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Fossil Focus: Stepping through time with tetrapod trace fossils

by Hannah C. Bird

Introduction:

Ichnology is the study of trace fossils, the physical evidence for the activities of organisms that lived millions of years ago. Trace fossils depict activities such as walking, resting, feeding and burrowing, which can be represented by tracks ranging from recognizable large footprints to long, grooved trails (Fig. 1). One organism can be responsible for multiple trackways: for example, the extinct invertebrate arthropods called trilobites are known to have produced the burrowing trace *Cruziana* as well as the resting trace *Rusophycus*.

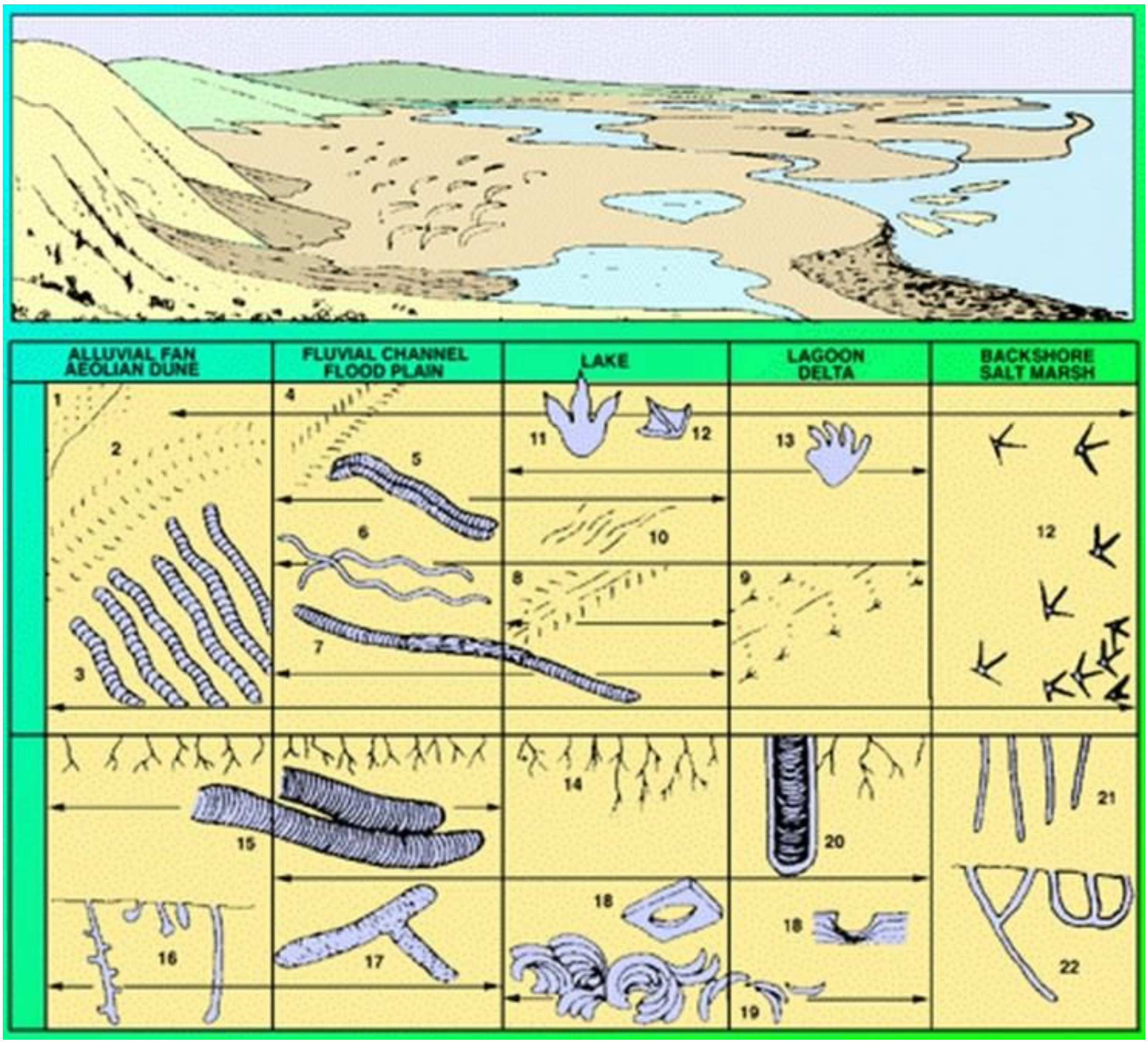

Figure 1 — Examples of trace fossils preserved in non-marine environments (after Bromley, 1996), including scorpion trackways (1), crustacean burrows (5; *Cruziana problematica*), arthropod trackways (8, 9), fish swimming traces (10), reptile tracks (11), amphibian tracks (13) and insect burrows (16, 17).

This field of study supplements the fossil record from preserved skeletons and soft tissue, allowing us greater insights into the lifestyles of ancient organisms and the environments they lived in. In particular, ichnology is known to be important when considering the footprints from tetrapods (extinct and living reptiles, amphibians and mammals with four limbs), which can enhance sparse records of skeletal material in the geological past. This article will focus on footprints from amphibians and reptiles, including some that are particularly abundant from the Carboniferous and Permian periods (356 million to 252 million years ago) of what is now Great Britain.

Globally, tetrapod footprints can be found in Nova Scotia in Canada, New Mexico in the United States, and numerous sites in Germany, Italy, France, Spain, Poland, Morocco and Argentina. Many types of footprints can be found across Europe and North America; these include the tracks that have been named *Amphisauropus*, *Dimetropus*, *Dromopus*, *Hyloidichnus*, *Ichniotherium* and *Limnopus (Limnopus)*, along with its smaller morph *Limnopus (Batrachichnus)*.

Key terminology

- Ichnite: fossilized footprint, including actual footprints, trackways and trails.
- Ichnotaxon (plural ichnotaxa): the name given to a particular fossil footprint, usually defined as ichnogenus followed by ichnospecies (see below).
- Ichnogenus and ichnospecies: ichnotaxa can be classified in a similar way to organisms, with Latin names for a genus and species. For example, in the trilobite burrowing trace *Cruziana problematica*, *Cruziana* is the ichnogenus and *problematica* is the ichnospecies.
- Manus: forefoot of a tetrapod (the 'hand').
- Pes: hindfoot of a tetrapod (the 'foot').
- Ichnofacies: a collection of trace fossils that can be used to get an idea of past environmental conditions, such as water depth, current energy, salinity and oxygenation.

Formation: making a fossil

Footprints are best preserved in soft mud or sand near to a body of water, with moist sediment enabling the particles to stick together and maintain the shape of the footprint. The imprint must be quickly covered by sediment to fill it in and preserve the impression before it can be eroded by water or wind. If the infilling sediment has different properties from the sediment the footprint is in — for example, if mud fills a sand mould — this can help to differentiate the impression. With time, burial and compaction from overlying sediment allow prints to be preserved along the bedding planes of rocks.

Methodology: if those feet could talk

Sometimes, when out in the field exploring geology, we can stumble on trace fossils. At other times, we search through literature to find particular rock types that yield trace fossils, then study geological maps to work out where there are outcrops of similarly aged rocks.

When we have found the trace fossils, we can make 3D models of them using techniques such as photogrammetry (taking multiple photographs of a specimen from different angles to input into software and generate a model) and digital scanning. This enables us to see more details of the trace fossils, which helps us to identify them and observe the interactions between the organisms that made them.

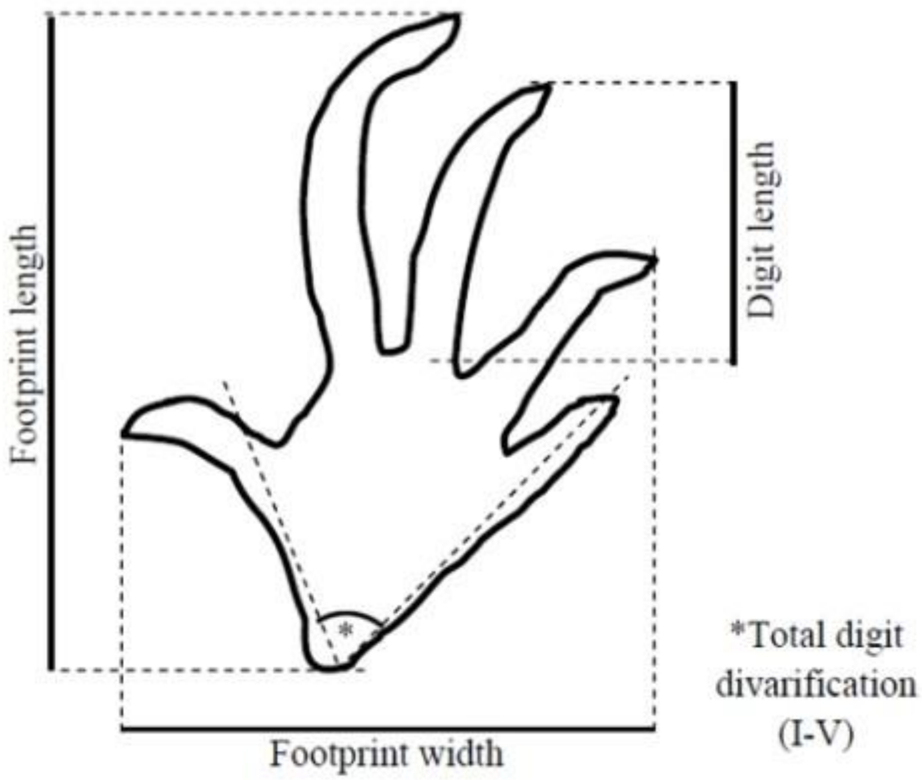

Figure 2 — Illustration of measurements made on a *Dromopus* ichnospecies pes (modified from Leonardi 1987). Total digit divarification: total angle between digits in the footprint.

We can also take measurements of the footprints and trackways (Figs 2, 3) to help estimate:

- Trackmaker size: measuring between the hands and feet estimates the distance between the shoulders and hips (called the glenoacetabular distance*), which can be doubled as an overall guide to the size of the animal including its head and tail.
- Trackmaker speed: the spacing between footprints can indicate the movement of the organism at the time of formation: the larger the spacing, the greater the speed.
- Gait: this refers to whether the limbs sprawl outwards to the sides of the body (as seen in tetrapods that walk by moving opposite limbs) or the animal has an erect stance, as seen in certain dinosaurs that walked on two feet (bipedal).

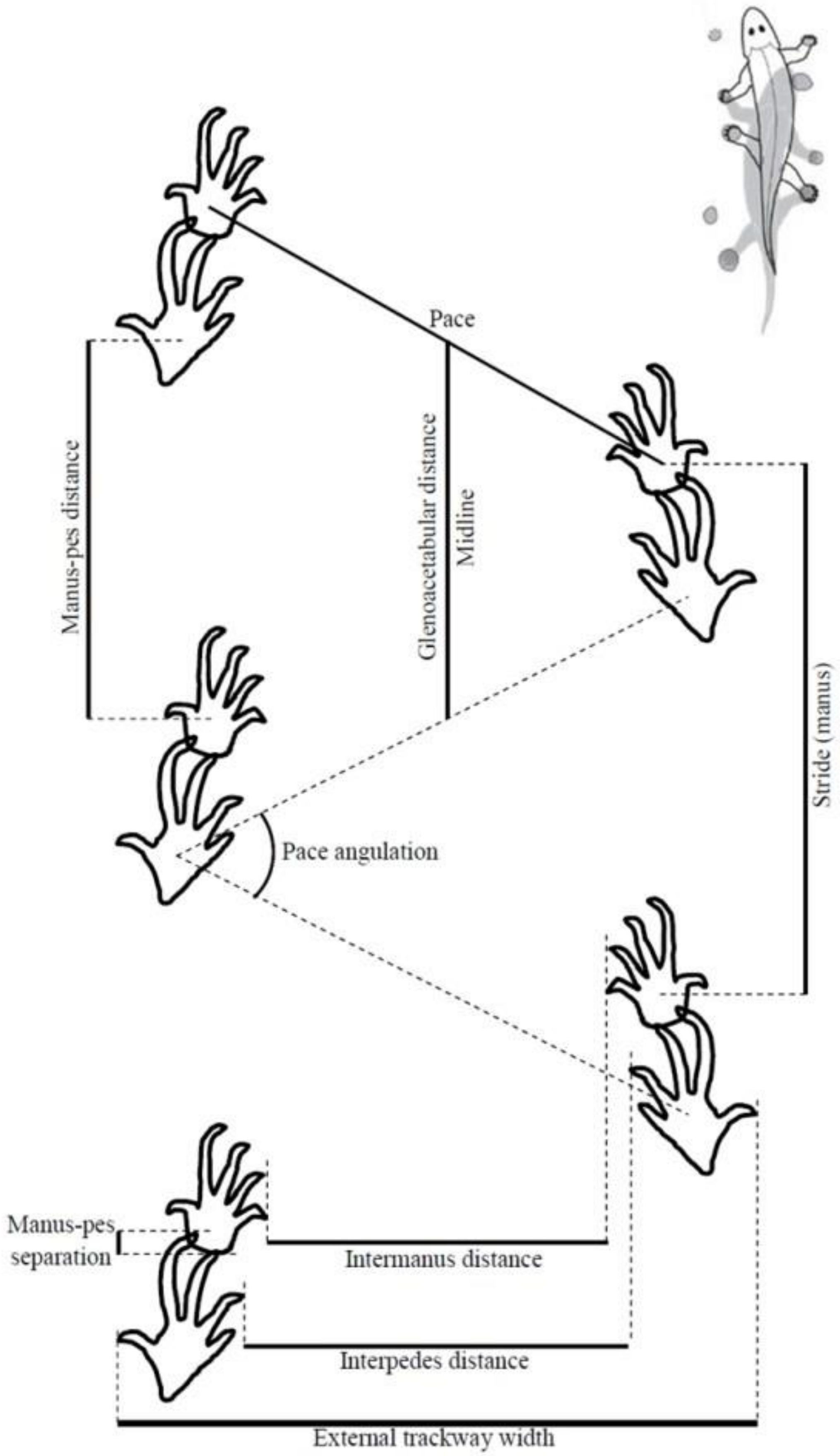
Pace
Manus-pes distance
Glenoacetabular distance
Midline
Stride (manus)
Pace angulation
Manus-pes separation
Intermanus distance
Interpedes distance
External trackway width

Figure 3 — Illustration of possible measurements made on a *Dromopus* ichnospecies trackway (modified from Leonardi 1987). Glenoacetabular distance: distance along the midline between a manus pair and pes pair, effectively the trunk length. Intermanus or interpedes distance: distance between the innermost margins of consecutive left–right manus or pes prints. Manus–pes distance: distance between the midpoints of the manus and pes in the same stride and side of the body. Manus–pes separation: distance between the longest pes digit tip and manus heel. Pace: oblique distance across the midline between the right and left manus or pes. Pace angulation: angle produced by three consecutive left–right–left footprints of the manus or pes. Stride: two consecutive prints on one side of the midline that show one complete cycle of movement from the foot being lifted off the ground to being placed back down again. Inset shows an amphibian reconstruction matching a footprint trackway (Niedźwiedzki et al. 2010).

Significance: the perks of being a trace fossil

The greatest benefit of ichnology is that it supplements the relatively limited record of tetrapod body fossils. Bones and footprints are preserved under different conditions, so the two are rarely found together. As a result, ichnology allows us to gain insights from a wider geographical distribution than do body fossils alone. It generates the possibility of reconstructing past environments and communities through snapshots of the organisms present in a given environment, and their abundance at a particular time.

Because the footprints are in a slab of rock, it is possible to analyse the composition of the sediment, which can provide more information about the past environmental conditions. It is also possible to study trace fossils left by other organisms in the vicinity, allowing more accurate recreation of palaeocommunities and the interactions between organisms living at a precise moment in time (Fig. 4). This could include evidence about movement in herds, predation and how organisms escaped environmental hazards. It might also help us to understand the environment, because certain organisms might be known to have lived in particular conditions of water depth, salinity and sediment oxygenation.

Furthermore, comparisons can be made with sites around the world where similar footprints are found, to help determine distributions of ichnotaxa (and therefore the trackmakers) and their migrations across continents in the geological past.

Figure 4 — Artistic reconstruction of the palaeoenvironment of a middle Carboniferous fossil-footprint site in New Brunswick, Canada (Falcon-Lang et al. 2010). Fossil and rock analysis leads to inference of a dryland river channel, with small tetrapods foraging on vegetation.

Issues: disappearing without a trace

A key issue with ichnology is that footprints can be affected by numerous factors that lead to different (or new) identifications, so a single type of track might be classified as more than one ichnotaxon. This makes identification — and attempts to match a footprint to the bones of a trackmaker — difficult. Confounding factors include differences in:

- Sediment wetness: the sediment must be sufficiently moist to hold the shape of the footprint.
- Clay content: sediment containing soft, wet clay can adhere to the organism's foot and create a sucker effect when the limb is lifted, causing deformation of the footprint.
- Environmental stability: wind and water erosion might occur before the mould is infilled, so the footprint isn't preserved, or is preserved incompletely.
- Subjectivity of researcher: those identifying the specimen might see differences in the footprint's features that affect their conclusions.

Multiple traces can be produced by a particular organism and a specific footprint morphology might have been produced by numerous biological taxa. Therefore, attributing footprints to a particular species can prove challenging and might not reflect genuine evolutionary patterns. Moreover, organisms that were more active than others or had larger footprints can be over-represented in the fossil record, hence biasing estimates of population sizes and the taxa present in a location.

We also see bias in distribution over time and location: only areas that experienced the right preservational conditions reveal the steps of ancient organisms. Additionally, there is human bias in terms of where people have explored the relevant-aged and exposed rocks through mining and engineering.

People who collected footprint fossils in the early days of geological exploration did not always make sufficient notes to give detailed information about which rock unit it came from, so we might not be able to ascertain the age and environmental conditions of the specimen. Similarly, some specimens are noted in early papers but have since been lost to science.

Case study: tetrapods of Great Britain

The Carboniferous period in Great Britain saw a shift in environmental conditions from humid rainforests to semi-arid climates, often linked to the formation of a mountain belt (the Variscan Orogeny) to the south of the country. The aridity created 'Red Beds' in Britain, notably red-tinged sandstones.

This environmental transition affected the biological development of organisms. Amphibians must lay their eggs in water, and so found the aridity unsuitable, whereas reptiles were better adapted to the emerging terrestrial environment because their eggs had hard shells and so could survive on land. Thus, we expect to see a marked change from amphibian to reptile dominated systems from the late Carboniferous Westphalian age (around 315 million years) and into the early Permian Cisuralian age (299 million to 273 million years ago).

Records of tetrapod footprints in Britain are limited, mainly occurring as a few specimens in various museums around the country. Notable exceptions include the extensive collection from the Warwickshire Group of the West Midlands, particularly the well-studied specimens from Alveley, Shropshire, and Hamstead, Birmingham.

Studies of British tetrapods, in fact, reveal a time and space bias towards specimens from between part of the Westphalian called the Westphalian D and the lower Stephanian age (311 million to 304 million years ago) of the West Midlands, highlighting that this area experienced optimal conditions for preservation at this time. However, the aforementioned issues with ichnology can explain some of this apparent bias.

Nevertheless, the period 311 million to 304 million years ago represents the greatest diversity of tetrapods in terms of ichnogenera and ichnospecies, including *Dimetropus leisnerianus*, *Dromopus lacertoides, Hyloidichnus bifurcates* and *Limnopus (Batrachichnus salamandroides)*. Other species found in Britain include *Dimetropus salopensis*, *Anthicnium salamandroides*, *Chelichnus duncani*, *Limnopus vagus*, *Limnopus (Batrachichnus plainvillensis)* and *?Laoporus ambiguous*.

Certain ichnotaxa in these assemblages, such as *Dromopus* (Fig. 5), are indicative of terrestrial ecosystems. They are often associated with dune environments, hence signalling the aridifying trend in the late Carboniferous.

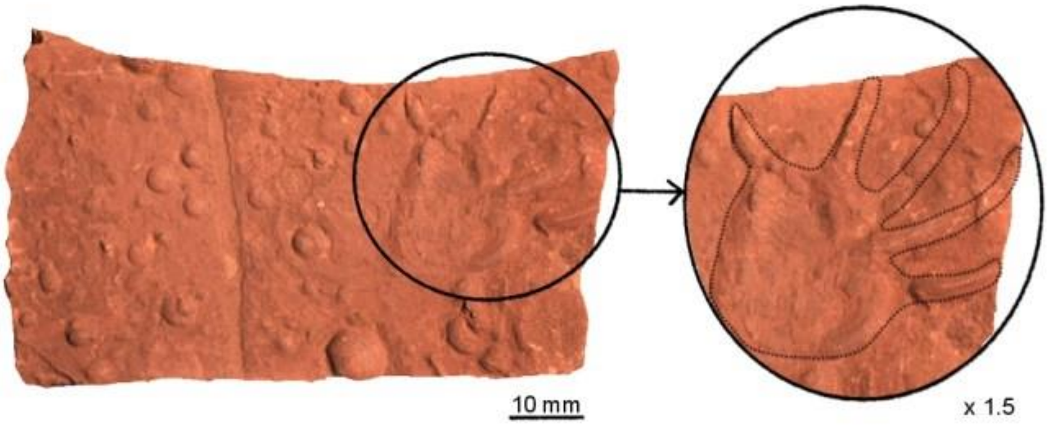

Figure 5 — Specimen housed in the collections of the Lapworth Museum of Geology, University of Birmingham, UK. Preserved in red sandstone is a footprint comparable to the ichnogenus *Dromopus*, along with a 'groove' running top to bottom that might be an invertebrate trace, and numerous circular raindrop impressions (author's own work).

However, as a standalone data set, British tetrapod trace fossils provide insufficient evidence to reconstruct evolutionary transitions from amphibians to reptiles in response to the changing environment. This does not necessarily oppose the hypothesis that this transition occurred, but rather is a lack of data to support it. By comparing British ichnotaxa with those found at sites around the world, it is possible to infer that Britain experienced the same aridification seen elsewhere, and that this would have resulted in the abundance of amphibians decreasing while reptiles diversified.

Summary

As a supplement to tetrapod body-fossil records, ichnology can offer an illuminating insight to the environment in which organisms lived and how the organisms interacted with each other. Through detailed study, footprints can be used to reconstruct palaeocommunities in ways that singular body fossils cannot, and comparison across global sites can highlight distribution and migratory patterns as well as evolutionary developments through key geological intervals. Although trace fossils are sometimes problematic to identify, ichnology has undeniable potential to enhance palaeontological interpretations.

One small step millions of years ago can now be one giant leap for science.

Suggestions for further reading

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