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Footprints in the Sands of Time. Vertebrate Footprints and the Interpretation of Past Environments

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Article abstract

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1. They provide direct evidence for the existence of animals not known fromosteological remains;

2. They furnish information on the locomotory and social behaviour of the trackmakers, — Information that could not be adduced from bones — and

3. Since they tell about the way of life of extinct animals, they tell us also about the environments those animals inhabited.

Results include recognition of the presence of small amphibians in the Triassic, yet unknown from bones, and of the existence of marsupials and wading birds in the Middle Cretaceous of North America; confirmation of the fashion of movement between drying-out pools of rhipistidean fishes and of the existence of tadpole-like larval stages in Mississippian (Late Carboniferous) amphibians; determination of the gait, speed, swimming abilities, and herd behaviour of dinosaurs; and demonstration that the running gait of horses was innate, not man-taught. Paleoichnology is indeed the only means for transforming our images of the past from still to moving pictures.

Footprints in the Sands of Time. Vertebrate Footprints and the Interpretation of Past Environments

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ABSTRACT

Vertebrate footprints are imprinted by the million daily into the world's beaches, dunes and river and lake margins. However, they survive as fossils only in special environmental circumstances. When fossil vertebrate footprints were first recognized by human eyes can never be known, but their scientific study commenced in the 1820s with discoveries in the New Red Sandstone (now known to be Permian) of Dumfries-shire, Scotland. These prompted Rev. William Buckland to try to simulate the tracks (the very earliest paleoecological experiments).

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RÉSUMÉ

Dans le monde, des vertébrés laissent des millions d'empreintes de pas à tous les jours sur les plages, les dunes, ainsi que sur les berges des rivières et des lacs. Cela dit, elles ne pourront être fossilisées qu'en des conditions environnementales bien particulières. On ne pourra jamais savoir quand les humains ont reconnu les empreintes de pas de vertébrés pour la première fois mais, leur étude scientifique a commencé en 1820 avec les découvertes faites dans les grès du *New Red Sandstone* (Permien) du comté de Dumfries en Écosse. Ces découvertes ont incité le révérend William Buckland à tenter de reproduire ces traces, ce qui a constitué les toutes premières expériences en paléoécologie.

Les empreintes de pas qui ont été découvertes un peu plus tard en Allemagne dans des couches triasiques, et incorrectement nommées « *Chirotherium* », ont été l'objet d'une longue controverse sur l'identité de leur auteur. Ce problème n'a été résolu que dans les années 1920 par les études de Wolfgang Soergel, ses déductions ayant été confirmées 40 ans plus tard par des découvertes ostéologiques. Les empreintes de pas trifides observées dans les grès de Wéaldien (Crétacé inférieur) de l'Angleterre du sud ont été mal interprétées initialement elles aussi, la bipédalité chez les dinosaures n'étant pas connue alors.

On reconnaît maintenant l'importance des empreintes de pas de vertébrés, et ce pour trois raisons:

1. Elles constituent des indices formels de l'existence d'animaux dont on ne connaît pas de restes ostéologiques ;
2. Elles nous livrent des informations sur le comportement moteur et social de leurs auteurs, informations que l'on ne saurait obtenir par l'étude des os ; et,
3. Puisqu'elles nous renseignent sur les modes de vie d'animaux disparus, elles nous renseignent donc sur les milieux de vie de ces animaux.

Parmi les résultats obtenus, on connaît maintenant l'existence de petits amphibiens au Trias malgré que l'on ne leur connaisse pas encore de restes osseux ; de la même façon, on a établi la présence de marsupiaux et d'échassiers du Crétacé moyen d'Amérique du Nord ; on a obtenu confirmation du mode déambulatoire de spécimens d'amphibiens à des stades larvaires (de type têtard) du Mississippien (Carbonifère supérieur) en comparant leurs empreintes à celles des déplacements de poissons rhipistidiens entre des mares d'eau en voie d'assèchement ; la détermination de la démarche, de la vitesse de déplacement, des habilités natatoires et du comportement social de troupeaux de dinosaures ; et, que la démarche en course des chevaux est un trait inné et non appris de l'homme. La paléoichnologie est vraiment le seul outil qui nous permette d'animer nos représentations statiques du passé.

Lives of great men all remind us
We can make our lives sublime,
And, departing, leave behind us
Footprints in the sands of time.

— *H.W. Longfellow*

The above words of the American poet were written in 1838. In the later years of the last century and the earlier years of this, they were much quoted by parents and schoolteachers trying to exhort reluctant children to apply themselves harder in their work. Yet, as a moment's reflection will show, Longfellow's image has undertones, advertent or inadvertent, that make it a dubious inducement. Footprints in beach sand will be obliterated by the next return of the tide, while footprints in dunes will be quickly blurred and destroyed by the shifting and settling of the sand grains and the movement of the dunes themselves. Of the untold millions of footprints impressed into sands daily by animals and men, only a very few, formed in certain special settings, have any least chance of surviving to become a part of the fossil record. Perhaps, indeed, Longfellow recognized how rare this was; perhaps he was hinting obliquely that fame was usually transient, only rarely persisting beyond a few brief hours or days.

Certainly Longfellow must have been aware that footprints were to be found in the geological record. In the 1830s, that fact was causing much excited comment in popular, as well as in scientific, journals on both sides of the Atlantic.

There must, of course, have been earlier observations of fossil tracks. The bushmen of southwest Africa had not only observed the fossil footprints of dinosaurs, but also conceived a trackmaker much like a dinosaur (F. Ellenberger, pers. comm. to D.J. Mossman). A German paleontologist, H. Kirchner (1941), speculated that it was the finding of dinosaur tracks in the Rhine valley that generated the legend of the dragon slain by Siegfried (Fig. 1). An example of later legends is furnished by the footprint-bearing slab in the porch of Christ Church, Higher Bebington, Cheshire, England, called locally "The Devil's Toenail" (Sarjeant, 1974, fig. 8). It is also on record that, in 1802, a Massachusetts farm boy called Pliny Moody noticed three-toed tracks in the red sandstones of the Connecticut Valley near South Hadley (Fig. 2) and thought them to be the footprints of Noah's raven. The folklore of footprints is indeed a fruitful field for investigation and speculation.

EARLY SCIENTIFIC STUDIES

It was in prosaic Scotland, however, that the scientific study of fossil vertebrate footprints commenced. About the year 1824, Mr. Carruthers of Dormont noticed, in the red sandstone quarries of Corncockle Muir, Dumfries-shire, a slab bearing 24 distinct imprints of the feet of a quadrupedal animal. He secured the slab and presented it to the Reverend Henry Duncan, the minister of Ruthwell church and perhaps the most erudite person in the neighbourhood. The Rev. Duncan was sufficiently impressed to build the slab into the wall of the summerhouse of his manse, where the footprints might easily be shown to visitors.

The discovery not only excited his curiosity sufficiently to cause him to visit the quarries and procure further footprint-bearing slabs (Fig. 3), but also to seek advice on the nature of the footprint maker from a recognized expert on fossils. Consequently, he wrote to an ecclesiastical colleague who was also a distinguished scientist — the Reverend William Buckland, Reader of Geology at the University of Oxford — and sent him casts of the footprints for study.

Buckland possessed one of the most fertile minds of any 19th century scientist. Among many other attainments, he contributed some of its basic concepts and terms to Jurassic stratigraphy, giving names to English strata that are still in use; he described the first dinosaur (*Megalosaurus*); he made pioneer observations on the fossil faunas of caves; he designed part of London's sewage

Figure 1 *The dragon of the Drachenfels, Germany. An illustration from Athanasius Kircher,* Mundus subterraneus *Book VIII, Amsterdam 1665.*

Figure 2 *The "Moody Foot Mark Quarry," South Hadley, Massachusetts. An illustration from Edward Hitchcock,* Ichnology of New England, *Boston 1858.*

system; he aided in the restoration of the fabric of Westminster Abbey and reorganized its choir school; and he demonstrated the use of mineral fertilizers in agriculture for the first time, also helping to found the Royal Agricultural Society. Naturally enough, the footprints excited Buckland's interest and set him speculating as to the nature of the trackmaker. Noticing the breadth of the trackway and the shortness of the stride, he conceived, whilst awake and writing in the early hours, that the trackmaker might have been a turtle. Well, Buckland had a pet turtle in the garden; so, having roused his wife and persuaded her to cover the kitchen table with flour paste, he fetched the reptile and induced it to traverse the prepared surface. The result was impressively like the Corncockle Muir tracks. Subsequently, Buckland made similar demonstrations before an audience which, while finding them hilarious (Anon., 1828; Gordon, 1894, p. 217; Murray, 1919, p. 7-8), also found them convincing.

These demonstrations were indeed epoch making, for they were the first occasions on which a scientist strove by experimentation to simulate a structure observed in ancient sediments. Yet Buckland was both right and wrong. Yes, the trackmaker had been a reptile and yes, it had had a wide trackway and short stride, much like Buckland's tortoise. However, that was not because it possessed a hard, broad carapace. Instead, it was because these were the early days of life on land. The trackmaker, certainly a primitive reptile and most probably a caseasaur (see Haubold, 1971, p. 36-37), had been simply an inefficient pedestrian, with legs sprawling outward from its body.

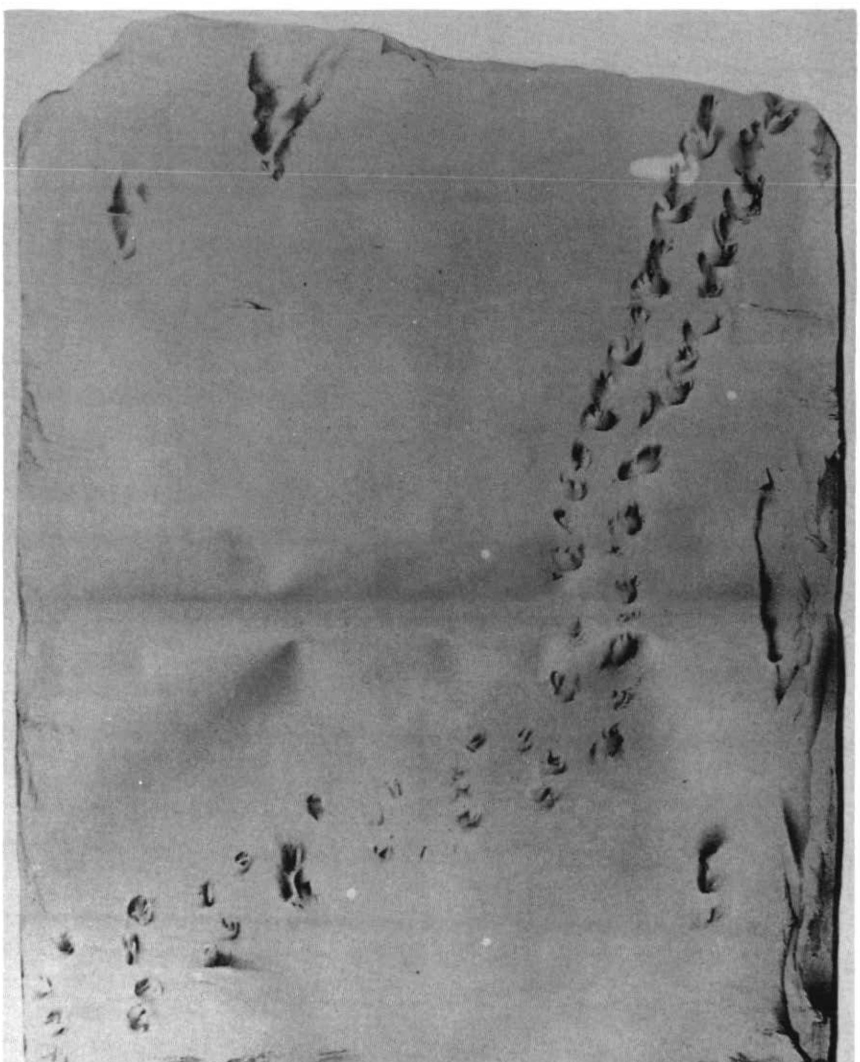

Figure 3 *Vertebrate tracks (*Chelichnus duncani *[Owen]) from the Triassic red sandstones of Annandale. An illustration from Sir W. Jardine,* The Ichnology of Annandale, *Edinburgh 1836.*

Duncan's account of the tracks to the Royal Society of Edinburgh on 7 January 1828, was reported in several scientific journals and, along with Buckland's experiments, sparked much popular interest in Scotland and elsewhere. This was intensified during the next decade by finds of beautifully preserved footprints in red sandstones in south Germany and Cheshire. The tracks were of an animal normally quadrupedal, intermittently bipedal, with one pair of feet much larger than the other. The larger footprints attracted closest attention. They were approximately the proportions of a human hand, having long, finger-like toes terminating in sharp claws; one digit, the outermost, was opposed and thumb-like. The smaller footprints had much shorter digits, the outermost again opposed (Fig. 4).

The sandstones in which they were imprinted were, like those in Scotland, then very imprecisely dated, a fact that permitted a wide range of speculation concerning the character of the trackmaker. The first suggestion was by Voigt (1835) who, noting the intermittent bipedality, considered the footprints had been made by a giant ape; but soon he changed his mind, suggesting instead (1836) that the trackmaker had been the cave bear, *Ursus spelaeus*. The great Alexander von Humboldt thought the trackmaker was a kangaroo-like marsupial (1835), while another German, Link (1835), suggested it had been a

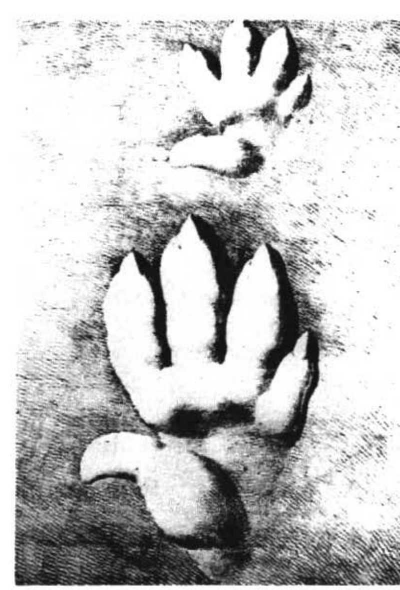

Figure 4 *One of the earliest illustrations of the hand-like footprints of south Germany (from Sickler, 1834).*

giant toad. Kaup (1835), when he decided on a Latin name for the tracks, was so uncertain whether the trackmaker was a mammal or a reptile that he proposed two generic names, calling the tracks *Chirotherium* or *Chirosaurus*. Inadvertently, he was setting a precedent for the future by giving a generic name, not to the remains of the actual body parts of an animal, but to the impression they had produced on a sediment surface. Unfortunately, since in Kaup's paper the name *Chirotherium* appeared first, that generic name was adopted by later investigators, even though it was becoming clear that the trackmaker could not have been a mammal.

In the decade that followed, it came to be perceived that the red sandstones were of pre-Jurassic, perhaps even Late Paleozoic, date. At this time, an even stranger idea developed concerning the trackmaker. The bones, and in particular the skulls, of huge amphibians had been found in European Coal Measures sediments. Because of the nature of their teeth, they had been named labyrinthodonts. It was proposed by Sir Richard Owen (1842) that the *Chirotherium* tracks must be those of such amphibians. Since the presumed thumb equivalents were pointing not inward, but outward, he believed that these were toad-like creatures that walked most awkwardly, crossing their feet at each step! (Fig. 5). Despite the absurdity of this idea, the trackmakers were long to be called "hand-footed labyrinthodonts."

Nowadays, any competent paleontologist glancing at the tracks would immediately perceive features to demonstrate the absurdity of that idea. First of all, such a gait is impossibly awkward; but, in addition, the morphology of the footprints is quite wrong. The great disparity in size between fore and hind feet, the conspicuous claws on all four feet, and the elaborate pattern of scales preserved on the better prints are features not to be found in any amphibian, living or fossil. However, in the mid-1800s when the post-cranial skeletons of amphibians were so poorly known, such a morphology — and even such a mode of progression — must have seemed perfectly possible.

What is harder to understand is the small account taken of the nature of the strata containing the impressions. By considering modern analogues, it should have been perceived that these were sediments of an arid environment: not full desert, perhaps, but at least semi-desert. Giant toads and, by extension, giant amphibians of any kind were scarcely likely to have lived under such conditions; moreover, although the giant kangaroos envisaged by Humboldt might have fared well enough, cave bears and giant apes would have been hard put to survive. Yet, so far as I am aware, none of the scientists of that time gave any thought to the environment when advancing their ideas. Only the morphology of the footprints themselves was considered.

This is the more surprising because not only a considerable awareness of the detail of the enclosing sediment, but also a willingness to make deductions from observations of that sediment, is apparent in some of the earliest writings about fossil footprints. George Fairholme was an avowed believer that all sediments had been laid down rapidly in the Noachian deluge. However, his discovery of footprints in the Coal Measures of Midlothian, Scotland, forced him to believe that some animals had survived that deluge, for a while at least. Reasonably enough, he thought that the survivors must have been amphibious creatures, like turtles. Even though we might nowadays scorn Fairholme's premises, his deductions (1833) remain reasonable:

> These *fossil* footmarks have all the appearance exhibited on a recent *sand-bank*. They, in some instances, indicate a short and shuffling gait, with the feet pressing *outwards*, and are such as we can suppose an amphibious animal to produce. Had the marks occurred in *clay*, instead of in *sand*, we can suppose the air to have completely *hardened* the impression, so as to have preserved it for a long time before being covered up. But such is not the case; and we can, therefore, have no manner of doubt that they were occasioned by some animal coming *ashore on a sand-bank left dry by the tide*; and that the returning waters, heavily charged as they must have been, by diluvial sediments, immediately covered up the former strata, and thus preserved entire those most interesting and solitary indications of a still living antediluvian race. (p. 344-345)

An even greater care in observation is evident in the writings of Hugh Miller, the eminent Scottish geologist and writer, when reporting a visit to Warwick Museum (1847):

> On one large slab...we may see the footprints of some betailed batrachian, that went waddling along, greatly at its leisure, several hundred thousand years ago, like the sheep of the nursery rhyme, 'trailing its tail behind it'. There is a double track of

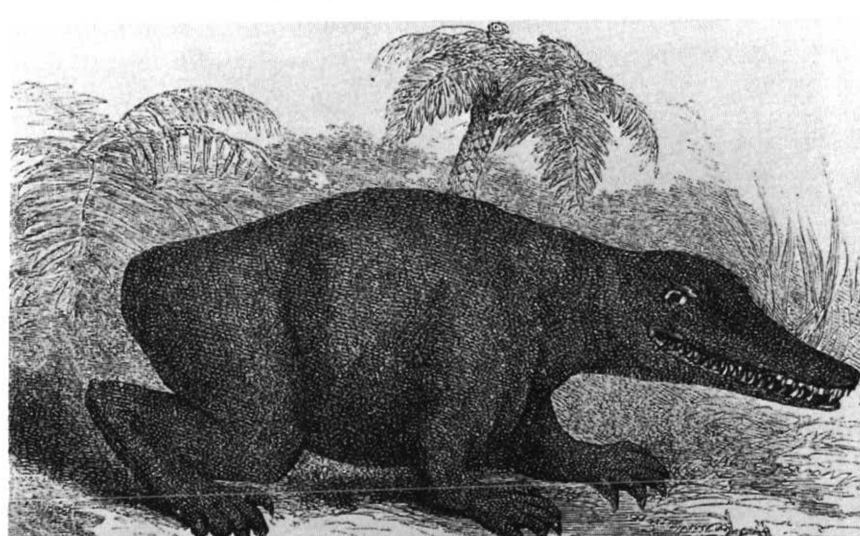

Figure 5 *The "hand-footed labyrinthodont." An illustration from Louis Figuier,* The World Before the Deluge, *London 1866.*

footprints on the flag — those of the right and left feet: in the middle, between the two, lies the long groove formed by the tail — a groove continuous, but slightly zig-zagged, to indicate the waddle. The creature half-way in its course lay down to rest, having apparently not much to do, and its abdomen formed a slight hollow in the sand beneath. In again rising to its feet, it sprawled a little; and the hinder part of the body, in getting into motion, fretted the portion of the surface that furnished the main fulcrum of the movement, into two wave-like curves. The marks on another slab of the same formation compose such a notice of the doings of one of the earlier chelonians as a provincial editor would set into type for his newspaper, were the reptile My Lord Somebody his patron. The chelonian journeyed adown a moist sandy slope, furrowed by ripple-markings, apparently to a watering-place. He travelled leisurely, as became a reptile of consequence, set down his full weight each step he took, and left a deep-marked track in double line behind him. And yet, were his nerves less strong, he *might* have bestirred himself; for the southern heavens were dark with tempest at the time, and a thunderous-like shower, scarce a mile away, threatened to wet him to the skin. On it came; and the large round drops, driven aslant by a gale from the south, struck into the sand like small shot, at an angle of sixty. How the traveller fared on the occasion has not transpired; but clear and palpable it is that he must have been a firm fellow and that the heavy globular drops made a much less marked impression on the sand consolidated by his tread than when they fell elsewhere on the incoherent surface around him. (p. 190-191)

Figure 6 *A "trifid body" of the type found in Sussex and later shown to be footprints of iguanodont dinosaurs. A specimen from the Oberkirchner Sandstein (Lower Cretaceous) in the University of Göttingen Museum, Germany (Photo: the author).*

The footprints from Germany were early recognized to be of Triassic date. By analogy of sediment character, a similar age was originally assigned to the footprint-bearing strata of Dumfriesshire and Cheshire (Harkness, 1850a, b). However, within six years it was coming to be perceived that, although this might be correct enough for the Cheshire strata, the Scottish strata were decidedly older, being of Permian date (Binney, 1856). The tracks themselves helped to evidence this, for the trackmakers of the Cheshire sandstones were all more efficient pedestrians than the slow-moving, heavy creatures whose footprints Duncan had found.

A few years earlier, another clergyman, the Reverend Edward Tagart, had discovered in the Wealden (Lower Cretaceous) sandstones of Sussex some three-toed footprints, of a size much larger than any found in the New Red Sandstone. He sent them for exhibition to the Geological Society of London in 1846 and, in his accompanying letter, noted that "Dr. Harwood suspects them to be the footmarks of the Iguanodon." However, this suggestion passed unmentioned in the Society's *Proceedings*; the footprints were not illustrated and were described only as "markings...of large size," with the comment that "there does not appear...any decisive evidence as to their origin."

A problem was that the "trifid bodies," as they were later called (Beckles, 1851; see also Fig. 6), were arranged in a pattern that showed them to have been produced by a biped. At that time, the dinosaurs in general and *Iguanodon* in particular were considered to be quadrupeds. (The reconstruction of *Iguanodon* made by Waterhouse Hawkins for the 1851 Exhibition, under Owen's instruction, well exemplifies the ideas then current: it can still be examined, for it survives in the Crystal Palace grounds at Sydenham).

Over in the United States, Edward Hitchcock had begun seriously studying the Connecticut Valley tracks. Believing them to have been made, if not by Noah's raven, then by birds of greater ancientry, he had styled similar imprints "ornithoidichnites" (1845). In the current state of knowledge, Beckles can scarcely be blamed for applying that term to the Sussex footprints (1852) and for presuming them to be made by a bird of even more gigantic size.

In a commentary on a fresh discovery in Sussex, "T.R.J." [T. Rupert Jones] (1862) questioned this deduction. Inadvertently echoing the percipient Dr. Harwood, Jones noted that the hind foot of *Iguanodon* likewise had three toes and was of the right size, concluding:

> We may therefore be allowed provisionally to refer these tracks to the Iguanodon, who certainly wallowed in the Wealden waters and frequented their sand-bars and mud-banks — who had a great three-toed foot — and who, like some other quadrupeds (such as the Tapir, &c.) may have usually, if not always, planted his footprints uniserially, leaving as his spoor a single row of thick-toed trifid imprints, sometimes showing the marks both of toes and heels, sometimes of the toes only, according to the firmness of the mud or sand on which he walked.

It is evident that Jones still assumed *Iguanodon* to have been a quadruped, for he refers to the "excellent models" at the Crystal Palace. His theory of the dinosaur's gait seems to have been that its hindfeet fell upon the exact positions where the forefeet had been set, obliterating the marks they had made.

Jones does not seem to have considered that *Iguanodon* might have been a biped, yet that idea ought to have been in his mind. Four years earlier, Joseph Leidy, describing bones of a dinosaur (*Hadrosaurus*) from New Jersey and noting the great disparity in size between its fore and hind limbs, had suggested it might have been at least partially bipedal (1858, 1859). Its analogy with *Iguanodon* was patent; if the one dinosaur was bipedal, might not the other have been bipedal also?

However, despite Jones's misconception of their locomotory attitude, it came to be taken for granted thereafter that the Wealden footprints were those of dinosaurs, not birds, and usually of *Iguanodon*. The question of the exact gait of this reptile long remained unresolved, however. A century later, when two parallel lines of prints were found on the bedding plane forming a quarry floor at Herston, Isle of Purbeck, Dorset, it was taken for granted that these represented the ponderous steps of the right and left feet of the same slow-moving dinosaur (Anon., 1962, p. 170). It was deduced that the short stride resulted from "the animal walking up what was then a steep incline; its weight was clearly taken on the ball of the foot" since, whereas the depressions left by the toes were up to 5 cm deep, "the heel marks are so shallow as to be barely distinguishable" (Swaine, 1962).

Unfortunately for these interpretations, further quarrying at Herston revealed that, a little farther along, the two lines of footprints diverged! (Charig and Newman, 1962). They had been made, not by a single *Iguanodon* shuffling laboriously along, but by two reptiles moving rapidly and setting one foot before the other in almost a straight line. The fact that the toes were so much more deeply impressed than the heels was because the two *Iguanodon*s were travelling so fast!

THE *Chirotherium* PROBLEM RESOLVED

The question of the identity of the *Chirotherium* trackmaker continued to be a focus for dispute. The botanist W.C. Williamson suggested (1867) that the hand-like footprints might be those of crocodiles, but this hypothesis attracted no support. Even after the zoologist L.C. Miall, in a report to the British Association (1874), had attacked Owen's theory and proposed instead that the tracks were those of dinosaurs, Owen's authority and renown made his opinions so unassailable that most zoologists continued to believe in the "hand-footed labyrinthodonts" (*e.g.*, Beasley, 1890; Matley, 1912). Only when another zoologist, D.M.S. Watson (1914), pointed out that the trackway was too narrow to have been made by an amphibian did Owen's theory at last drop from favour.

The most searching study of *Chirotherium* was made by a German paleontologist, Wolfgang Soergel (1925). His work deserves to be better known, for it is one of the very finest pieces of paleontological detective-work. By making comparison with the foot skeleton of the South African Triassic reptile *Euparkeria*, Soergel showed that the opposed digit was not digit I (the human thumb) but digit V (our "little finger"); thus there was not the least need for the elaborate, cross-footed gait earlier envisaged by Owen. The relative depth of the impressions of *manus* (hand) and *pes* (foot) demonstrated that the trackmaker, although essentially a quadruped, had short, light forelimbs and larger, more powerful hindlimbs. Consequently, it must have borne its greatest weight on the pelvis and must have had, as counterbalance to the body weight, a large, heavy tail. Moreover, since there were never tail-drag impressions, its tail must have been carried clear of the ground. The body length of the animal making the most typical tracks *(C. barthi)* was computed by Soergel, on the basis of stride and footprint size, to have been approximately 1 m, with a tail of comparable length. Allowing for head and neck, a total length of 2.5 m seemed likely. Soergel concluded that the trackmaker was a pseudosuchian reptile, member of a group ancestral to both the crocodilians and the dinosaurs.

At that time, no pseudosuchians of so great a size were known. Within a decade, however, Friedrich von Huene had described from Brazil the genus *Prestosuchus*, a reptile actually much bigger than Soergel's postulated trackmaker, for it had a length of fully 4.7 m (see von Huene, 1942). Eventually in 1965, Bernard Krebs reported from the Swiss Triassic an ideal candidate as trackmaker for *Chirotherium barthi*: the pseudosuchian reptile *Ticinosuchus*. His restoration of *Ticinosuchus* is so much like Soergel's restoration of *Chirotherium* as to demonstrate beyond question the possibility of reconstruct-

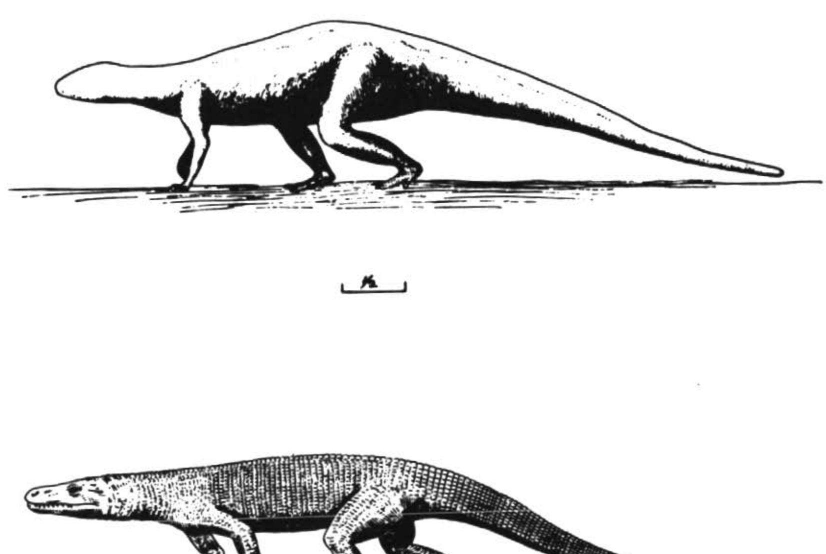

Figure 7 *Theory and actuality: Soergel's reconstruction of the* Chirotherium *trackmaker (1925) compared with Krebs's restoration of* Ticinosuchus *(1965).*

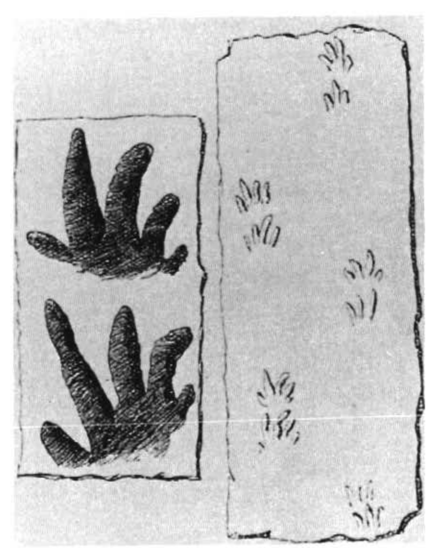

Figure 8 *Vertebrate footprints (*Hylopus logani *Dawson) from the Coal Measures of Nova Scotia. These furnished the earliest-discovered evidence for terrestrial life in the Carboniferous. An illustration from J. William Dawson,* Some Salient Points in the Science of the Earth, *London 1893.*

ing an animal from its tracks alone (Fig. 7).

FOOTPRINTS AS EVIDENCE FOR UNDISCOVERED CREATURES

From their earliest discovery, fossil footprints have been important as indicators of the presence of animals at time intervals when, and in regions where, skeletal remains have not been found. The circumstances under which bones are preserved do not, in general, accord with those under which footprints are preserved. Osteological remains survive most often when there has been an immediate accumulation of sediments, burying the bones rapidly enough to prevent their destruction by scavengers or their attack by bacteria, algae, fungi and other decay-inducing organisms. Footprints, to survive, require a moderately lengthy period of exposure, permitting the thorough drying-out of the substrate before a storm causes an inrush of waters (an inrush sufficient to bury them under new sediment before the substrate has become saturated and the indentation infilled). Most remains of dead animals would have been destroyed or removed by scavengers during that interval of drought. Should any still persist on the margins of the now reflooding stream, they would surely be carried away by the swirling waters and buried somewhere downstream or downslope.

Certainly, circumstances can be envisaged in which both footprints and bones might be preserved in the same stratum, but this is so rare an event that I cannot call to mind a single example. In contrast, there are very many instances in which footprints have afforded the first evidence of vertebrate life at a particular period or in a particular region.

Sometimes the discovery has served to upset preconceived ideas. When William Logan exhibited footprints from the Pennsylvanian Coal Measures of Nova Scotia to the Geological Society of London on 23 March 1842, he was demonstrating for the first time the existence of terrestrial vertebrate life during the Carboniferous period (Fig. 8). The idea was so novel that it was disbelieved. No account of his find was published in the Society's *Transactions* and Logan gained no credit whatsoever for his discovery: rather the converse. Acceptance of this disconcerting revelation came only when bones of terrestrial vertebrates were found in the German and United States Coal Measures two years later (see Sarjeant and Mossman, 1978).

Sometimes the footprints fill a major gap in the osteological record. Small amphibians of several types are abundantly represented by bones in Late Paleozoic strata and are known sparsely from the Middle Jurassic onward; yet, between those times, their skeletal remains are unknown. However, since their footprints are to be found in Triassic strata, we know there were indeed small, salamander-like amphibians during that "barren" interval (see Sarjeant, 1975, p. 303).

In Brazil and northern Argentina, the Botucatu Formation crops out over a vast area; it is a terrestrial deposit of Late Triassic to Early Jurassic date but has, as yet, yielded no bones. From their abundant footprints, however, we know that small and large dinosaurs, other reptiles and, in particular, protomammals were abundantly present (see Leonardi and Sarjeant, 1986; also Fig. 9).

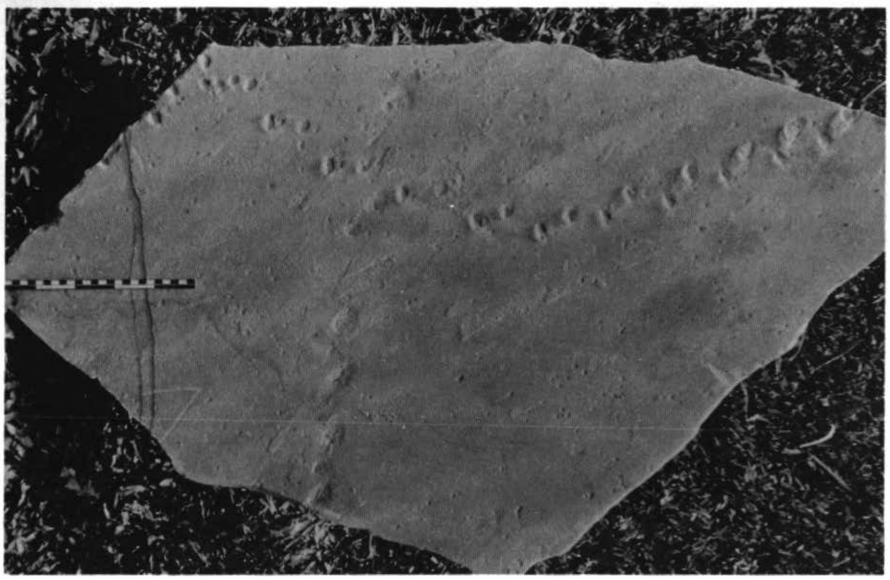

Figure 9 *The trail of a protomammal (*Brasilichnium elusivum *Leonardi) from the Botucatu Formation of Brazil. (Photo: G. Leonardi).*

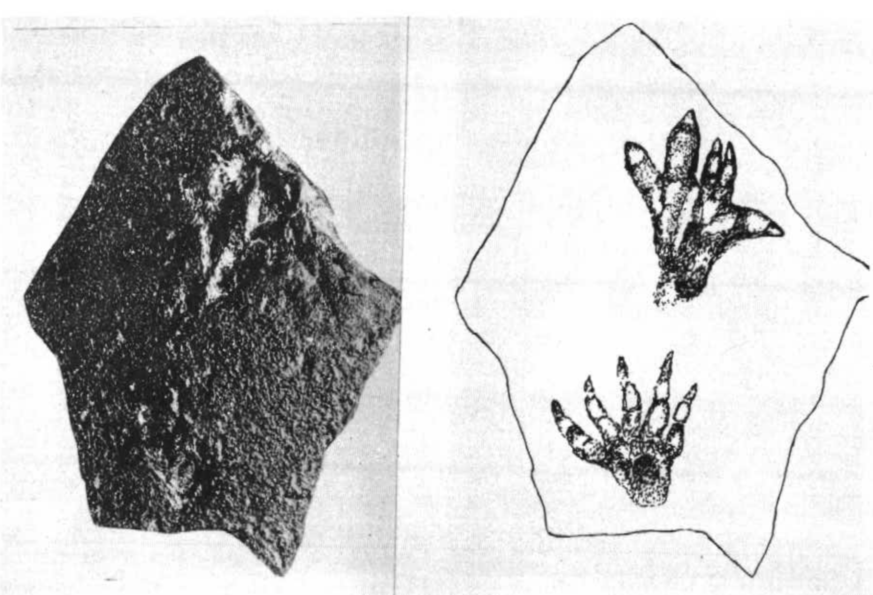

Figure 10 *The oldest known marsupial footprint (*Duquettichnus kooli *Sarjeant and Thulborn) from the Middle Cretaceous of British Columbia. This footprint is very like that of the living brush-tailed possum of Australia (after Sarjeant and Thulborn, 1986).*

In the Early Cretaceous of North America, bipedal herbivorous dinosaurs related to *Iguanodon* are widely represented by fossils while, in the Late Cretaceous, hadrosaurs are abundant. It is evident that the later group of dinosaurs must have descended from the earlier, but intermediate forms are not known from skeletal remains. However, in the Peace River Canyon of eastern British Columbia, a superabundance of footprints demonstrates that dinosaurs having an intermediate foot structure were abundant during the Middle Cretaceous. In the same region, fossil footprints have provided the earliest evidence for wading birds yet found (Currie, 1981) and, more recently, for the presence of marsupials at that time (Sarjeant and Thulborn, 1986). Both these groups are unrepresented by skeletal remains until much later in the Cretaceous, although in both instances the character of those skeletal remains implies an earlier origin. The marsupial footprints, moreover, provide the first evidence for the occurrence of syndactyly — a reduction and partial fusion of the second and third digits of the hind foot, designed apparently for the combing of fur — among Mesozoic mammals (Fig. 10).

Sometimes the tracks of vertebrates indicate morphological features in the feet whose presence is not determinable from the bones alone. A single footprint from the Late Triassic of Nottinghamshire, England, is the only direct evidence we have for the existence of an ample webbing between the digits of early crocodiliform reptiles (Sarjeant, 1967; Sarjeant, 1995b). The careful study of a hadrosaur footprint from Alberta demonstrated that those dinosaurs, like elephants, had pads on their feet to help cushion their great weight (Langston, 1960). And remember the scale patterns on those *Chirotherium* footprints (p. 80)? Such details cannot be determined from the fossil record by any other means.

FOOTPRINTS AS EVIDENCE FOR LOCOMOTORY BEHAVIOUR

However, the most important point about footprints is that they record the animal in dynamic action. From bones, we may deduce how an animal might have behaved, but its footprints carry us much farther, for they show us how it *was* behaving

Some living reptiles, such as the whiptail lizards of the southern United States, travel on all fours while walking or while running at a slow pace. However, while running at speed, they travel on hind limbs only, the forepart of the body being carried clear of the ground and the long tail serving as counterbalance.

A comparable behaviour is evidenced as far back as the Late Permian, where tracks from Texas show the presence of a reptile travelling at speed on its hind feet only. Intriguingly, moreover, only two digits were utilized, the impression of one (probably digit IV) being much larger and deeper than that of the other (probably digit III), of which only the innermost phalange is impressed (Fig. 11). Essentially, the little trackmaker was running on a single digit, as did the horses many millions of years later.

At the time when Roy Moodie described these Texas tracks (1930), and even 40 years later when I redescribed them (1971), no bipedal reptiles were known from the Permian, although the morphology of the Younginiformes suggested a potential for such behaviour. However, in 1982 a bipedal, lizard-like reptile was described from the Late Permian of South Africa by Robert Carroll and Pamela Thompson. Since the Atlantic Ocean did not exist at that time, this was close enough to Texas; and, once again (as with *Chirotherium*) a footprint discovery had amply anticipated one from bones!

Footprints may serve to confirm a deduction made from bones alone. From their osteology it was concluded that the rhipistideans, a group of early freshwater fishes, should have been able to use their fins — fins that had strong bony axes — to haul themselves laboriously from one pool to another in the beds of drying-out streams. A track from the Old Red Sandstone of the Isle of Hoy, Orkney Islands, Scotland, demonstrates exactly this behaviour, for it exhibits a broad central drag furrow formed by the fish's belly, with alternating fin impressions on either side (see Wilson *et al.*, 1935, p. 141; Sarjeant, 1974, p. 282-283, fig. 5).

At the other extreme of terrestrial vertebrate evolution, tracks in volcanic ash that had freshly fallen on the Laetoli Plain of Kenya, some 3,500,000 years ago, show that our ancestors the australopithecines, earliest of humankind, could walk freely in an upright posture, as indeed their skeletons had already caused their discoverers to suppose (Leakey and Hay, 1979).

Footprints may serve also to settle a disputable point. The running walk of horses has been thought by some zoologists to have been a man-taught gait. Not so; trails of the Pliocene horse *Hipparion*, formed in the surfaces of soft lava at Laetoli, show exactly that gait Renders, 1984), and no-one has claimed

Figure 11 Moodieichnus didactylus *(Moodie, 1930) Sarjeant 1971; imprints of a reptile which, while running bipedally at speed, impressed only one principal and one subsidiary digit of the hind foot. Late Permian, Texas, United States.*

that the australopithecines had domesticated the horse!

Footprints may even serve to contradict unwarranted presumptions. For example, it was long considered likely that herbivorous dinosaurs, when pursued by predators, would take refuge in rivers or lakes, into which the theropods (carnivorous dinosaurs) could not follow them. Indeed, it has been widely considered that a majority of herbivorous dinosaurs were essentially aquatic, despite the lack of any appropriate modifications of their skeletons. Such erroneous theories are difficult to disprove, for direct evidence for swimming ability is rarely to be expected. Yet, by chance, the Lower Jurassic strata of Rocky Hill, Connecticut, show patterns of claw traces that can only have been made by swimming strokes of the hind feet of a large theropod, probably a megalosaur (Coombs, 1980). Rivers and pools, then, were no refuge, unless the herbivores chanced to be able to swim faster than the carnivores, and for that we have no evidence!

It was long supposed by paleontologists that the huge, long-necked, long-tailed sauropod dinosaurs of the Jurassic and Cretaceous were too massive ever to have walked on land, and that, as with whales, their great weight needed to be sustained by the buoyant support of water. This hypothesis entirely contradicts the detail of their skeletal anatomy, for the massive, pillar-like limbs and the superbly designed vertebrae, combining as they do maximum attachment surfaces for muscles (and thus, maximum stress-bearing capacity) with the lightest possible weight, are osteological adaptations that make sense only if the dinosaurs were habitual pedestrians. Yet, it was a hypothesis that long held sway.

The conclusive evidence enforcing its abandonment came from sauropod tracks studied and collected by Roland T. Bird, from West Verde and Paluxy Creeks, Texas. These showed sauropods sometimes wading in water too shallow for their bodies to be immersed, sometimes walking across sand banks entirely out of the water (Bird, 1944, 1954, 1985, p. 162-189). Quite evidently, these dinosaurs were perfectly able to sustain their great bulk in air! Moreover, they were efficient walkers, having a narrow trackway and a stride of up to 2 m. The long tail was only rarely dragged along; usually, as might be expected in animals so mobile, it was carried high.

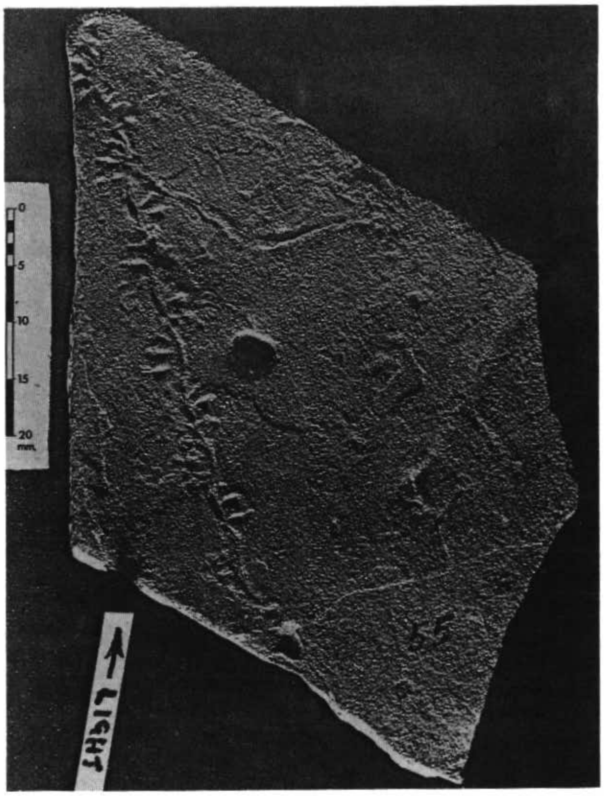

Figure 12 *A track of a larval amphibian (*Oklahomaichnus millsi *Sarjeant, 1976) from the Pennsylvanian (Late Carboniferous) strata of Oklahoma, United States.*

FOOTPRINTS AS EVIDENCE FOR SOCIAL BEHAVIOUR

These tracks from Texas served also to establish a further important point. From the finds of massive accumulations of bones at localities such as the Howe Quarry in Wyoming, there had been reason to suspect that the sauropods lived in herds (see Bird, 1985, p. 47-59). The Texas tracks demonstrated this beyond doubt; the sauropods were moving together, in the same direction and at the same time (Bird, 1944, 1954, 1985, p. 162-163). Moreover, the sauropods in the herd had been of varying sizes, juveniles and adults travelling together, an indication of social behaviour among dinosaurs that was so startling as to be long disbelieved. Yet, like Bird's other deductions, this behaviour has been confirmed by subsequent finds of sauropod tracks, in particular by the discovery of more than 100 trackways in the Purgatoire valley, southeastern Colorado (Lockley *et al.*, 1986), where the efficiency of the sauropods as pedestrians and their herding behaviour is unequivocally demonstrated.

Social behaviour in other dinosaurs is being increasingly evidenced by tracks from a variety of other localities. The herbivorous bipedal dinosaurs, whose tracks occur so abundantly in the Peace River Canyon of British Columbia, were emphatically social. Juveniles were gregarious and stayed together until large enough to join herds of more mature animals. In those herds, the dinosaurs — most unexpectedly — walked side by side, seldom crossing paths, and changed direction together, almost with the smooth co-ordination shown by a marching line of soldiers (Currie and Sarjeant, 1979; Sarjeant, 1981; Currie, 1983). When one of the dinosaurs lurched sideways, the three others walking beside it veered away to avoid a collision before resuming step!

If herbivorous dinosaurs foraged in herds, some of the smaller carnivores hunted in packs; this has been demonstrated from the Late Triassic-Early Jurassic of Massachusetts (Ostrom, 1972) and is apparent also in the Middle Cretaceous trackways of the Peace River Canyon. These smaller carnivores might be thought of as the wolves of the dinosaur world; the largest of the theropods, the tyrannosaurs, hunted like tigers, in pairs or alone (Sarjeant, 1981, p. 171).

FOOTPRINTS AND INDIVIDUAL BEHAVIOUR

Finally, vertebrate footprints can provide information of a sort that can never be obtained from skeletons. The old idea that dinosaurs were slow-moving, slow-thinking creatures, like inadequately activated automata, has clouded the thinking of paleontologists for too long, but to be able to determine their actual speed of movement is an unexpected bonus. Yet this is perfectly possible from study of their tracks. Utilizing a calculation formulated by Alexander (1976), one may show that the bipedal, herbivorous dinosaurs moved habitually at rates ranging between a leisurely amble, at approximately 3 km per hour, to a fast walk at 9 km per hour. The carnivores seem to have been habitually faster moving than the herbivores, normally proceeding at between 6 km per hr and 9 km per hour, but attaining speeds of more than 16 km per hour when running (equal to the fastest running speed of a human athlete). Demathieu (1984) has extended this technique to assess the speed of dinosaurs with a leaping, rather than running, mode of progression; he has determined speeds of 6 km per hr to 13.2 km per hour.

Another way in which footprints can be utilized is to study the changes in proportions of the foot during ontogenesis. More than 40 years ago, Richard S. Lull (1953) showed how, by plotting footprints onto Cartesian diagrams, such changes in shape might be analyzed, but little work has yet been done in this regard. The early hadrosaur footprints of the Peace River Canyon, mentioned earlier (p. 84), show an inverse relation between the relative breadth to length ratio of the foot and the degree of maturity of the individual dinosaur (Currie and Sarjeant, 1979, p. 113). Larval tracks of amphibians are known; these include the smallest fossil vertebrate tracks yet reported, from the Pennsylvanian of Oklahoma (Sarjeant, 1976; see Fig. 12). Such tracks promise to give insights on vertebrate development that cannot be gained from bones.

There is even promise that we may use footprints as a means for assessing the number of animals of a particular species in a region. A formula for this purpose has been developed and successfully applied in determining the numbers of African elephants today from footprints in alluvial plains. As Lockley *et al.* (1986) pointed out, it might be used equally successfully, from the examination of bedding-planes where footprints are abundant, for determining numbers of dinosaurs.

Paleoichnology — the study of fossil traces — has risen in scientific estimation during the last few decades. From being a study despised by those vertebrate paleontologists brought up on the dogmas of comparative anatomy, it has come to be a prime means for establishing the facts about long-extinct animals. It provides a window through which we may peer into the past and see those animals in action.

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