Dinosaur tracks in the computer age

Kevin Padian

A three-dimensional record of dinosaur feet and movement comes from 200-million-year-old footprints made in wet mud. Comparisons of these prints with the tracks made by living birds clear up some of the mysteries about dinosaur toes and the tracks that they left.

It was no accident that Sherlock Holmes had the habit of rousing his faithful companion off to another adventure with the exhortation, "Come, Watson! The game is afoot". Their creator, Arthur Conan Doyle, was fond of footprints — even fossil ones — and he knew how they could be useful forensically[1]. Alas for the many palaeontologists who, through the years, have looked down their noses at such tracks and traces. For footprints have revealed many secrets of locomotion, ecology and behaviour to those who have been patient and sharp enough to study them[2–4]. And on page 141 of this issue, Stephen M. Gatesy and his colleagues[5] bring the science of fossil trackways into the twenty-first century, in ways that Conan Doyle and his creations could never have dreamed.

The story begins as the researchers explored the tree-barren fields of East Greenland. Lured to the Triassic (over 200-million-year-old) exposures near the Fleming Fjord Formation by the prospect of discovering early mammals and their relatives, Gatesy *et al.* found a surprisingly diverse fossil fauna, the components of which are still being described[6]. As well as the bones and teeth of various vertebrates, the authors uncovered strange trackways with features that would have been ignored by most workers because they are so indistinct. Instead, Gatesy and colleagues turned the find into a model for future work.

Baird's 'First Law' of ichnology — the science of footprints — states that a trackway is not a simple record of anatomy. Instead, it is a record of how a foot behaves under a particular locomotory pattern as it makes contact with a particular substrate[7]. The varying conditions of the substrate can have a substantial effect on the features of the trackway, as anyone who has walked along a beach, both close to and above the strand line, can tell — and aching calf muscles, after a good walk along the shore, attest to the influence of substrate on locomotion.

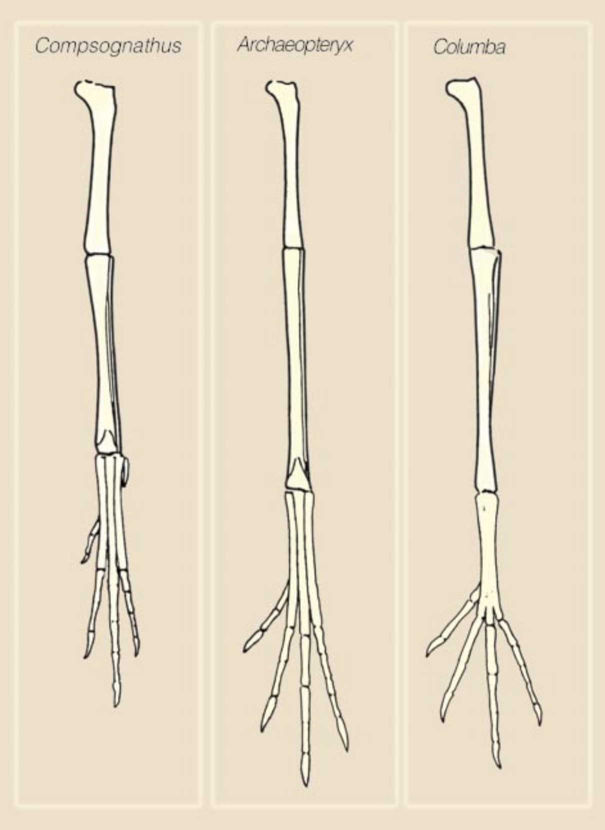

Figure 1 **Putting your foot in it — feet from a theropod dinosaur (*Compsognathus*), the first known bird *Archaeopteryx*, and a pigeon (*Columba*). Gatesy *et al.*[5] studied the footprints made by theropods in wet mud, and worked out how the feet of these dinosaurs compare with those of living birds. Their results show that living birds walk much like their ancestors did, although the dinosaurs carried their heels just a bit lower. (Adapted from ref. 12.)**

The tracks studied by Gatesy and colleagues ranged from clear imprints to virtually indistinct traces, depending on the condition of the substrate. They were made by a theropod (carnivorous) dinosaur in mud that was often so sloppy that there was little chance of preserving precise records of individual joints or skin impressions. But this sloppiness preserved the entry and exit 'wounds' made by the foot, which led to an interesting discovery — the deeper you sink, the more of the movement that normally occurs above ground level can take place below it instead.

In theropod dinosaurs, the fifth toe is completely reduced and lost. The first toe (hallux) is short, and it is suspended from the second metatarsal (sole bone), a bit less than halfway up the sole. In those theropods that are closer to birds, the first toe has descended in the course of evolution, eventually hanging from near the end of the sole. For instance, in *Archaeopteryx*, which is the first known bird, the first toe is fully opposable (that is, it faces the other digits on the same foot), and in later birds the claws enlarge for perching, suggesting the start of true arboreality[8]. So, the distinction between bird and other dinosaur tracks has sometimes been assessed on the basis of the imprint of the hallux — if it extends backwards and towards the midline, the maker of the track is often regarded as avian[9].

In the Greenland tracks, the hallux seems to make such an impression going in — in apparently avian fashion — but on the way out it disappears. To find out why, Gatesy *et al.*[5] sectioned the fossilized footprints and traced the disappearance to the fact that the toes were brought together as the animal lifted its foot. They then ran guineafowl and turkey through successively more sloppy mud to demonstrate that this kinematic pattern is simply inherited by today's birds from their theropod ancestors[10]. Moreover, the footprints elongate as the mud becomes sloppier. In Mesozoic Era trackways, this feature has sometimes promoted the inference that some dinosaurs were plantigrade (that is, they walked on their soles)[2,3]. But the sloppiness of the sediment now reveals that, in these dinosaurs, the heel was just carried a bit lower than in birds today (Fig. 1). This finding indicates that the stride was more strongly powered by the femur in basal theropods than in birds, where the femur is more stable and the lower leg and foot provide more of the power thrust.

The results of Gatesy and colleagues' investigation are dramatically shown by computer graphics (Fig. 3 of their paper on page 143), which graft the anatomy of a typical basal theropod foot onto the footfall pattern of living birds, allowing for differences in proportions and kinematics. The conclusions are clear — early Mesozoic theropods walked much, but not exactly, like their living avian descendants. And, more importantly, locomotion and limb function have evolved like any other features[10].

Most of the fossil footprint literature documents new tracksites, describes the form and proportions of tracks, and tries to assign such tracks to trackmakers, usually with little in the way of direct anatomical reference[2]. At a landmark conference[11] in 1985, there was consensus that two frontiers should receive renewed attention: kinematic patterns and 'competency' of the sediment. Unfortunately, few studies have since done so. But Gatesy *et al.*[5] set the standard for future work, and show just how much we have to gain from such analyses. ☐

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Earth science

Radon and rock deformation

Evelyn Roeloffs

What happens when stress is applied to rocks in the Earth's crust so that the crust deforms? This is a question tackled by Trique *et al.* on page 137 of this issue[1]. They have used a natural laboratory in the French Alps — the Roselend reservoir — to monitor the geophysical signals that result from the greater or lesser pressure on the underlying crust exerted by the weight of water in the reservoir. This area is not itself prone to earthquakes. But the broader interest of this work is in what it may tell us about the events, induced by crustal deformation, that precede earthquakes.

The ability to predict earthquakes is of course highly desirable. But progress in this difficult and highly contentious science will depend on detecting and interpreting physical changes stemming from the processes of earthquake generation. Many possible precursors have been reported, but seismologists are sceptical of those that are not clearly linked to crustal deformation. This 'unproven' category includes the well-documented precursory decrease and increase of radon concentration before the 1978 Izu–Oshima earthquake in Japan[2] (Fig. 1), as well as the controversial assertion that moderate earthquakes in Greece have been predicted from variations in the local electric field[3].

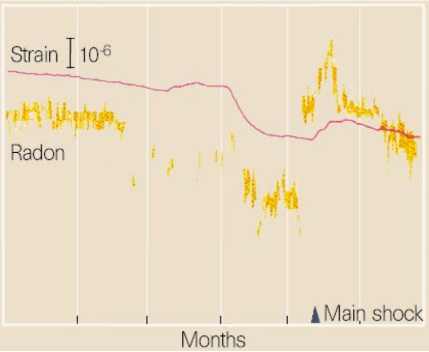

Figure 1 **The radon and strain data for the magnitude-7 Izu–Oshima earthquake[2,9] of 14 January 1978 show changes preceding the earthquake. But they do not match the model shown in Fig. 2; in particular, neither change is monotonic, and in both cases the pre-earthquake change exceeds that produced by the earthquake itself.**

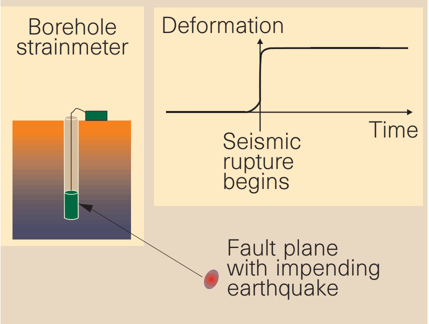

Figure 2 **Rock friction, which depends on slip rate and sliding-induced changes on a fault surface, implies that seismic slip should be preceded by accelerating aseismic slip near the hypocentre of an impending earthquake. Sufficient aseismic slip would produce near-surface deformation detectable by a borehole strainmeter. Compared with the strain step recorded at the time of the earthquake, the precursory strain signal would be in the same direction but of much smaller amplitude. A magnitude-5 earthquake, 10 km deep, produces maximum near-surface strain of about 10^{-7} at a site 5 km from its fault plane; strain increases 30-fold for each unit increase of magnitude, but falls off as the third power of distance from the source. Estimates of pre-seismic slip duration and amplitude range widely because frictional parameters of natural faults are poorly known.**

Trique *et al.*[1] now report that various phenomena — bursts of radon gas, changes of electric potential, and departures of ground tilt from that predicted on an assumption of linear rock elasticity — consistently accompany water-level variations behind the Roselend dam. These phenomena occur together, usually within days after an abrupt change in the reservoir's filling or emptying rate. At Roselend, radon emissions and electrical changes are produced by a well-quantified driving force — the lake 'load', or weight of water — instead of the poorly understood processes that precede earthquakes. But the observations do provide indications of the relationship between radon and electrical anomalies, and the deformation of crustal rocks.

Seismologists expect earthquake precursors to take the form of transient crustal-strain signals from 'aseismic' fault slip near the earthquake's nucleation point (that is, fault slip that is too slow to radiate seismic waves) (Fig. 2). Numerical simulations show, however, that such signals would be exceedingly small[4]. Even the best existing instruments — borehole strainmeters with resolution exceeding a part per billion — would need to be within a few kilometres of the impending earthquake's epicentre to detect this aseismic strain. Although strain changes preceding two California earthquakes have been identified[5,6], they don't resemble the expected signals.

Proponents of earthquake prediction maintain that changes in radon emission, or in electrical or magnetic fields, represent a natural amplification of pre-earthquake deformation under special geological conditions. For example, the conductance by rock fractures of water or gas is proportional to the third power of the fracture's aperture[7]. Fluid flow past ions adsorbed on rock surfaces produces an electric field, termed a 'streaming potential', that varies with pressure gradient and permeability[8]. Fluid, gas or electromagnetic measurements might thus detect deformation indirectly, albeit at localized sites and with amplitudes related nonlinearly to strain.

Silver and Wakita[9] list many potential examples of such pre-earthquake 'strain indicators'. Unfortunately, these indicators are irreproducible: they can be detected only in certain locations, but in any one location earthquakes recur infrequently. What is needed is evidence that transient strain leads consistently, if not linearly or uniformly, to observable phenomena. The radon, electrical and ground-tilt measurements from Roselend lake constitute this kind of reproducible evidence.

The shallow crust's reaction to large changes in lake level may also illuminate the