle on top without causing it to degrade (McKee, 1947; Sadler, 1993). Some of the morphologies observed in the dry subaerial protocol do resemble some fossil trackways, such as the '*Permichnium*-like' trackways with poorly defined tracks produced by the discoid cockroach (Fig. 5), and *Octopodichnus raymondi* track arrangement in Chilean rose tarantula trackways (Fig. 9). However, evidence of the anatomical features that only make imprints in dry conditions is very rare in fossil trackways. Imprints made by cerci of cockroaches (and other insects), and the palps and spinnerets of spiders have not been positively identified in the fossil record.

5.5. Interpreting producers

Producers are rarely found at the end of their trace fossils (Abel, 1935) and so the majority of producer attributions are interpretations. Producers can sometimes be assigned on the basis of comparative morphology between trace fossils and body fossils, but the degree of confidence with which this can be done varies depending on the distinctiveness and complexity of the trace fossil morphology in question (e.g. Walker et al., 2003). Neoichnology provides a particularly useful approach for relating producers to fossil trackways and subsequent palaeoecological reconstructions. Neoichnological studies sometimes have unexpected results such as the observation that limulids can produce *Nereites*-like traces, in contrast to the more traditional viewpoint of vermiform animals being the culprits (Martin and Rindsberg, 2006).

The results presented herein demonstrate that one producer can generate several different trackway morphologies due to variations in substrate conditions and behaviour, and equally different producers can generate similar trackways; which is in agreement with previous arthropod neoichnological studies (e.g. Brady, 1947; Sadler, 1993). In those arthropods that produce discrete trackway series, loss of tracks, or change in their morphology along a moisture gradient can lead to similar trackways being produced by different arthropods. This is most evident with the emperor scorpion and Chilean rose tarantula trackways, where similar track morphologies and series arrangements are produced (Figs. 7–10). Brady (1947) and Sadler (1993) both produced *Paleohelcura* trackways, but with different scorpion species. This study highlights that it

is not just scorpions that are capable of producing *Paleohelcura*. Many of the Chilean rose tarantula trackways are more reminiscent of *Paleohelcura* than *Octopodichnus*, and both can produce a variation of *Paleohelcura* consisting of two tracks per series (Figs. 7–10). Similarly, trackways of different multi-limbed arthropods can resemble each other. For example, despite the size difference, the common woodlouse trackway produced after 30 min following siphoning in the transitional subaqueous–subaerial protocol on fine-grained sand (Fig. 14) is superficially like that of the African giant black millipede produced after 60 min following siphoning (Fig. 12). The medial impressions produced by the uropods of the common woodlouse indicate that medial impressions may not always be produced by an elongate tail or abdominal feature. *Helminthoidichnites* is typically attributed to worms grazing or insect larvae (Buatois et al., 1997), but insects have previously been noted to make similar traces (Metz, 1987) and the evidence presented herein suggests that isopods are also capable of producing such traces in waterlogged coarse-grained sand.

These results highlight the need for a cautious approach to interpreting the producers of fossil trackways. An understanding of the trackways, and the variation therein, of modern arthropods will facilitate palaeoecological reconstructions based on trace fossils. The results of these experiments also demonstrate that the mass of an arthropod influences the range of moisture levels and sediment grain sizes on which it can produce trackways; heavier arthropods produce trackways across a greater moisture range and the time frame for trackway production is also greater. In the subaerial protocol, continuous spraying of moisture produces a surface crust, as noted by Brady (1947) and Sadler (1993), which becomes progressively harder to deform or break. Consequently, heavier arthropods can produce trackways further along a moisture gradient than lighter arthropods. Similarly, in the transitional subaqueous–subaerial protocol, the substrate hardens as it dries, becoming progressively more difficult to make trackways on, and so heavier arthropods will be able to produce trackways for a greater time period. The African giant black millipede also produced the same trackway morphologies at the same moisture levels regardless of grain size (Figs. 11–12), hinting at a threshold whereby producer mass becomes too large for grain size to have a significant affect on trackway morphology. Additionally, this study has shown that on coarse-grained sand, the common woodlouse cannot produce trackways in the subaerial protocol (Fig. 13), indicating a grain-size threshold above which arthro-pods of certain mass do not produce trackways. It has previously been suggested that trackways are useful for determining diversity and relative abundance of track-makers (e.g. Lockley, 1986), although unless this concerns large animals such as dinosaurs, caution is advised for such interpretations. This study shows that there is a bias towards heavier arthropods, which can produce trackways across greater moisture gradients (Fig. 3). Where arthropods are too light to produce trackways, because the grain size or substrate firmness were too great, it does not necessarily mean that they were not present in such ancient environments, rather they just never left their mark.

5.6. Palaeoenvironmental inferences

Neoichnology also facilitates palaeoenvironmental inferences. The trace (trackway or trail) morphologies documented herein can be used to infer the moisture level of the substrate in subaerial depositional settings, or the time of trace production after a surface was exposed in transitional subaqueous–subaerial settings. For example, the difference between the African giant black millipede trail at 0 min following siphoning on fine-grained sand in the transitional subaqueous–subaerial protocol and the trackway 120 min later (Fig. 12), provides evidence that *Dendroidichnites* trails and *Diplichnites* trackways can be used to distinguish between soft and firmground substrates in ancient depositional environments. It should be noted that the times following exposure and surface moisture levels should not be taken as absolute values, but as a relative scale because the different trace morphologies produced are also dependent on the environmental temperature and mass of the producer. This is particularly useful where different morphologies of essentially the same traces are found together on single bedding planes. Comparing these to the surface moisture taphoseries of different arthropods presented herein enables inferences on the relative substrate moisture levels when the traces were produced, which can facilitate reconstructions of surface colonization sequences (e.g. Buatois et al., 1997). Here, using arthropod trackways, the soft to firmground gradation corresponds to the moisture gradient in the transitional subaqueous–subaerial protocol, which can be related to depositional environments such as tidal flats and floodplains (Figs. 6, 8, 10, 12, 14). Additionally a "dryground to dampground" gradation is proposed herein for the subaerial protocol, which corresponds to depositional settings such as aeolian dunes (Figs. 5, 7, 9, 11, 13). It is often the case that one fossil trackway morphology can grade into another (e.g.

Johnson et al., 1994) and in such cases it is possible to infer that an arthropod was moving from one substrate moisture level to another, which may be interpreted as representing movements between land and water, or from water margin to more distal areas.

5.7. Utility of neoichnology in ichnotaxonomy

Neoichnology is a useful tool in ichnotaxonomy, providing an approach for investigating the processes that can result in morphological variation in trackways. As demonstrated herein, neoichnology can be used to systematically investigate the affect of substrate conditions, such as grain size, moisture content and depositional regime, as well as undertracking, on trackway morphology. The affect of producer behaviour on resultant trackway morphology can also be investigated through observations during the production of individual trackways. This can enable the identification of the features of trackways and other trace fossils that are least affected by such variation, and consequently lead to the selection of the most informative ichnotaxobases when diagnosing new ichnotaxa (Minter et al., in press). Neoichnology can also be used to highlight potential synonymies whereby minor morphological variation results from minor behavioural or preservational variation, although the justification for synonymy of arthropod trackway ichnotaxa should be restricted to intergrading fossil specimens (Minter et al. in press).

Individual trackways produced by discoid cockroaches demonstrate that a variety of morphologies of existing ichnotaxa such as *Lithographus hieroglyphicus*, '*Hexapodichnus casamiquelai*' and various ichnospecies of '*Permichnium*' can occur within individual trackways. The co-occurrence of *L. hieroglyphicus* and '*H. casamiquelai*' within individual discoid cockroach trackways demonstrates that these different morphologies can arise from minor behavioural variation in terms of the placement of the limbs. A similar scenario occurs in the emperor scorpion trackways whereby both *Paleohelcura tridactyla* and '*P. dunbari*' occur within the same trackway, which can be attributed to minor behavioural variation in terms of the gait parameters. *L. hieroglyphicus* and various ichnospecies of '*Permichnium*' also occur within individual discoid cockroach trackways, which highlights that these different morphologies can result from minor preservational variations, such as substrate moisture content. Undertrack fallout can also result in '*P. völckeri*' and '*P. bidirectum*' morphologies following an original *Lithographus* trackway.

6. Summary

Comprehensive systematic neoichnological investigations were conducted using a range of modern terrestrial arthropods, representing a range of body forms and higher taxa, under subaerial and transitional subaqueous–subaerial experimental protocols, which simulate aeolian and tidal flat or floodplain environments respectively. The results of these experiments demonstrate a change in the morphology of arthropod trackways along a dry to dampground or soft to firmground moisture gradient, due to increasing firmness of the substrate, which can be represented as a "surface moisture taphoseries". General features include a decrease in track width (or width of the track row for multi-limbed arthropods) and a loss of tracks within series. The moisture level has a greater affect than grain size on resultant trackway morphologies. Surface moisture taphoseries are very similar in the subaerial and transitional subaqueous–subaerial protocols. The morphological trends are compressed into shorter moisture ranges with increasing sediment grain size.

Many modern arthropod trackways produced herein are very similar to those in the fossil record, although this requires careful interpretation. It is important to be aware that there may be multiple producers of single trackway morphologies. There are also potential biases towards heavier arthropods in palaeoecological reconstructions because they can produce trackways across a greater moisture and grain size range. Neoichnology demonstrates that certain trackway and trail morphologies can be related to substrate moisture content at the time of production, which can facilitate palaeoenvironmental inferences, reconstructing colonization sequences, and movements relative to water margins.

The phenomenon of undertrack fallout can influence observed trackway morphologies, and the loss of tracks in the undertrack taphoseries for the discoid cockroaches mimics that of the surface moisture taphoseries. The sequence of track loss can be related to the posture and resultant pressure exerted by the different limbs. Survivorship of trackways subjected to an air current in a subaerial depositional environment is enhanced exponentially by increasing the clay content of a sand substrate, whereas increasing the moisture level of the substrate surface enhances trackway survivorship linearly. The combination of small amounts of clay and moisture results in trackways being highly resistant to any degradation. It is unlikely that trackways formed in pure dry sand will survive into the fossil record, thus explaining why such morphologies are so rare. Neoichnology provides a particularly useful approach for

understanding the substrate-related and behaviourally-related factors involved in minor morphological variation within and between trackways and is therefore a useful tool in ichnotaxonomy. The results of this investigation are fundamental to the study of fossil arthropod trackways.

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