

A re-appraisal of some supposed dinosaur footprints from the Triassic of the English Midlands

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Abstract: When vertebrate footprints were first discovered more than twenty years ago in the Triassic strata of Worcestershire and Nottinghamshire, seven morphological types were considered to be probably the footprints of small dinosaurs. Their restudy is reported. None can now be attributed to dinosaurs; instead, one is considered to be of lacertoid, two of chirotherioid and four of crocodyloid character. The new combination *Paratetrasauropus swinnertoni* (Sarjeant, 1970) is proposed for one of the latter; five of the others are re-attributed to alternative, more appropriate, ichnogenera.

Introduction

Although the first scientific studies of fossil vertebrate footprints were made in Scotland during the late 1820's, it was in Germany and England — especially Cheshire — that most major subsequent discoveries were made during the latter part of the nineteenth century and the first decades of this century. In Germany, the scientific study of fossil vertebrate footprints has continued almost without interruption up to the present. In the United Kingdom, their scientific study came to a virtual end after the First World War, a hiatus enduring for some forty-eight years.

My own interest in vertebrate footprints was aroused by a series of chances. After an early-winter executive meeting of the East Midlands Geological Society in the Nottingham Technical College, I was descending the stairs with the late Richard E. Elliott when he said to me, "I could never understand why, when your Department left this building to move to the new University campus, they didn't take along that slab of vertebrate footprints". I replied with surprise, "What slab of footprints?" Dick answered by taking me behind the building and showing me by torch-light a large slab exhibiting the tracks of a quadrupedal reptile, secured by rusting stanchions to an outer wall beside what had been the door to the original Geology Department of the University of Nottingham. This proved to be a specimen of great historic interest, eventually re-described and illustrated in an early issue of *The Mercian Geologist* (Sarjeant, 1966); it is now lodged in the Natural History Museum, Wollaton Park, Nottingham and is still the only reptile trackway to be discovered in the Permian of the English Midlands.

My concern with footprints might have ended there. However, during a second move of the Geology Department, more vertebrate footprint specimens were found. These had been collected within the city of Nottingham and had hitherto received only brief published mention (Swinnerton, 1913). Together with some other specimens rediscovered subsequently, they were re-described in two further papers (Sarjeant, 1967; 1970).

In writing all three papers, considerable problems were encountered. No attempts to standardize the approaches to the description, illustration and classification of fossil vertebrate footprints had been made at that time. Consequently, the techniques used

were decided upon arbitrarily. The footprints were photographed under darkroom conditions, in oblique illumination from a succession of different angles. The interdigital angles were measured and illustrated in diagrammatic sketches (it should be stressed that this was done as a descriptive procedure rather than as a basic tool for vertebrate footprint classification since, from studies of modern footprints, it is known that the angle varies according to the animal's speed and gait and the hardness of the substrate). The size, shape, relative length and (in the case of digit V) degree of opposition of the digits were considered of much greater importance in determining both behaviour and affinity. Though these approaches were to be refined greatly in ensuing years (see Sarjeant, 1989), they have undergone no essential changes.

At that time, trace fossils were a nomenclatural "no-man's-land", excluded from consideration in either the zoological or the botanical codes of nomenclature. Though I was later to become very much involved in the question of trace fossil classification (Sarjeant and Kennedy, 1973; Basan, 1979), I had not yet begun to formulate any philosophical principles, instead adopting existing nomenclatural procedures and ideas of biological affinity. My present view — that fossil footprints, being essentially sedimentary structures, should be named entirely on the basis of their morphology and **not** upon the presumed identity of the trackmaker (see Sarjeant, 1990) — had not yet been formulated; nor is it shared by all vertebrate palaeoichnologists.

Difficulties with descriptive procedures and nomenclature reached an apogee when I was invited by the late Leonard J. Wills to collaborate in the study of some footprints he had discovered in cores from boreholes put down by the East Worcestershire Waterworks Company. As I have written earlier (Sarjeant, 1981, p. 145):

"When I saw his specimens, I was not much impressed. Yes, there did appear to be imprints on a few of the slabs, but their quality seemed poor; and, in some specimens on which he claimed to see footprints, I could see nothing at all. It was more as a courtesy to a venerable geologist than from any other motive that my technician and I took the specimens back to the University of Nottingham for full examination. When we examined them under oblique

illumination in a dark room, my astonishment was great; in every instance, the slab did indeed bear footprints, many so extremely shallowly imprinted that I still marvel at his having perceived them in the field.”

In our joint paper, the difficulties encountered in studying those specimens were stressed (Wills and Sarjeant, 1970, p. 411):

“The footprints described here presented difficulties of recognition, illustration and description, since they are generally shallowly impressed. The majority are single prints, but, in the cases where trackways are present, their study was not greatly eased — in one instance, because the wet nature of the sediment, when imprinted, has blurred the form of the tracks; in two other instances because, even under the most favourable illumination, only one print was clearly visible at a time.”

For those reasons, although several of the Worcestershire specimens represented undescribed types, no new taxa were proposed. Instead, after being described and illustrated, the footprints were given very tentative systematic attributions, then used optimistically to assess the likely mid-Triassic fauna of that region.

After our work was completed, the Worcestershire specimens were lodged in the collections of the Geology Department of the University of Birmingham, with which Wills had been long associated. The Nottingham specimens remained in the collections of that University and were on display at a public “open day” early in 1969. That proved unfortunate since, while they were still out in a laboratory on open tables, the Geology Department was badly damaged by fire and the laboratory almost wholly destroyed. The specimens were recovered from the rubble and re-identified, but they had been severely discoloured and many had suffered other damage, such as cracking and flaking. Subsequently they were lodged in the collections of the Natural History Museum, Wollaton Park, Nottingham.

The Identity of the Trackmakers

Both in my reports of the Nottingham footprints (Sarjeant, 1967; 1970) and in my work with Wills (Wills and Sarjeant, 1970), I believed I had recognized the footprints of dinosaurs. At that time, the correlation of Triassic sediments, not just in Britain but worldwide, was still a subject for much dispute and the presence of dinosaurs in Middle Triassic strata seemed likely enough. Moreover, though some of the footprints were tiny, the coelurosaurs would surely have been just as tiny after hatching; indeed, most never attained great size, even in adulthood. The present consensus, that newly hatched dinosaurs remained long in their nests, being fed and tended by adults (see various papers in Carpenter *et al.*, 1994), was behaviour unsuspected by scientists at that time.

By 1991, correlations were becoming firmer and the knowledge of early dinosaurs very much greater. In a paper presented at the IInd Georges Cuvier Symposium

in France that year, Dr Tony Thulborn (University of Queensland, Australia) critically reassessed the supposed evidence for pre-Carnian (Late Triassic) dinosaurs, as furnished by footprints reported from Britain and other countries. He concluded that it was uniformly unreliable, dismissing in particular the supposed evidence from the English Midlands. Moreover, the evidence from bones indicated that, though their ancestors the thecodonts were present much earlier, the dinosaurs proper did not appear till the late Carnian (Hunt, 1991). It was as a consequence of Thulborn’s cogent criticisms that this restudy was undertaken.

Stratigraphy

The Worcestershire footprints are present on complete or broken slabs from boreholes drilled at Bellington, near Kidderminster (National Grid reference SO 877 768). These boreholes penetrated the entire thickness of strata then assigned to the Bunter Formation (Bunter Pebble Beds and Upper Mottled Sandstone), passing downward into the Permian Dune Sandstone. Footprints were present in both Triassic units — in the Bellington No. 3 borehole at depths of 165m (540ft) and 270m (886ft) and in the No. 4 borehole at depths of 70m (229ft), 190.5m (625ft), ca. 305m (ca. 1000ft), 306m (1005ft) and 351m (1152ft).

Because the original correlations between England and Germany are now considered dubious, the name “Bunter Formation” has been abandoned. The former ‘Pebble Beds’ are now included in the Kidderminster Formation (Warrington *et al.*, 1980, p. 58), while the Upper Mottled Sandstone is now termed the Wildmoor Sandstone Formation (Warrington *et al.*, 1980, pp. 62-63); the two units are regarded as being lateral equivalents, at least in part. Both are placed in the Scythian (Lower Triassic).

The Nottingham footprints came from a temporary outcrop located by Swinnerton (1913) as either “the Sherwood suburb” or “Mapperley Park”. His specimens bear the latter label (Swinnerton’s original photographs, preserved in the Geology Department collections at Nottingham, give no locality details). Subsequently Elliott (1961, p. 212) stated that they came from “near the northern end of Cyprus Road, Mapperley Park” (National Grid reference SK 4575 3423). However, Elliott’s basis for identifying the locality so confidently was not made clear. Consequently, this precise locality was not quoted in my papers (Sarjeant 1967; 1970). That area of the city is now built over and no outcrops are visible.

Elliott (1961) stated that the footprint bed was “a few feet below the Waterstones”, which would place it in his Woodthorpe Formation. Elliott’s ‘Waterstones Formation’ was subsequently renamed the ‘Colwick Formation’ by Warrington *et al.* (1980, p. 57); more recently, Charsley *et al.* (1990) have combined the Colwick and Woodthorpe formations, naming their new unit the Sneinton Formation. The date assigned earlier (Sarjeant, 1970, p. 329) was early Ladinian; however, Warrington *et al.* (1980) have since given an older date — middle Anisian — within the Middle Triassic.

Systematic Reconsideration

1. The Supposed 'Dinosaur Footprints' from Worcestershire

These are reconsidered under the names, and following the text order, utilized by Wills and Sarjeant (1970). Ichnotaxa names in single quotation marks are reclassified in this account.

'*Coelurosaurichnus* cf. *ziegelangernensis* Kuhn, 1958' (Pl. I, no. 4; Fig. 1a)

This small tridactyl impression was originally considered to be that of a bipedal reptile, apparently a coelurosaur, and likened to pes prints of the ichnospecies *Coelurosaurichnus ziegelangernensis* Kuhn (1958) from the Semionotensandstein (Late Triassic; Norian) of Germany. A restudy of this footprint shows it to be more informative in morphological terms than hitherto supposed (Pl. I, no. 4). It is here redrawn (Fig. 1a). There is no residual similarity to *Coelurosaurichnus*, to which ichnogenus the footprint cannot now be assigned, while an apparent similarity to *Anchisauripus* extends only to the digital impressions, no heel being impressed.

The relative lengths and curvature of the digits indicate that this is a left, not a right, pes; the digits are re-numbered accordingly (Fig. 1a). A comparison with Haubold's illustration of pedal osteology (1984, Fig. 26) indicates a strong similarity to the functionally tridactyl foot structure of the primitive crocodylian *Trialestes* (= *Triassoolestes*) and, though rather less strikingly, to the central, functional three digits of the thecodont *Euparkeria*. In terms of footprint ichnogenes, greatest similarity is found (in digit shape, size and proportionate length) with the tridactyl pes of *Tarsodactylus caudatus* Hitchcock, 1858, a presumed crocodylian imprint from the Late Triassic of Massachusetts (see Haubold, 1984, Fig. 105, no. 4). Though the Nottinghamshire footprint is not attributable to that ichnospecies (digits II and IV are too slender, the claws also too slender and the divergence of digits too small), it is better named *Tarsodactylus* sp. and considered most probably the footprint of a primitive crocodylian.

'*Coelurosaurichnus* spp. A and B'. (Plate I, nos. 2, 3; Figs 1b-c)

These constitute an isolated cast (sp. A) and mould (sp. B), both of diminutive size (type A being 1.7cm long and type B only 0.75cm long). Both were originally considered trifid and identified as footprints of small, presumably juvenile, coelurosaurs. It was suggested earlier (Wills and Sarjeant, 1970, p. 406) that type A corresponded closely with two small traces described by Beasley (1896, pl. 2, Figs. H2 and H3) from the 'Keuper' of Weston Point in Cheshire. However, Beasley (1896, p. 408) doubted that these "were really tridactylate".

Restudy of the Worcestershire footprints confirms the presence of unguis and digital pads, showing that these are indeed vertebrate footprints and contradicting the earlier idea of Thulborn (1990, p. 227) that they were produced by limulids (Xiphosurida). However, it

demonstrates also that dinosaurs were certainly not the trackmakers.

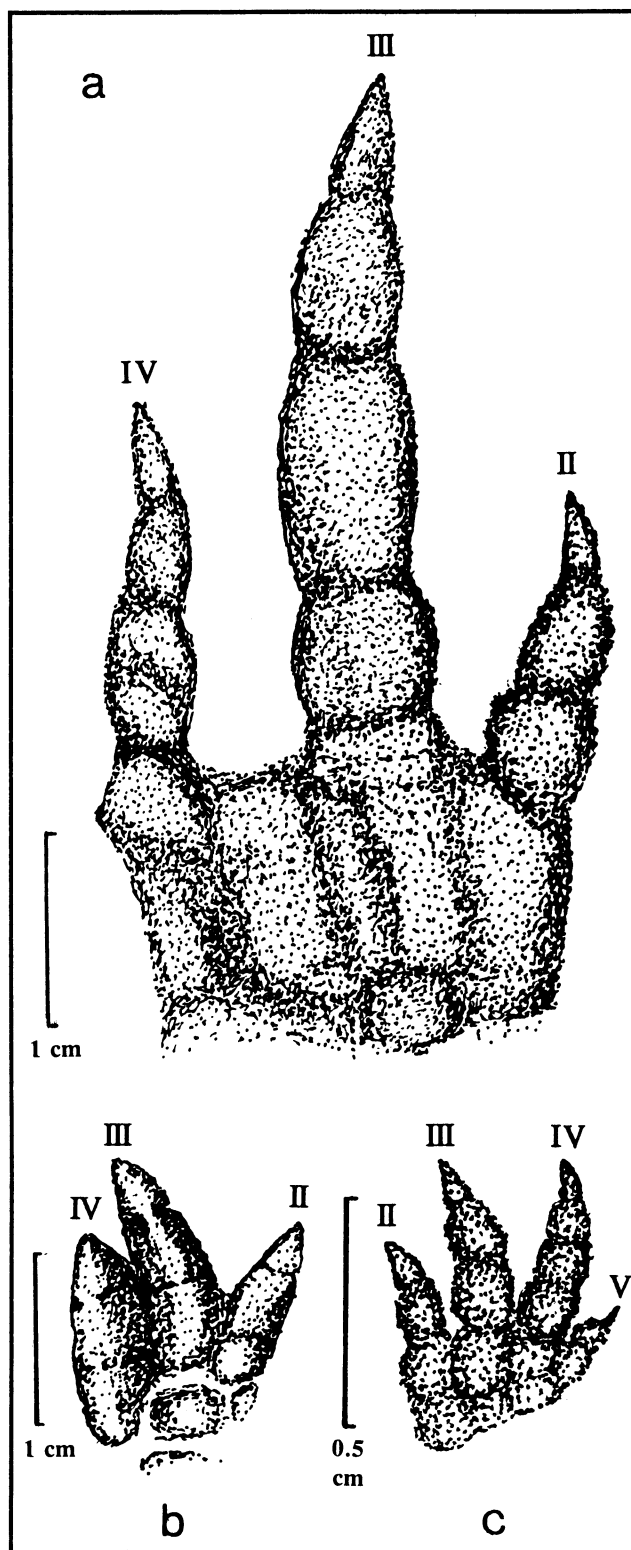


Fig. 1. Supposed dinosaur footprints from the Triassic of Worcestershire, England; redrawings showing identification of digits. (a) *Tarsodactylus* sp. (formerly *Coelurosaurichnus* cf. *ziegelangernensis* of Wills and Sarjeant, 1970); left pes $\times 2.5$; (b) *Batrachopus* sp. (formerly *Coelurosaurichnus* sp. A of Wills and Sarjeant, 1970); probably the left manus $\times 2.5$; (c) *Plectopterna* sp. (formerly *Coelurosaurichnus* sp. B of Wills and Sarjeant, 1970); right manus $\times 6$.

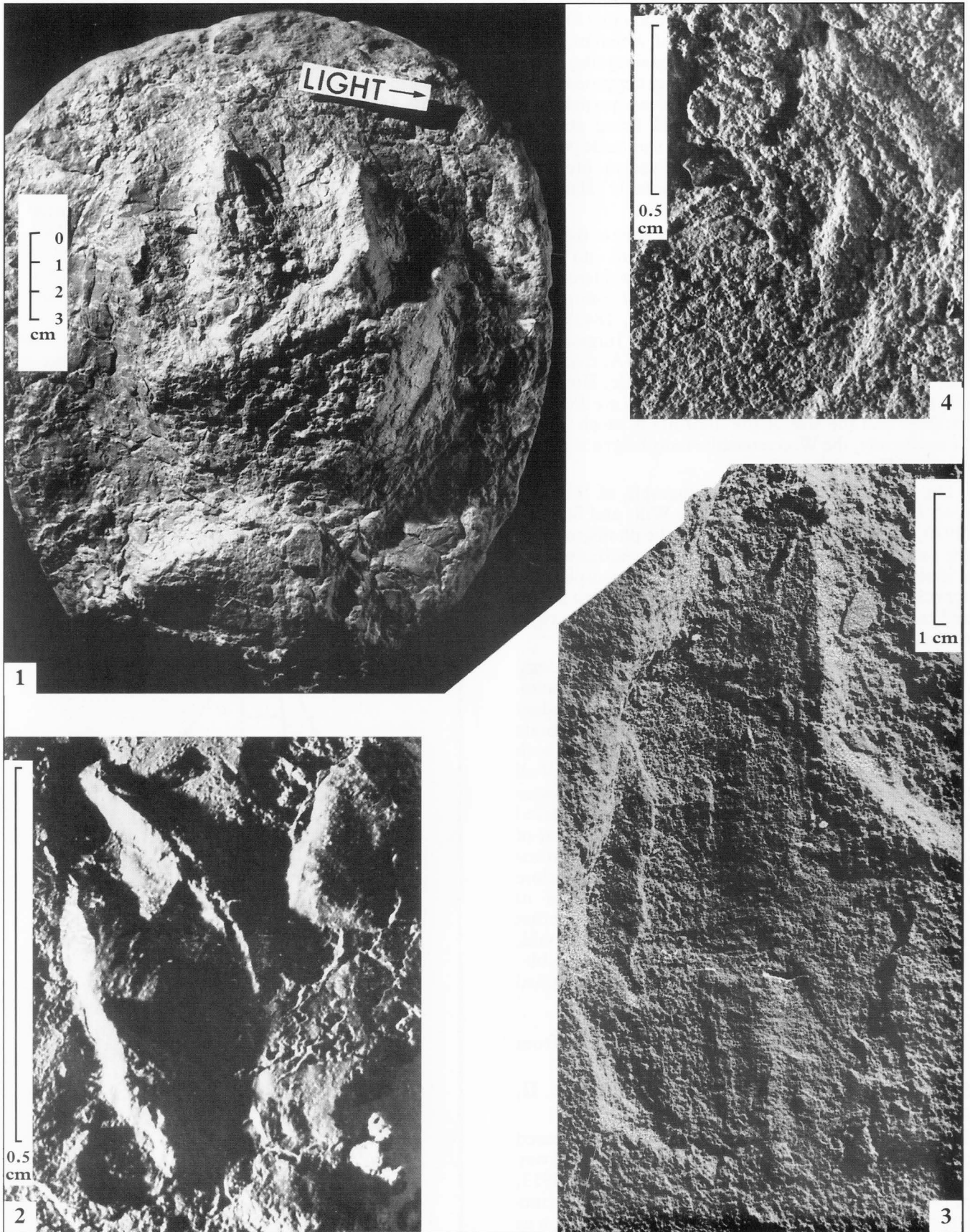


Plate I 1. *Paratetrasauropus swinnertoni* (Sarjeant, 1970), comb. nov. The holotype (formerly ?*Otozoum swinnertoni*); right manus. 2. ?*Batrachopus* sp. (formerly *Coelurosaurichnus* sp. A of Wills and Sarjeant, 1970); probably the left manus. 3. ?*Plectopterna* sp. (formerly *Coelurosaurichnus* sp. B of Wills and Sarjeant, 1970); right manus. 4. *Tarsodactylus* sp. (formerly *Coelurosaurichnus* cf. *ziegelangermensis* of Wills and Sarjeant, 1970); left pes.

'*Coelurosaurichnus* sp. A' is here re-illustrated (Pl. II, no. 2). Re-interpretation of its morphology (Fig. 1b) suggests that it is an impression of a manus (most probably a left manus) of a quadrupedal reptile, rather than the right pes of a biped, as earlier supposed. Two digits are slightly convergent. These are provisionally interpreted as III and IV, digit II being strongly divergent. This revised interpretation was made possible by the availability of a more extensive literature illustrating tetrapod trackways (notably Haubold, 1984).

Haubold's (1984, Fig. 26) reconstructions of the pedal anatomy of Triassic footprints afford no close comparisons. However, the footprint considered here is so similar to the manus impressions of *Batrachopus* (ex: *Sauroidichnites*) *deweyi* (Hitchcock, 1843) Lull, 1904, from the Late Triassic-Early Jurassic red sandstones of the Connecticut valley, USA, that it too may be a manual print of a small crocodile. However, the manual digital impressions of *B. deweyi* are distinctly stubbier and the size of the imprints is much larger. Consequently, the Worcestershire morphotype is named merely ?*Batrachopus* sp.

Only a sketch, and not a photograph, of '*Coelurosaurichnus* sp. B' was published by Wills and Sarjeant (1970, Fig. 3G). Re-examination of the photographs of the footprint (see Pl. I, no. 3) brought realization that it is not tridactyl but tetradactyl, with an inconspicuous, short fourth digit (Fig. 1c). On the bases of digit length and curvature, this is considered the imprint of a right manus, the fourth digit being digit V.

The small size of this footprint (length only 0.75cm) makes a dinosaur affinity improbable. Rhynchocephalian (sphenodontoid) footprints are an abundant component of Middle to Late Triassic vertebrate ichnofossil assemblages but, typically, digit IV of both manus and pes is unusually long, while digits II-IV all tend to be curved inward. These features are not seen in the Worcestershire footprint and it is considered instead, therefore, that this represents the imprint of a lacertoid manus. Of lacertoid footprints described from the Middle to Late Triassic, none shows close similarity; the manual impressions of species of *Plectopterna*, an ichnogenus accommodating tracks that are more often bipedal than quadrupedal (Haubold, 1971, p. 50-51), are perhaps most comparable. Consequently this footprint is provisionally reclassified as ?*Plectopterna* sp.

2. The Supposed 'Dinosaur Footprints' from Nottingham

Swinertonichnus mapperleyensis Sarjeant, 1967. (Pl. II, no. 1; Fig. 2)

The type and only species of this ichnogenus is based upon a single pes print surviving from a partial trackway on a slab illustrated and described by Swinnerton (1913, p. 67, pl. IV, Fig. 4). The specimen shows two prints almost superimposed, characterized by Swinnerton as follows:

"The presence of strong claws at once strikes the eye and points to reptilian affinity. Further study shows that the toes, which had a span of five

inches, were more parallel than but not so evenly balanced as in print A. The curved line between some of the toe marks suggests that the feet were webbed. It is evident that the sole was not placed on the ground for marks only of digits occur, and the impression of one foot has not seriously disturbed the other, though the two are quite close to one another. A slight disturbance is however observable in that the claw mark of the hind print has been flattened sideways by the pressure which made the front print. The latter must therefore have been made by the hind foot which has been placed on the ground in front of the impression of the fore foot, a peculiarity which may be noticed in almost any common animal."

The remainder of the slab described by Swinnerton is lost. The surviving specimen from that trackway was earlier considered (Sarjeant, 1967) to be the footprint of a biped, envisaged as "a web-footed coelurosaur". That opinion cannot now be maintained.

Swinertonichnus mapperleyensis is morphologically unique, since it shows a prominent 'heel' and three narrow, blunt-tipped and weakly divergent digits connected by a large web. It differs from typical theropod tracks in having an almost U-shaped rear margin, parallel-sided digits and well-rounded toe-tips with no indication of claws. The pattern of digital nodes, apparently 0-3-4-4-0, is without parallel among dinosaurs.

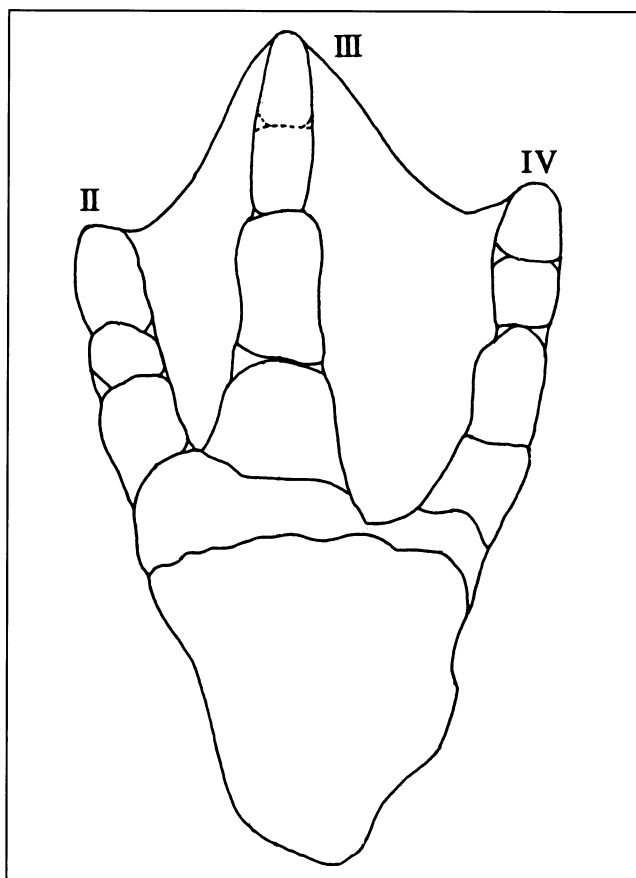


Fig. 2. *Swinertonichnus mapperleyensis* Sarjeant 1967, from the Triassic of Nottinghamshire, England; sketch of right pes, showing revised identification of digits, \times approx. 0.9.

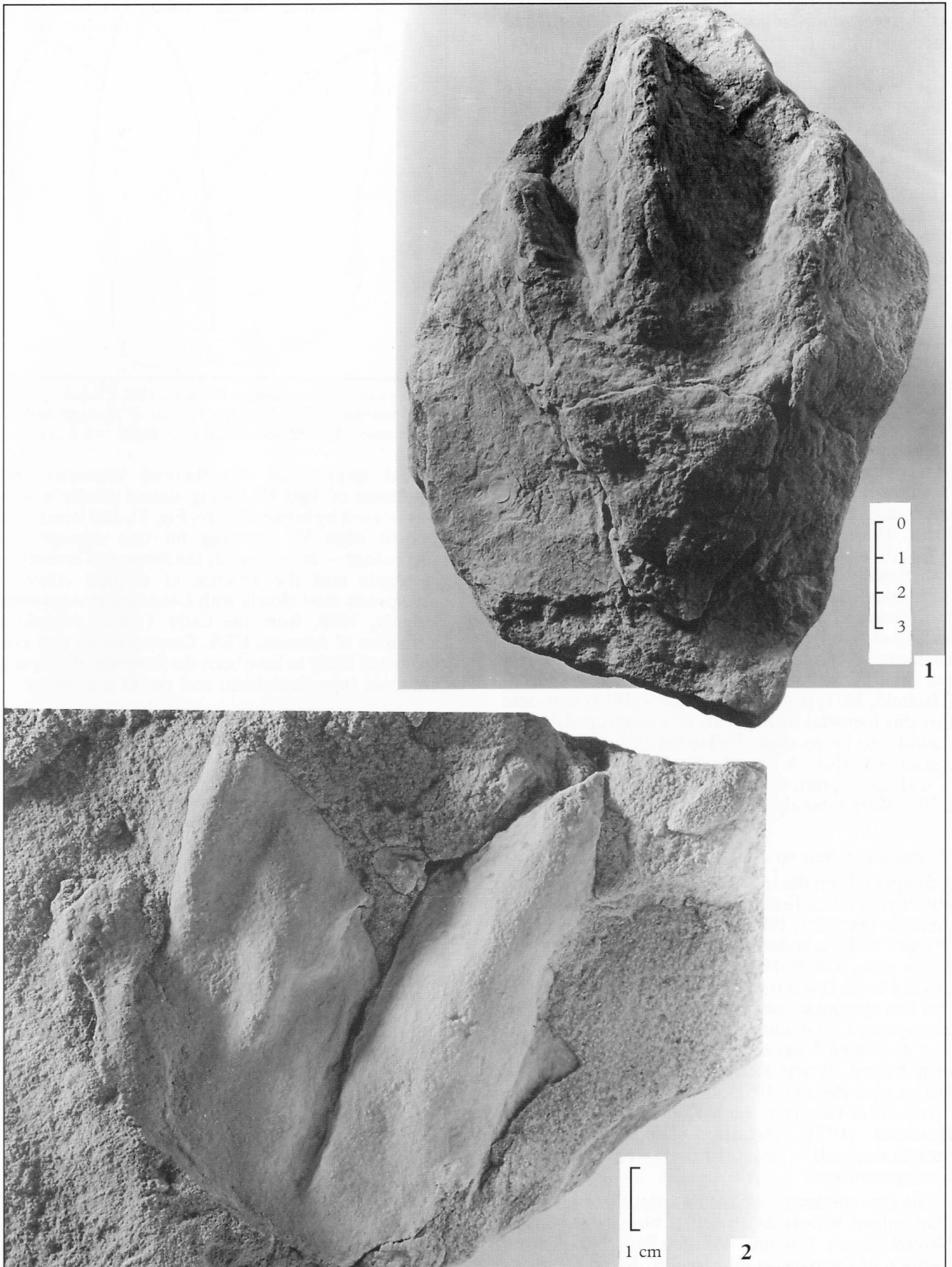


Plate II 1. *Swinertonichnus mapperleyensis* Sarjeant, 1967. The holotype; a right pes. 2. *Chirotherium maquinense* Peabody, 1948 (formerly *Coelurosaurichnus* sp. of Sarjeant, 1967); impression of right manus, lacking the opposed digit V.

The type specimen is a natural cast, identified as a pedal impression (Sarjeant 1967, p. 333). It suffered discoloration and surficial flaking in the Nottingham University fire of 1969 and is now lodged in the Natural History Museum, Wollaton Park, Nottingham (specimen PC3315). Fortunately, photographs were taken before the fire from several different angles and were available for study; one is reproduced here (Pl. II, no. 1).

In the original description (Sarjeant, 1967), the numbering of the digits was transposed; this is now corrected (Fig. 2). Several features of digit IV (=digit II of Sarjeant, 1967) confirm that the specimen is a right pes, namely its weak curvature (convex to the exterior), its relatively large number of nodes and its slight preponderance in length over digit II (=digit IV of Sarjeant, 1967). The first two features are characteristic of digit IV in dinosauroid tracks, while the third feature parallels the ectaxonic condition that prevailed in pes prints of chirotherioid type. The flattened bulge at the base of digit IV may represent a vestige of digit V.

The most remarkable feature of *S. mapperleyensis* is its webbing (Pl. II, no. 1; Fig. 2), a feature unknown in dinosaur footprints but present in some crocodyloid tracks, e.g. *Apatopus* (ex: *Otozoum*) *lineatus* (Bock, 1952) Baird, 1957, an ichnogenus considered by Haubold (1971, p. 59) to comprise the footprints of a phytosaur. Functionally tridactyl phytosaur footprints have not been reported, however. In contrast, pedal imprints of two Triassic ichnogenes, *Tarsodactylus* Hitchcock, 1858 and *Agialopous* Branson and Mehl, 1933, are tridactyl; the former is considered by Haubold to be crocodylian, the latter classed among "Tetrapoda triadica indet." (Haubold, 1971, p. 63). Swinnerton's (1913) statement that this footprint formed part of a quadrupedal track should also be recalled. Following this restudy, it is considered that *S. mapperleyensis* is probably a crocodylian imprint, to be placed alongside *Tarsodactylus* in the Morphofamily Batrachopodidae Lull, 1904.

'*Coelurosaurichnus* sp'. (Pl. II, no. 2; Fig. 3)

A footprint from the same locality as *Swinnertonichnus* was attributed earlier to a small, bipedal carnivorous dinosaur (Sarjeant, 1967, p. 338). This was originally thought to be a tridactyl pes print, 8.5cm long and 8.7cm wide, with stubby triangular digits of extremely unusual form. It was considered (Sarjeant, 1967, p. 339) that this specimen "corresponds in morphology to the ichnogenus *Coelurosaurichnus*", but it was recognized that it differed "significantly" from all ichnospecies then known. It was likened also to the ichnogenus *Dinosauripus* Rehnelt (1952), from the Benker Sandstein (Carnian) of Germany; both Kuhn (1958, 1963) and Haubold (1971) classified *Dinosauripus* as a morphologically indeterminate equivalent of *Coelurosaurichnus*.

The type specimen suffered no serious damage in the Nottingham University fire; it is now lodged in the Natural History Museum, Wollaton Park, Nottingham. Restudy of the photographs (see Pl. II, no. 2) shows it to be not a tridactyl pes impression, as originally supposed (Sarjeant, 1967, p. 337), but a damaged right

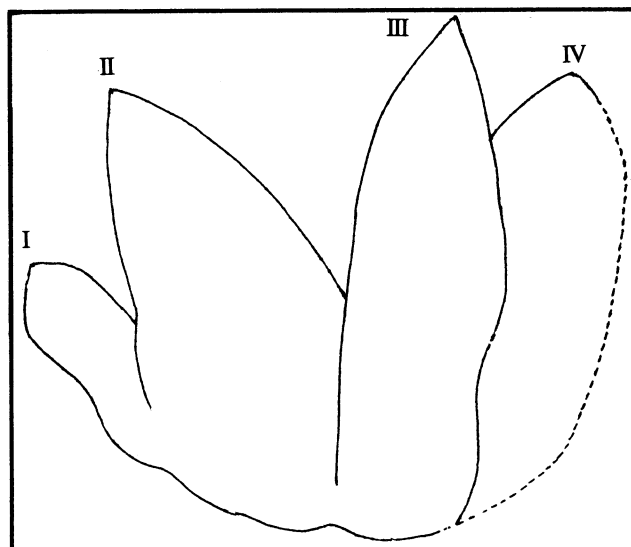


Fig. 3. *Chirotherium maquinense* Peabody, 1948 (*Coelurosaurichnus* sp. of Sarjeant, 1967), from the Triassic of Nottinghamshire, right manus, showing identification of digits, $\times 0.9$ approx.

manual imprint of chirotherioid character, the impression of digit IV having almost wholly broken away (shown by broken line on Fig. 3), and lacking the opposed digit V. Allowing for this damage, the morphology — in particular, the shape and breadth of the digits and the absence of distinct claws — corresponds most closely with *Chirotherium maquinense* Peabody, 1948, from the Early Triassic Moenkopi Formation of Arizona, USA. Consequently, it is now considered likely to have been the footprint of a bipedal thecodont (pseudosuchian) and not of a dinosaur.

'*Brachychirotherium coburgense* Aumann, 1957'. (Fig. 4)
Another chirotherioid footprint is present in the Nottinghamshire assemblage. This was originally

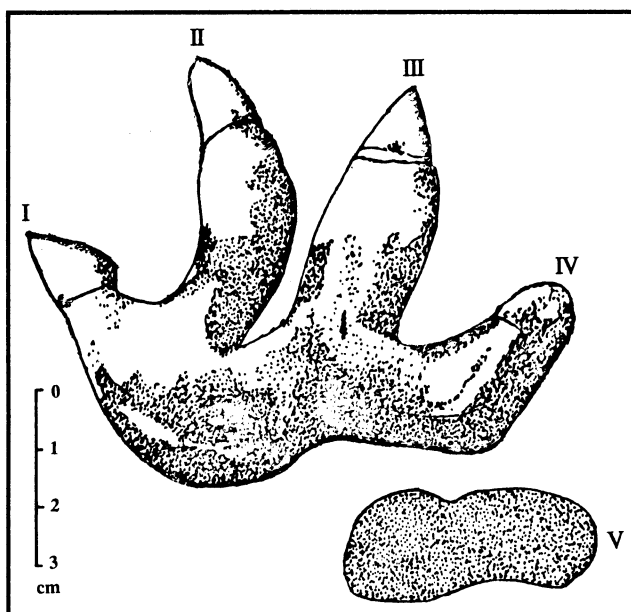


Fig. 4. *Synaptichnium diabloense* Peabody, 1948 ('*Brachychirotherium coburgense*' of Sarjeant, 1967), from the Triassic of Nottinghamshire, England; right manus, showing identification of digits, $\times 1$.

considered to be a pedal impression and attributed (Sarjeant, 1967, p. 337-338) to *Brachychirotherium coburgense* Aumann, 1957, an ichnospecies believed by Haubold (1971) to be a junior synonym of *B. thuringiacum* (Rühle von Lilienstern, 1939) Beurlen, 1950. However, that attribution was based upon a misreading of the original German text. The Nottinghamshire footprint is of a manus, not a pes, and the manus of *B. thuringiacum* is quite dissimilar to the footprint here considered (Fig. 4), its digits being more closely set and blunter. In contrast, the Nottingham footprint is strikingly like the manual imprint of *Synaptichnium diabloense* Peabody, 1948, reported from the Moenkopi Formation (Lower to Middle Triassic) of Arizona, USA. (Points of resemblance are the relative lengths and claw shape of digits I-IV and the rather sausage-shaped digit V, apparently lacking a claw.) It is thus to be considered the footprint of a pseudosuchian reptile — a thecodont, not a dinosaur.

?*Otozoum swinnertoni* Sarjeant, 1970. (Pl. I, no. 1; Fig. 5)

This species was established on the basis of a plantigrade, tetradactyl pes print, believed to have formed part of another trackway described by Swinnerton (1913, p. 66-67, pl. IV, Fig. 3). The trackmaker was envisaged as “a basically bipedal and plantigrade, occasionally quadrupedal animal, with manus much smaller than pes and with pes blunt-clawed, the sole being clearly impressed” (Sarjeant,

1970, p. 271). On account of the form and spacing of its digits, the footprint was confidently identified as a new ichnospecies, but referred only tentatively to the ichnogenus *Otozoum* of Hitchcock (1847). It was suspected that the trackmaker was possibly an early prosauropod dinosaur (Sarjeant, 1967). Haubold (1971, p. 85) noted that *Otozoum* was confined to the Upper Triassic, but nonetheless included ?*O. swinnertoni* in his systematic listing for that ichnogenus; he likewise considered *Otozoum* to comprise the tracks of prosauropods.

This type specimen also suffered surficial flaking and cracking during the Nottingham University fire (p. 23); its restudy is again based upon photographs taken before the fire from different angles, one being reproduced here (Pl. I, no. 1). This restudy does not result in any new morphological interpretations. However, the attribution of this ichnospecies to *Otozoum*, always tentative, cannot now be maintained, since the pedal digits are too short and do not have the stout, often inwardly curving claws of that genus. A much closer comparison is to be found in the pedal imprints of an ichnogenus reported from the Molteno Formation (Late Triassic) of South Africa, *Paratetrasauropus* Ellenberger, 1972, which has comparably short, pointed pedal digits and is considered to be a crocodyloid track (see Haubold, 1984, Fig. 116, no. 2). Moreover, the sprawling gait implicit in the imprinting of the calcaneus accords more closely with that of a crocodile, or perhaps a phytosaur, rather than an early prosauropod. Accordingly, the following new combination is proposed: *Paratetrasauropus swinnertoni* (Sarjeant, 1970) Sarjeant, comb. nov. (= ?*Otozoum swinnertoni* Sarjeant, 1970, p. 270-271, 274, pl. 20, text-figs. 1, 2B). Triassic (Middle Anisian: Sneinton Formation), Mapperley Park, Nottingham, England. Holotype: specimen PC4238, lodged in the Natural History Museum, Wollaton Hall, Nottingham.

Conclusions

This restudy has resulted in the systematic re-attribution of seven types of footprints reported earlier. The ichnotaxa represented are now considered to include footprints of lacertoid, chirotherioid and crocodyloid character; that is, of a lacertilian (?*Plectopterna* sp.), of two pseudosuchians (*Chirotherium maquinense* and *Synaptichnium diabloense*), and of four reptiles that were either crocodylians or phytosaurs (*Tarsodactylus* sp., ?*Batrachopus* sp., *Swinnertonichnus mapperleyense* and *Paratetrasauropus swinnertoni*). Other footprints described earlier from Nottinghamshire (Sarjeant, 1967) included another lacertilian (*Varanopus* aff. *curvidactylus* Moodie, 1929), what may have been a small salamander-like amphibian (*Microsauropus* aff. *acutipes* Moodie, 1929), and a quadrupedal reptile of problematic affinity (*Deuterotetrapous plancus* Sarjeant, 1967). Other vertebrate footprints reported from Worcestershire by Wills and Sarjeant (1970) were attributed to small sphenodonts (*Rhynchosauroides* cf. *pisanus* (Fucini, 1915) von Huene 1941, *Rhynchosauroides* sp. and possibly *Hamatopus* sp.), a possible cotylosaur (?*Procolophonipus* sp.) and a quadrupedal reptile, perhaps an aëtosaur (?*Aëtosauripus* sp.).

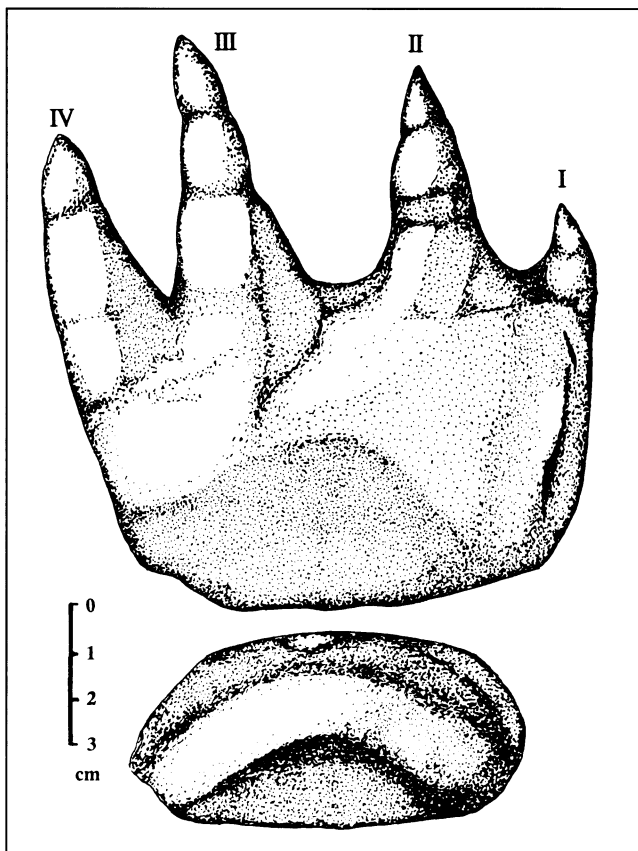


Fig. 5. *Paratetrasauropus swinnertoni* (Sarjeant, 1970), comb. nov. The holotype (formerly ?*Otozoum swinnertoni*); left pes, showing identification of digits, $\times 0.75$ approx.

From the Worcestershire and Nottinghamshire localities, respectively in Lower (Scythian) and early Middle Triassic (middle Anisian) strata, fifteen footprint ichnotaxa have thus been recognized. The predominance of small reptiles is noteworthy but predictable in a semi-arid environment; the presence of aquatic reptiles around pools also occasions no surprise. (The Mapperley pool, in drying out, furnished fish remains in quantity; see Swinnerton, 1913, p. 66). However, this restudy entirely supports Thulborn's contention (see p. 23) that none of the footprints from the Lower or Middle Triassic strata of the English Midlands are truly those of dinosaurs.

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