New techniques let scientists analyse ancient footprints to understand how our forebears' physiques and lifestyles changed over time. Matthew R Bennett, Robin Huw Crompton and Sarita Amy Morse describe recent breakthroughs in the science of fossilised movement.

Tracking our ancestors

A key part of being human is our 'bipedal' posture – we walk upright on two legs. The development of bipedalism was a critical stage in our evolution. Another was the later transition from early habitual bipeds such as *Australopithecus africanus*, made famous by the skeleton 'Lucy', to more modern humans like *Homo erectus* and *Homo sapiens*, which were, and are, endurance walkers and runners.

Our ancestors' ability to walk efficiently influenced how they foraged and hunted for food, how they gathered raw materials for tools and how they migrated across the globe. But despite more than a century of research, our understanding of the modern foot is still relatively poor, and our knowledge of our ancestors' feet is even more uncertain.

The foot is a complex structure of 26 bones held in place by a lattice of soft tissue. It interfaces with the ground to create pressures which decelerate, balance and accelerate the body during walking and running. Little wonder this complex machine has not given up its secrets easily.

Fossil foot bones are rarely found with skeletons of known species, and the fossil record is fragmentary. When we do find part of one of our ancient ancestors' feet, it has usually been badly chewed by scavengers. And fossil foot bones rarely give a definite indication of how our early ancestors walked, since they act through a series of complicated soft tissues which are rarely preserved – from ligaments to the outer skin – so they interact only remotely with the ground.

Fossilised motion

We believe human footprints provide a better record of our ancestors' feet than foot bones – a record of 'fossilised motion' formed as they walked across soft ground. The prints directly record the forces our forebears applied to the ground to balance and propel their bodies.

Our team is a collaboration between field scientists at Bournemouth University led by Professor Matthew Bennett, who have expertise in excavating and recording footprints, and experts in biomechanical modelling at the University of Liverpool under Professor Robin Crompton. Our goal is to meld field science with computational analysis and simulation to reveal the fossilised motion of our ancestors.

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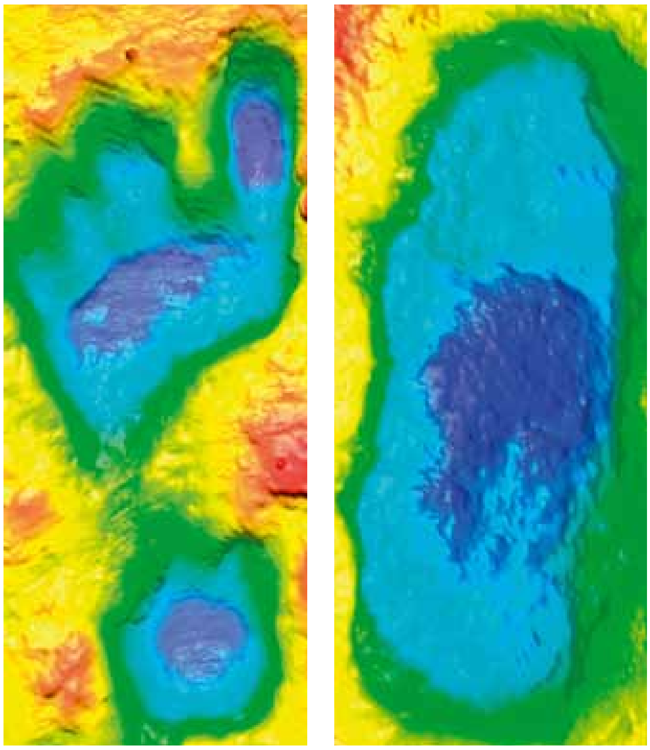
Until relatively recently, human and animal footprints were thought to be rare in the geological record – freak occurrences of sedimentary preservation, with each one holding a rare glimpse of locomotive behaviour. But we're coming to realise that footprint sites probably aren't so scarce; it's just that they haven't been properly identified and analysed before.

The oldest and most famous ancient footprints are at Laetoli in Tanzania, made some 3.75 million years ago by an ancestor similar to 'Lucy' (*Australopithecus africanus*). Last year we published in *Science* details of the second-oldest human footprint site, found in northern Kenya, dating from 1.5 million years ago.

We think these footprints were made by *Homo erectus*, one of the first of our ancestors capable of long-distance walking and running. Comparing these sites and prints will help us understand the transition in locomotive style between species of *Australopithecus* and *Homo*. There are also other more recent human footprint sites around the world, and lots still to be discovered, with prints made by *Homo sapiens* in diverse settings like coastal mudflats, caves and layers of volcanic ash.

These sites help us understand the data on 'fossil locomotion' from ancient footprints. For example, some team members have just

Matthew Bennett and the team scanning footprints at Ileret, Kenya.



3-D scans of a human footprint from Formby, UK (left), c3500 years old, and one of the prints from the quarry at Valsequillo, Central Mexico.

returned from Namibia, where one of the richest footprint sites in the world recently came to light. The site contains many human trails and a plethora of animal prints including elephants, giraffe, buffalo, cattle, goats/sheep and a range of birds. The site is in a large dune field, and each day the team used quad bikes to reach it – a former mudflat over which the dunes have migrated. The footprint surfaces are only exposed for a few years at a time as they are revealed and then covered again by the mobile dunes.

The site's age will not be known until the results of our dating programme are completed later this year, and it is probably only a few thousand years old. But it contains important information to help us interpret ancient footprints, since the prints reveal the subtle influence of the surface they are made in. In one case there is a trail of more than 70 prints formed by an individual walking across a shallow channel and mudflat. The individual prints vary in their anatomy and with the type of sediment they were made in, particularly its moisture content. Adding sites with different properties to our database of knowledge is crucial if we want to understand the patterns of foot pressure caused by different styles of locomotion and foot anatomy. The team will also be returning to northern Kenya and the second-oldest footprint site in the coming year to continue excavating these ancient prints.

Capturing the information held in a footprint has long involved casting it in a medium like latex or plaster, a destructive process that does not readily provide quantitative data that we can analyse objectively. Our team has pioneered the use of an optical laser scanner to capture footprints in the field. Mounted on a custom-made rig which controls light and dust levels, the laser scanner provides digital elevation models of individual prints that are accurate to less than a millimetre. The scans record each print, preserving them for the scientific community even if these fragile sites with their prints erode in future. More importantly, the scans provide the basis for statistical analysis of print anatomy.

One of our goals is to develop objective methods for interpreting footprints. First, we needed to be able to tell for sure whether or not a mark in the ground is really a human footprint. Working at controversial sites in Mexico, and closer to home in South Wales, we have developed a simple numerical test using scans of footprints of various ages and species, formed in different materials.

Objectivity is critical, especially as prints within a single trail may vary from one another; we need a way of effectively determining what the mean print looks like, eliminating the bias associated with the interpretation of individual prints. Professor Crompton's team did some lateral thinking and realised that methods used to analyse chemical patterns in the brain are also ideal for comparing footprints. They have developed a new approach which lets us calculate an 'average' footprint from a whole trail, and then compare it statistically to other print populations.

This lets us objectively compare prints made by different species at different times and helps develop models of how human locomotion has evolved. For example, the technique has helped resolve a 30-year debate over the Laetoli footprints, showing they were made not by a creature that walked with bent hips and knees, but by a more modern version with a gait not so far from our own.

Studying these footprints has greatly improved our knowledge of our ancestors. We can more accurately place them on the map chronologically, see what fauna they interacted with – even make them walk through computer modelling. We can't research our forebears' feet directly, but our work may ultimately mean the prints they left behind are just as good.

MORE INFORMATION

Matthew Bennett is Professor of Environmental & Geographical Sciences at Bournemouth University. Robin Huw Crompton is Professor in the Institute of Ageing and Chronic Disease at the University of Liverpool. Sarita Amy Morse is a student of the anthropology department at Rutgers, State University of New Jersey.
Email: mbennett@bournemouth.ac.uk