ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 122 (1996) 213–225

PALAEO

Dinosaurs in the Early and Mid Triassic?—The footprint evidence from Britain

Michael J. King, Michael J. Benton

Department of Geology, University of Bristol, Wills Memorial Building, Queens Road, Bristol, BS8 1RJ, UK

Received 20 December 1994; revised and accepted 12 September 1995

Abstract

The oldest skeletons of dinosaurs date from the Late Triassic (Carnian), but supposed dinosaur footprints have been reported from Lower and Mid Triassic rocks, dated up to 20 m.y. earlier. Supposed Lower Triassic dinosaur footprints from Britain are reinterpreted as ripple marks, mud rip-up clasts, and possible limulid prints. The Middle Triassic material is reinterpreted as partial specimens of *Chirotherium*, presumably produced by rauisuchians, and one indeterminate specimen, possibly also of chirotheroid affinities. The oldest dinosaur footprints from Britain come from the marginal Triassic (Norian, Upper Triassic) in South Wales. Elsewhere in the world, the oldest dinosaur footprints appear to be Carnian, corresponding in age to the oldest skeletal remains.

1. Introduction

There have been several reports of supposed dinosaur footprints from the Lower and Middle Triassic of Britain. These include the earliest record of dinosaurs from Europe, footprints of small theropod dinosaurs from Lower Triassic sediments in borehole cores from Bellington pumping station, Worcestershire, England (Fig. 1; Wills and Sarjeant, 1970). Supposed dinosauroid footprints were also recorded (Sarjeant, 1967, 1970) from the Middle Triassic of Mapperley Park, Nottingham (Fig. 1), ascribed to the theropod ichnotaxa *Coelurosaurichnus* and *Swinnertonichnus*, and the possible prosauropod footprint ?*Otozoum*.

At the time of these publications, the assignment of Lower and Middle Triassic footprints to dinosaurs did not seem unusual, as it was then widely accepted (e.g. Huene, 1932; Romer, 1966, 1970; Cox, 1967; Charig, 1972) that dinosaurs had been present from the Early Triassic. More recent studies indicate that the oldest reliable skeletal evidence of dinosaurs now dates from the Late Triassic (early late Carnian) (Benton, 1990, 1993, 1994a,b; Sereno et al., 1993), with a suggested radiometric date of 228 m.y. for the best-represented forms, from the Ischigualasto Formation in Argentina (Rogers et al., 1993).

There is now a substantial mis-match in the age of the earliest skeletal evidence of dinosaurs and these supposed dinosaur footprints, an apparent gap of 20 m.y. between first footprints and first skeletons. Thulborn (1990) proposed that there is no reliable footprint evidence for dinosaurs in the Lower and Middle Triassic of the British Isles. This idea is tested here.

Museum acronyms are: BU = Lapworth Museum, Department of Geology, University of

SSDI 0031-0182(95)00095-X

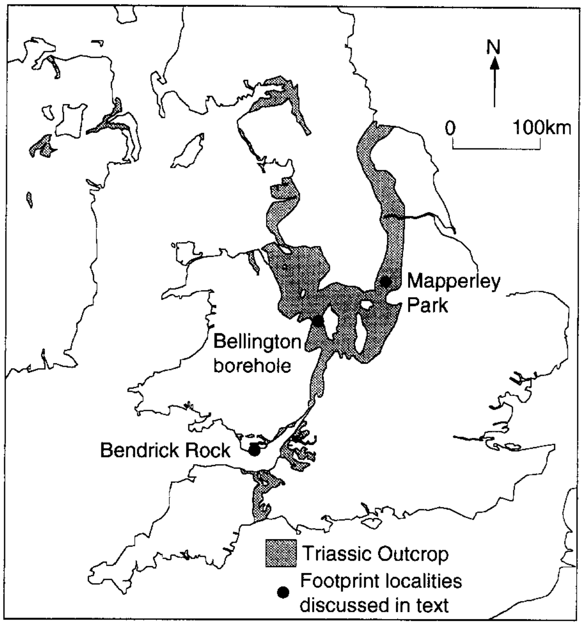

Fig. 1. Triassic outcrop of England and Wales, with footprint localities indicated.

Birmingham; NOTNH = Natural History Museum, Wollaton Hall, Nottingham.

2. The earliest skeletal evidence of dinosaurs

Until the 1970s, there was apparently a rich record of dinosaur skeletons dating from before the Late Triassic. For example, Von Huene (1932) listed ten dinosaurs, based on skeletal remains, from the German Muschelkalk (Mid Triassic), while other authors (Romer, 1966, 1970; Cox, 1967) noted the occurrence of dinosaurs in Middle Triassic formations from South America. These erroneous records resulted from the lack of a precise definition of Dinosauria, the misidentification of thecodontian remains as those of dinosaurs, and the incorrect dating of formations containing genuine dinosaur remains. The German Muschelkalk "dinosaurs", for example, have all been reidentified as prolacertiforms (*Macrocnemus* or *Tanystropheus*), unidentifiable basal archosaurs, or even placodonts (Wild, 1973; Benton, 1984b, 1986a). One of the key groups of supposed early dinosaurs was the Teratosauridae from the Middle and Late Triassic of Europe, as well as the Late Triassic and Early Jurassic of South Africa and China. However, these specimens turn out to be an assemblage of skulls and teeth of rauisuchid thecodontians (*Teratosaurus*) or Archosauria inc. sed., together with the skeletons of prosauropods (Benton, 1984a,b, 1986a,b; Galton, 1985).

Early "dinosaurs" have also fallen by the wayside because of firm application of a cladistic definition of Dinosauria in recent years (Gauthier, 1986; Benton, 1990). This has had the effect of excluding some doubtful "dinosaurs" that in fact lack any apomorphies of the clade. Finally, recent stratigraphic work, particularly in South America, has caused re-dating of some dinosaur-bearing beds from the Mid to the Late Triassic. In particular, Romer (1970) dated the Santa Maria Formation of Brazil and the Ischigualasto Formation of Argentina as Mid Triassic, since both contain abundant fossils of rhynchosaurs, as well as rare dinosaurs. These are now both regarded as Late Triassic in age (e.g. Bonaparte, 1978; Benton, 1986b, 1994a,b; Hunt and Lucas, 1991).

The oldest dinosaurs date from the earlier part of the late Carnian, the early Tuvalian substage (*welleri* and *dilleri* palynological zones), or the middle Carnian (Julian substage, *nanseni* palynological zone), the *Paleorhinus* biochron of Hunt and Lucas (1991), and there appear to be a number of records of this age (Benton, 1993, 1994a,b). The best-known fauna consists of the small theropods *Eoraptor lunensis* and *Herrerasaurus ischigualastensis* (Sereno and Novas, 1992, 1994; Sereno et al., 1993; Novas, 1994; Sereno, 1994) and the small ornithischian *Pisanosaurus mertii* (Bonaparte, 1976), all from the Ischigualasto Formation of San Juan Province, Argentina (Rogers et al., 1993). Of similar age is the theropod *Staurikosaurus pricei* from the Santa Maria Formation of Rio Grande do Sul Province, Brazil. Late Carnian dinosaurs are known also from the Maleri Formation of India, the Chinle Group of North America, and the Timesgadiouine Formation of Morocco. *Saltopus elginensis* from the Lossiemouth Sandstone Formation (late

Carnian) of Elgin, Scotland, if it is truly a dinosaur, is the oldest from Europe.

3. Defining dinosaur footprints

Most of the characters used to diagnose the Dinosauria are based on modifications to the hip, knee and ankle bones (Gauthier, 1986; Benton, 1990; Sereno and Novas, 1992, 1994; Sereno et al., 1993). Some of these are expressed in the characteristics of the footprint and more especially, the trackway. Thulborn (1990, pp. 216-7) noted the key distinctions between footprints made by basal archosaurs (thecodontians) and dinosaurs: "thecodontians with a sprawling posture had plantigrade hindfeet with five toes and an ectaxonic pattern of foot structure, whereas theropods and ornithopods had digitigrade hindfeet with three or four toes and a mesaxonic pattern of foot structure". Thus, the features of dinosaur footprints correspond to certain aspects of the cladistic diagnosis of the clade Dinosauria.

In some cases, the distinction between dinosaur and non-dinosaur footprints is unclear. Certain advanced thecodontians, such as *Ornithosuchus*, were probably capable of making footprints that would be difficult to distinguish from dinosauroid forms. Poorly preserved, or incomplete, chirotheroid tracks can also be mistaken for tridactyl dinosaur footprints. Likewise, theropod and ornithopod prints may be hard to distinguish from bird footprints of the Late Jurassic and Cretaceous.

4. The Bellington borehole "dinosaur" footprint specimens

Wills and Sarjeant (1970) described a Lower Triassic ichnofauna consisting of eight vertebrate ichnotaxa (?*Aetosauripus*, *Coelurosaurichnus* cf. *ziegelangernensis*, *Coelurosaurichnus* sp. A, *Coelurosaurichnus* sp. B, *Rhynchosauroides* cf. *pisanus*, *Rhynchosauroides* sp., *Hamatopus* sp. and ?*Procolophonipus* sp.), including three dinosaurian forms (*Coelurosaurichnus*), as well as running tracks of insects, *Permichnium*. Pollard (1985) also noted abundant specimens of the arthropod resting trace *Isopodichnus* on one horizon. The specimens were observed on sandstone and siltstone blocks extracted from wide-diameter (0.45 m) boreholes drilled in the late 1960s at Bellington Pumping Station, Bellington, near Kidderminster, Worcestershire (Wills, 1970; National Grid Reference SO 877768; Fig. 1).

The footprints were found at depths of 70–350 m in sediments of the Kidderminster Formation (formerly the Bunter Pebble Beds) and of the overlying Wildmoor Sandstone Formation (formerly the Upper Mottled Sandstone). These formations (Fig. 2) are of mid and late Scythian age respectively (Warrington et al., 1980). The apparent dinosaur footprints came from a depth of c. 1000 ft (310 m) from Borehole 4, hence presumably in the Kidderminster Formation, since the overlying Wildmoor Sandstone Formation is up to 150 m thick (Warrington et al., 1980).

We have re-examined the material, on several occasions, and in a variety of lighting conditions, and we can find no unequivocal evidence for any tetrapod tracks. The postulated tracks occur largely on well-preserved siltstone horizons, many of them bearing ripple marks, wind flurries, mud cracks, and burrows and trails of invertebrates. In addition, the specimens of *Permichnium* and *Isopodichnus* are found on such surfaces, and tetrapod tracks would not be unexpected in such a setting. However, such tracks would be expected to be sharply defined, based upon our studies of extensive collections of Triassic tetrapod tracks from other localities. However, all the specimens described by Wills and Sarjeant (1970) are indistinct and irregular, and the most plausible explanation is that they are inorganic sedimentary structures. The specimen of ?*Aetosauropus* may be a set of aligned flute marks, while the specimens of *Rhynchosauroides*, *Hamatopus*, and *Procolophonipus* are probably chance associations of shallow inorganic pits. The three postulated dinosaur prints, *Coelurosaurichnus*, consist of a draped ripple, a small group of mud flakes, and a possible limulid print.

Coelurosaurichnus cf. *ziegelangernensis* Kuhn, 1958

Wills and Sarjeant (1970, pp. 402–404, figs. 2a, 3e, pl. 32, fig. 4) tentatively assigned the first

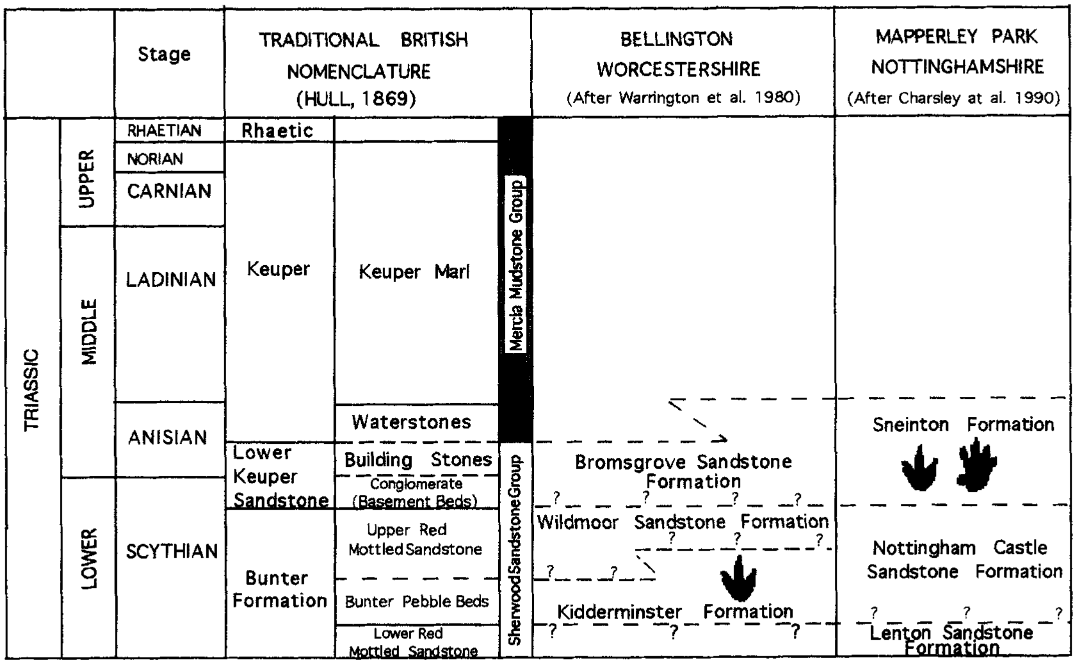

Fig. 2. Stratigraphy of footprint-bearing units of the Lower and Middle Triassic of Central England (based on Warrington et al., 1980).

specimen (BU 2016) to a species named from the Late Triassic of Germany. Haubold [1971, pp. 68-9, fig. 42 (2)] refigured the type specimen of the German ichnospecies, which he mistakenly called *C. ziegelangerensis* (omitting the letter "n").

Wills and Sarjeant (1970) figured one "footprint", which is ringed in white on the specimen. They did not state whether the "footprints" were preserved as moulds or casts. The inference is that they are original impressions, or moulds. They noted that the Bellington "impressions are extremely shallow, being clearly visible only under very low-angle illumination, and few details are afforded; the presence of rather blunt claws is clear, but phalangeal pads are scarcely suggested", although clearly defined phalangeal pads are shown in their figure (Fig. 3A).

The specimen is re-interpreted as inorganic. Examination of the whole core surface shows that it bears numerous impressions of the sort interpreted by Wills and Sarjeant (1970) as a footprint. The impressions are elongate, slightly sinusoidal markings, each measuring about 10 mm wide, and 50–100 mm long. They lie parallel to each other and they are set off from the background fine sandstone by a capping of siltstone. The impressions are clearly the crests of low-amplitude symmetrical sinusoidal-crested wave ripples, spaced with a wavelength of about 20 mm. The ripples have been draped with siltstone, and then covered by a subsequent deposit of fine-grained sandstone. The borehole core has broken across horizontally, hence exposing siltstone-clad ripple crests here and there emerging through the overlying fine sandstone which resides in the ripple troughs.

Coelurosaurichnus sp. A

The second postulated dinosaur footprint (BU 2023; Fig. 3C) was interpreted by Wills and Sarjeant (1970, pp. 404-5, figs. 3d, 4d, pl. 32, fig. 5) as "probably the right pes of a bipedal reptile". This interpretation is not further substantiated.

We reinterpret BU2023 as a chance grouping of tiny mudflakes. The supposed digits and palmar

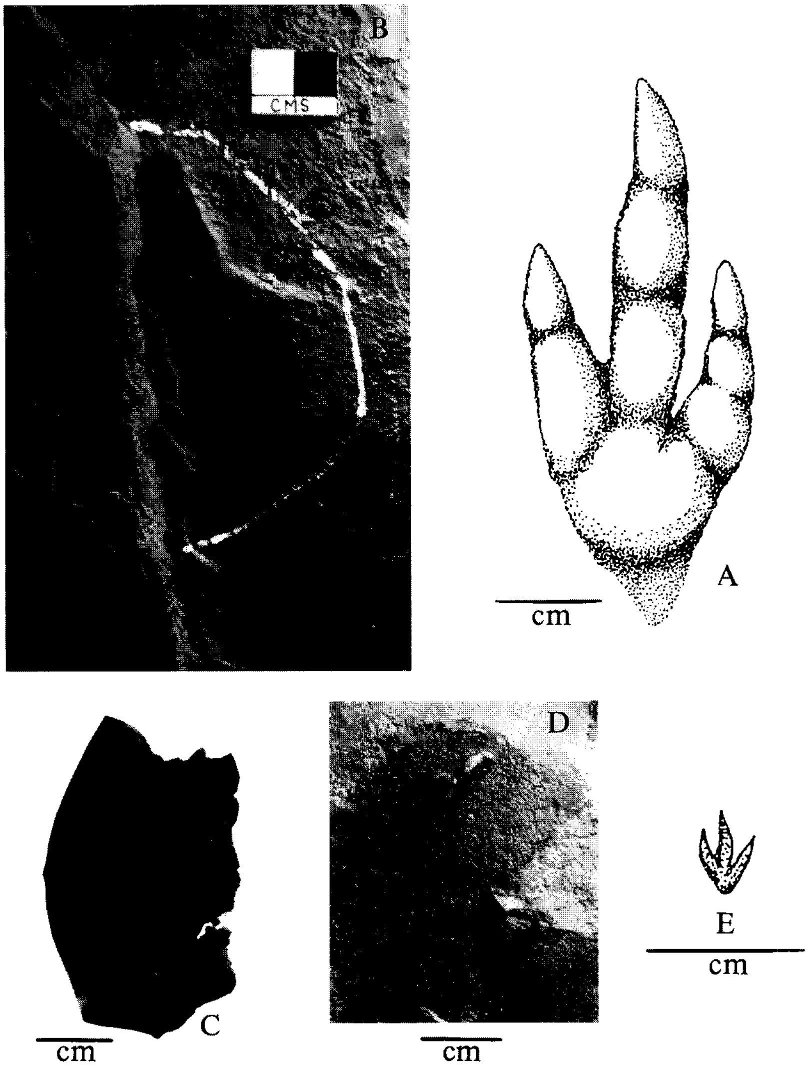

Fig. 3. Supposed dinosaur footprints from the Lower Triassic Kidderminster Formation of the Bellington Borehole, Worcestershire. The identifications given by Wills and Sarjeant (1970) are indicated. A,B. *Coelurosaurichnus* cf *ziegelangerensis* (BU 2016), the original illustration (Wills and Sarjeant, 1970, fig. 2a)(A) and photograph (B) (Scale bar = 2 cm); physical breaks in laminae. C. *Coelurosaurichnus* sp. (BU 2023); mud rip-up clasts. D. Mud rip-up clasts in sandstone (BUGD 2030), for comparison. E. *Coelurosaurichnus* sp. B (BU specimen lost/no catalogue ref) (Wills and Sarjeant, 1970, fig. 3h, 4c); ?indentations left by mud clasts or an invertebrate footprint (photographs by M.J. King).

imprints are isolated rhomboid and rectangular flakes of dark red mudstone in a matrix of fine-grained sandstone. The "digits" do not show any regular form, all three being different in size and shape, and they do not meet. It is impossible to imagine how a footprint could be preserved as sharp-edged isolated mudstone flakes set in an undisturbed sandstone matrix. Mud flakes of this kind are abundant in many specimens from the same borehole, such as BU2030 (Fig. 3D), and we suggest that the most parsimonious explanation of BU 2023 is that it is inorganic.

Wills and Sarjeant (1970, pl. 32, fig. 2) show another small tridactyl print (BU 2019), but do not describe it. This also appears to consist of a group of mud clasts.

Coelurosaurichnus sp. B

Wills and Sarjeant (1970, p. 406, Figs 3h, 4c) interpreted this specimen (Fig. 3E) as the footprint of a "small (young)" coelurosaur dinosaur. The specimen could not be located in the BU collections, and it is presumed lost.

The specimen is re-interpreted here as either inorganic, or, following Thulborn (1990), as an invertebrate trace, primarily because of its tiny size and overall shape. The specimen measured 5 × 3 mm, which implies a hip height of 20 mm, when the scaling formula of Alexander (1976) is applied. Thulborn (1989, p. 42) noted that juvenile animals have relatively large feet, and his modified formula yields a hip height of 25 mm, but this is still much smaller than any known dinosaur. Thulborn (1990, pp. 225-7) interpreted this specimen as that of a limulid (horseshoe crab), and noted specifically that this might be true "for tiny 'coelurosaur' tracks, some no more than 5 mm long, which came to light in borehole cores from the Lower Triassic of the English Midlands".

Fig. 4. The temporary exposure at Cyprus Road, Mapperley Park, Nottingham in 1911. Swinnerton's footprint B (NOTNH PC3440) was found on a loose block from a bed that cannot be precisely located. Swinnerton's footprint A (NOTNH PC4238) was found two beds below the white cross on the photograph (scale can be roughly estimated from lamp post, on right of photo) (after Swinnerton, 1912).

5. The Mapperley Park "dinosaur" footprint specimens

Footprints were reported from the Middle Triassic of Mapperley Park, Nottingham by Swinnerton (1912), and noted again by him (Swinnerton, 1960, p. 115) as "cheirotheroid prints". Sarjeant (1967, 1970) formally described the assemblage of seven specimens as including material of prints made by small amphibians (*Microsauripus* aff. *acutipes*, *Varanopus* aff. *curvidactylus)*, by a thecodontian (*Brachychirotherium coburgense*), by small theropod dinosaurs (*Swinnertonichnus mapperleyensis*, *Coelurosaurichnus* sp.), and by a prosauropod (?*Otozoum swinnertoni*).

The Mapperley Park footprints were discovered in a temporary exposure of the Woodthorpe Formation. This formation, and the overlying Colwick Formation ("Waterstones"), were recently combined, and renamed the Sneinton Formation (Charsley et al., 1990). Warrington et al. (1980) dated the Woodthorpe Formation as early–mid Anisian (Mid Triassic)(Fig. 2), which is older than the early Ladinian age suggested by Sarjeant (1967, 1970). Swinnerton (1912, pl. 3, Fig. 1) included a photograph of the exposure, entitled "Exposure of Waterstones in Mapperley Park" (Fig. 4). A more precise lithostratigraphic position and location were noted by Elliott (1961, p. 212): "from the Woodthorpe Formation near the northern end of Cyprus Road, Mapperley Park (National Grid Reference SK 575424) a few feet below the Waterstones".

We have re-examined the Mapperley Park collection, and confirm that they are tetrapod footprints, but we assign them to the two commonest ichnotaxa in the British Middle Triassic, namely *Chirotherium* (NOTNH PC3315, PC3316 (?), PC3317, PC3437, PC3440, PC4238) and *Rhynchosauroides* (NOTNH PC3365). We discuss the postulated dinosaurian ichnotaxa here, and will consider the *Rhynchosauroides* specimen elsewhere.

The specimens were once lodged at the University of Nottingham, and Sarjeant (1974, p. 323) records that "a fire swept the top floor of the geology building of the University of Nottingham in late March 1970. The Nottingham footprints, which had been on display for the University Open Day, were all discoloured and the holotypes damaged through flaking of their surfaces in the intense heat". The specimens were then moved to the Wollaton Hall (NOTNH) collection. We have compared the specimens carefully with the photographs in Sarjeant (1967, 1970), and find no evidence of any flaking or loss of detail. The only visible effect of the fire is slight blackening round the edges of some specimens.

?Otozoum swinnertoni Sarjeant, 1970

Sarjeant (1970, p. 269) noted that this specimen (NOTNH PC4238; Fig. 5A, B) was "probably the footprint of a bipedal saurischian dinosaur, perhaps a prosauropod". If the identification of *Otozoum* were correct, this specimen would represent the oldest record of the ichnogenus. *Otozoum* is generally interpreted as a prosauropod footprint (Haubold, 1971; Lockley, 1991), although Thulborn (1990, pp. 178, 193) argued that some specimens could have been produced by thecodontians, early crocodilians, or ornithopod dinosaurs.

We reinterpret NOTNH PC4238, the type specimen of *O. swinnertoni*, as a partial *Chirotherium* pes print, for four reasons. Firstly, the footprint is much smaller than typical Early Jurassic specimens of *Otozoum*, being only 235 mm long (compared to 490 mm for the pes of *Otozoum moodii*). Secondly, the foot is plantigrade, and hence not that of a dinosaur, since dinosaurs had digitigrade posture. Thirdly, there are no phalangeal pads on the specimen, a key feature of *Otozoum*, although Sarjeant (1970, p. 271) notes that the "phalangeal pads are poorly marked", and he shows them in his drawings. Fourthly, the digits are straight and distally tapered, whereas *Otozoum* has broad digits and curving claws.

The key to the correct identification of PC4238 lies in the supposed sole impression, which lies behind the digits Sarjeant (1970) interpreted the structure behind the digital impressions (Fig. 5A) as a sole, and his drawings (Figs. 1 and 2) mistakenly indicate that it is located symmetrically with respect to the digits (compare with his plate 20). If, as is the convention (Leonardi et al., 1987, p. 46), the long axis of the foot is drawn through digit III, it can be seen that the inner edge of the "sole" is in line with the middle of digit III (Fig. 5B). The "sole" is in fact, the curved fifth digit of a *Chirotherium* right pes. This is part of a broad *Chirotherium* form, with measurements similar to Beasley's (1904) A2 form.

Re-identification of the supposed *Otozoum* print as *Chirotherium* resolves the problem of its age. Beasley's A2 *Chirotherium* form has been recorded from the upper part of the Helsby Sandstone Formation and the lower part of the Tarporley Siltstone Formation in Cheshire (Beasley, 1904, p. 227; Tresise, 1993), dated as late Scythian–early Anisian. The Sneinton Formation (Woodthorpe Formation) is the approximate lateral equivalent of these units (Fig. 2).

Swinnertonichnus mapperleyensis Sarjeant, 1967

Sarjeant (1967, pp. 333–5, pl. 14, Fig. 3) established specimen NOTNH PC3315 (Fig. 5C, D) as the holotype of a new ichnogenus and ichnospecies, *Swinnertonichnus mapperleyensis*. The new ichnotaxon was classified as the footprint of a small theropod dinosaur, and it was said to differ from *Coelurosaurichnus* in the presence of webbing between the digits. We re-interpret the specimen (Fig. 3C, D) as a partial *Chirotherium* footprint, preserving only digits II, III, and IV.

Sarjeant's (1967) interpretation of NOTNH PC3315 as a dinosaur footprint, and as a footprint bearing webbing, is problematic, since the proximal end of the footprint is broken. There is a distinct change in level on the surface of the cast, indicating that part of the original footprint cast is missing. The outer edge of "digit IV" is poorly preserved, and may also be missing, especially towards the proximal end.

Measurements of the digits show that *Swinnertonichnus* has more in common with *Chirotherium* than with Triassic dinosaur footprints (Table 1). The toe extension (T/E) value for NOTNH PC3315 (33 mm) is about half the

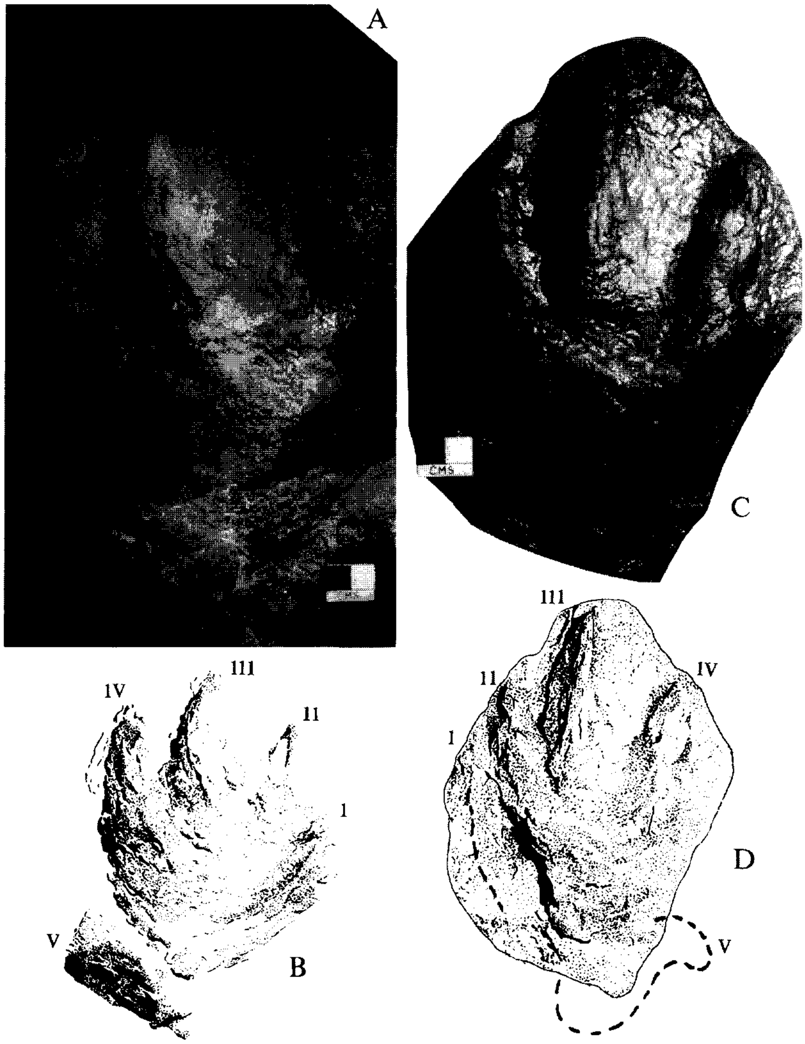

Fig. 5. Supposed dinosaur footprints from the Middle Triassic Woodthorpe Formation of Mapperley Park, Nottinghamshire. The identifications given by Sarjeant (1967, 1970) are indicated. A,B. ?*Otozoum swinnertoni* Sarjeant, 1970 (holotype, NOTNH PC4238), (A) photograph (scale bar= 2 cm), (B) sketch reinterpreting the "sole" as the fifth digit of a *Chirotherium* sp.; right pes of *Chirotherium*. C,D. *Swinnertonichnus mapperleyensis* Sarjeant, 1967 (holotype, NOTNH PC3315), (C) photograph (scale bar= 2 cm), (D) sketch inferring position of digits I and V, which are believed to be missing; partial left pes of *Chirotherium* (photographs and sketches by M.J. King).

value for specimens of *Anchisauripus* and *Grallator* of similar size (54–81 mm), but equivalent to that for complete *Chirotherium* (24–34 mm).

The supposed webbing on *Swinnertonichnus mapperleyensis* was drawn connecting the distal tips of the digits (Sarjeant, 1967, Fig. 3). Webbing extending to the tips of the claws is anatomically impossible. Further, if the conditions of preservation were good enough to preserve an impression of an interdigital web, the terminal claws typical of theropod footprints such as *Coelurosaurichnus*, should also be clearly visible. Only digit III appears to show the cast of a claw.

There are two problems in understanding the nature of webbing in fossil footprints, first the definition of the term, and second, its appearance

Table 1
Comparison of dimensions of footprints of *Swinnertonichnus mapperleyensis* with those of chirotheroids (basal archosaurs) and Triassic theropods. The toe extension (*T/E*) measure is the excess length of digit III, measured perpendicularly from a line joining the tips of digits II and IV (Weems, 1987). Data on basal archosaurs based on specimens. Measurements for dinosaur tracks *Anchisauripus* and *Grallator* from Weems (1987), and of *Coelurosaurichnus* from Haubold (1971)

Taxon	Length (all in mm)	Width	T/E
Swinnertonichnus mapperleyensis (NOTNH PC3315)	168	100	33
Swinnertonichnus mapperleyensis (NOTNH PC3437)	146	78	28
Chirotherium storetonense (Bootle Town Hall Museum, 10)	184	130	24
Chirotherium sp. (Univ. Keele, Department of Education)	196	149	28
"?*Otozoum swinnertoni*" (NOTNH PC4238)	227	162	34
Anchisauripus parallelus	167	80	56
Anchisauripus sillimani	168	79	65
Anchisauripus tuberosus	175	100	56
Anchisauripus crassus	158	140	54
Grallator formosus	165	102	66
Grallator formosus	193	116	81
Grallator cuneatus	130	75	54
Grallator cuneatus	129	78	54
Coelurosaurichnus sassandorfensis	175	110	60
Coelurosaurichnus toscanus	70	40	30
Coelurosaurichnus ziegelangerensis	100	55	23
Coelurosaurichnus moeni	90	60	33

in the fossils. Thulborn (1990, p. 80) notes that "The term 'interdigital web' often causes some confusion. Strictly speaking, this anatomical term denotes any sheet of flesh connecting the bases of two adjoining digits—even the small web between two fingers of the human hand. In this strict sense, traces of interdigital webs are commonplace in the footprints of dinosaurs. More often, however, the term is taken to indicate very extensive webbing, such as that between the toes of a duck". Brown et al. (1992, p. 18, 178) propose more precise terminology for the webbed footprints of extant species, namely proximal, mesial, or distal webbing. Thulborn (1990, p. 80) reports only two examples of distal webbing in dinosaur footprints: *Otouphepus magnificus* Lull, 1953, a theropod dinosaur from the Lower Jurassic of Massachussetts, USA and *Talmontopus tersi* De Lapparent and Montenat, 1967, a theropod dinosaur from France. However, M.G. Lockley (pers. comm., 1994) cannot confirm the presence of webbing in either taxon.

If the animal that made the *Swinnertonichnus* print truly had distal webs, the impression should be clear. Lightweight birds such as gulls, often fail to leave an impression of the web, unless the substrate is soft. Heavier birds, such as swans and geese more commonly leave distinct web and claw impressions, even on relatively firm substrates. The relief shown on *Swinnertonichnus mapperleyensis* is relatively high, especially on the distal end of the footprint, but the so-called 'webbing' impression is indistinct, and it does not display features seen in modern analogues. A plaster cast of a bird's footprint (Fig. 6B) shows a clear proximal web between digits III and IV, and a smaller web between digits III and II. The webbing produces a raised cast, with a concave structure between the digits, because the web is forced upwards between the digits, when the digits themselves sink into the substrate.

Other *Swinnertonichnus* specimens

Two further Mapperley Park specimens are labelled "*Swinnertonichnus*", although they are not described by Sarjeant (1967, 1970). The first is Swinnerton's (1912, p. 67, pl. 4, Fig. 4) "Footprint B" (NOTNH PC3440), which Sarjeant (1967, p. 333) misidentified as NOTNH PC3315. Swinnerton's (1912) "specimen B" (NOTNH PC3440; Fig. 6A) is a natural cast of two incompletely preserved *Chirotherium* pes prints, one overprinting the other. The curved digit V of a right pes is possibly present on the underlying print. This is overlain by ?three digits of another *Chirotherium* pes, ?digit III of which displays an excellent claw which, as Swinnerton (1912, p. 67) noted, is "flattened sideways". No evidence of webbing between the digits was observed, although Swinnerton (1912) suggests that he saw such a feature.

A second specimen, also labelled *Swinnertonichnus mapperleyensis* (NOTNH PC3437; Fig. 6C) from Mapperley Park, was

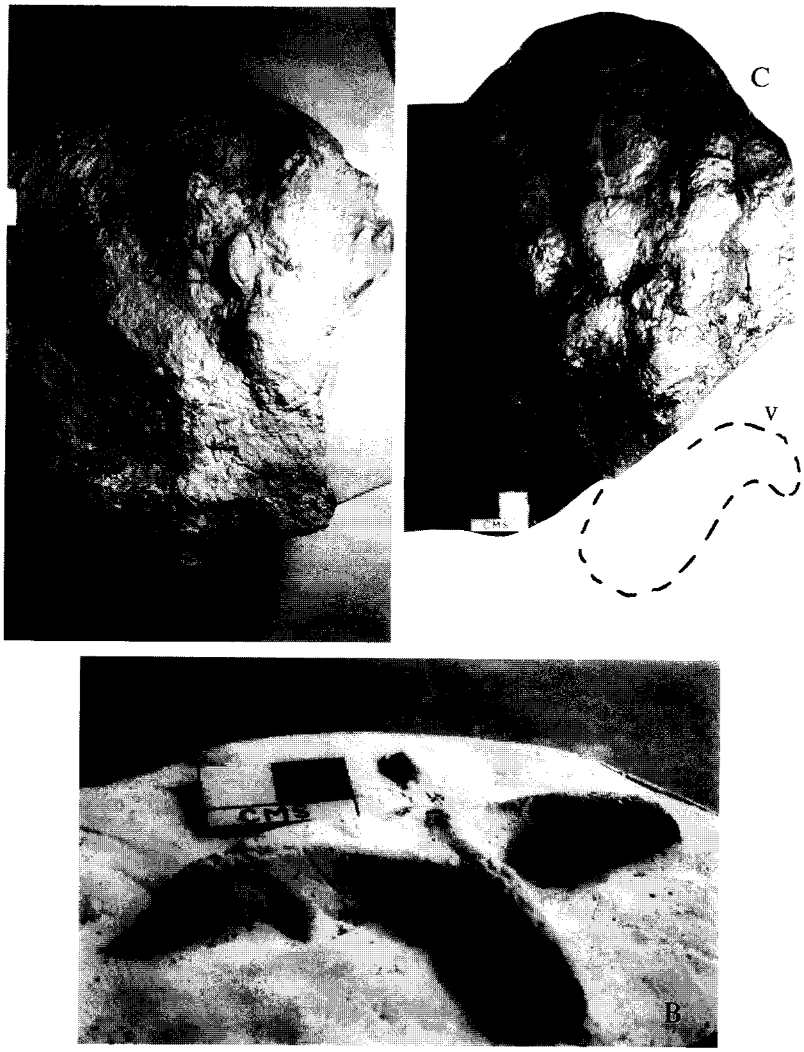

Fig. 6. A. Swinnerton's (1912) footprint "B" (NOTNH PC3440), which appears to show two incompletely preserved *Chirotherium* sp. pedes, one overprinting the other. Scale bar (top left) = 1 cm. B. Plaster cast of a footprint made by a wading bird on the banks of the River Severn, Gloucestershire, showing proximal webbing between digits III and IV. Note how the web produces a concave structure between the digits. In the original mould this would be convex, indicating that the web is forced upwards when the digits sink into the substrate. No such structure exists on *Swinnertonichnus mapperleyensis*, despite the fact that it is a footprint cast of relatively high relief at the distal end. Scale bar = 2 cm. C. *Swinnertonichnus mapperleyensis*, according to the label, but not mentioned by Sarjeant (1967, 1970) (NOTNH PC3437), the position of missing digit V is inferred; part of a *Chirotherium* left pes. Scale bar = 2 cm (photographs, cast and sketch by M.J. King).

not described by Sarjeant (1967), and it is not clear who identified it. Although labelled *Swinnertonichnus mapperleyensis*, this is obviously not a tridactyl print. It exhibits four digits with prominent digital pads (nodes), and is interpreted here as part of a *Chirotherium* left pes.

Coelurosaurichnus sp.

Sarjeant (1967, pp. 338–339, fig. 2A, 4b; pl. 16, fig. 2) described another specimen from Mapperley Park (NOTNH PC3316; Fig. 7) as the footprint of a small bipedal theropod. It is re-interpreted

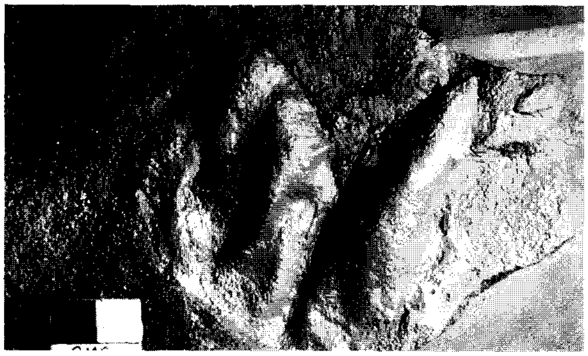

Fig. 7. *Coelurosaurichnus* sp. Sarjeant, 1967 (NOTNH PC3316); the conformation of the digits suggest a poorly preserved chirotheroid form, but owing to the imperfect preservation, it has been reassigned to "Ichnotaxon indet". Scale bar = 2 cm (photograph by M.J. King).

here as possibly part of a chirotheroid print, or possibly even inorganic.

The specimen lacks six key features of "coelurosaur" footprints (Thulborn, 1990, pp. 152–162): it is not mesaxonic (digit III longest); it is not longer than wide, measuring as it does 85 mm long and 87 mm wide; the total divarication (splay of all digits) is high (69.5°), in comparison to typical "coelurosaur" specimens (45–50°); the interdigital angles are far from being approximately equal (II–III = 41.5°, III–IV = 28°); the digits are not narrow, slightly tapered, and bearing nodes; and there are no metatarso-phalangeal pads behind any of the digits.

The specimen shows chirotheroid digit shapes preserved as dark red siltstone on a background matrix of fine-grained sandstone. If this is a footprint, there appears to have been some slippage of the digits when the foot was impressed. However, the "digit" impressions have very low relief, and they are indistinct, so the specimen might represent an inorganic sedimentary structure.

6. Discussion

The earliest dinosauroid footprints from the European mainland (Massif Central, France) were reported in rocks of mid Anisian age (Demathieu, 1970, 1989). Although rare in rocks of this age, dinosauroid footprints become increasingly common in the early Ladinian (Demathieu, 1989, p. 201). These age assignments for the French footprint specimens require critical analysis. The dinosaur affinity of specimens such as *Coelurosaurichnus* described by Demathieu (1970, 1989) is also unclear, and requires re-investigation. In areas such as the Western USA, where excellent Lower and Middle Triassic ichnofaunas are known, no dinosauroid tracks have been reported (Lockley and Hunt, 1995).

The oldest genuine dinosaur footprints from Britain are Norian in age, and they come from two localities in South Wales. Abundant specimens in the marginal Triassic (Mercia Mudstone Group; ?Norian) at Bendrick Rock, near Barry, South Wales represent *Anchisauripus* (Tucker and Burchette 1977), presumably produced by small theropods. Rarer large tetradactyl tracks from this site may represent the footprints of a prosauropod. A trackway of similar age, consisting of five large *Anchisauripus* sp. footprints, was recorded last century (Sollas, 1879; Thomas, 1879) from Newton, near Porthcawl, Mid Glamorgan, South Wales, and a further prosauropod footprint has also been found there. These ichnofaunas will be re-described shortly (Lockley et al., in prep.; King, in prep.).

7. Conclusions

This study supports Thulborn's proposal (1990) that there is no reliable footprint evidence for dinosaurs in the Lower and Middle Triassic rocks of the British Isles. It is now recognised that there is no convincing skeletal evidence for dinosaurs before the late Carnian (Upper Triassic). Consequently the assumed dinosaur affinity of other imperfectly preserved, or isolated, Lower-Middle Triassic footprints from the rest of Europe and North America, also now requires critical reappraisal.

Acknowledgements

We thank Tony Thulborn (University of Queensland, St Lucia, Australia), whose proposal provided the initial impetus for this study, for his support and encouragement. Thanks also go to Paul Smith (Lapworth Museum, University of Birmingham), Neil Turner (Wollaton Hall Natural History Museum, Nottingham), Stephen Howe (National Museum of Wales, Cardiff), David Thompson (University of Keele, Staffordshire), and Lynn Broadbridge (Education Office, Town Hall, Bootle, Merseyside—formerly Bootle Museum) for access to specimens. Martin Lockley (University of Colorado, Denver, USA) and David Thompson (University of Keele, Staffordshire) provided valuable comments on the draft manuscript. We also thank Bill Sarjeant (University of Saskatchewan) and Maurice Tucker (University of Durham) for comments on the MS. Supported by NERC Grant GT4/91/GS/130.

References

Alexander, R. McN., 1976. Estimates of speeds of dinosaurs. Nature, 261: 129–130.

Beasley, H.C., 1904. Report on footprints from the Trias: Part I. Rep. Br. Assoc. Adv. Sci., 1903: 219–230.

Benton, M.J., 1984a. Rauisuchians and the success of dinosaurs. Nature, 310: 101.

Benton, M.J., 1984b. Fossil reptiles of the German late Triassic and the origin of the dinosaurs. In: W.-E. Reif and F. Westphal (Editors), 3rd Symp. Mesozoic Terrestrial Ecosystems, Tübingen, 1984, Short Pap. Attempto, Tübingen, pp. 13–18.

Benton, M.J., 1986a. The late Triassic reptile *Teratosaurus*—a rauisuchian, not a dinosaur. Palaeontology, 29: 293–301.

Benton, M.J., 1986b. The Late Triassic tetrapod extinction events. In: K. Padian (Editor), The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic–Jurassic Boundary. Cambridge Univ. Press, pp. 303–320.

Benton, M.J., 1990. Origin and interrelationships of dinosaurs. In: D.B. Weishampel et al. (Editors), The Dinosauria. Univ. Calif. Press, Berkeley, pp. 11–30.

Benton, M.J., 1993. Reptilia. In: M.J. Benton (Editor), The Fossil Record 2. Chapman and Hall, London, pp. 681–715.

Benton, M.J., 1994a. Late Triassic terrestrial vertebrate extinctions: stratigraphic aspects and the record of the Germanic Basin. Paleontol. Lombarda, N.S., 2: 19–38.

Benton, M.J., 1994b. Late Triassic to Middle Jurassic extinctions among tetrapods: testing the pattern. In: N.C. Fraser and H.-D. Sues (Editors), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge Univ. Press, New York, pp. 366–397.

Bonaparte, J.F., 1976. *Pisanosaurus mertii* Casamiquela and the origin of the Ornithischia. J. Palaeontol., 50: 808–20.

Bonaparte, J.F., 1978. El Mesozoico de America del Sur y sus tetrapodos. Opera Lilloana, 26: 1–596.

Brown, R.W., Lawrence, M.J. and Pope, J., 1992. Animal Tracks, Trails and Signs. Hamlyn, London, pp. 1–320.

Charig, A.J., 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. In: K.A. Joysey and T.S. Kemp (Editors), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh, pp. 121–155.

Charsley, T.J., Rathbone, P.A. and Lowe, D.J., 1990. Nottingham: a geological background for planning and development. Br. Geol. Surv. Tech. Rep., WA/90/1, pp. 1–82.

Cox, C.B., 1967. Changes in terrestrial vertebrate faunas during the Mesozoic. In: W.B. Harland et al. (Editors), The Fossil Record. Geol. Soc. London, pp. 77–89.

Demathieu, G.R., 1970. Les empreintes des pas de vertébrés du Trias de la bordure nord-est du Massif Central. Cah. Paléontol. C.N.R.S., pp. 1–211.

Demathieu, G.R., 1989. Appearance of the first dinosaur tracks in the French Middle Triassic and their probable significance. In: D.D. Gillette and M.G. Lockley (Editors), Dinosaur Tracks and Traces. Cambridge Univ. Press, New York, pp. 201–207.

Elliott, R.E., 1961. The stratigraphy of the Keuper series in southern Nottinghamshire. Proc. Yorks. Geol. Soc., 33: 197–234.

Galton, P.M., 1985. The poposaurid thecodontian *Teratosaurus suevicus* v. MEYER, plus referred specimens mostly based on prosauropod dinosaurs from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. Stuttg. Beitr. Naturkd., Ser. B, 116: 1–29.

Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. Mem. Calif. Acad. Sci., 8: 1–55.

Haubold, H., 1971. Ichnia amphibiorum et reptiliorum. Handb. Paläoherpetol., 18: 1–124.

Hunt, A.P. and Lucas, S.G., 1991. The *Paleorhinus* Biochron and the correlation of the nonmarine Upper Triassic of Pangaea. Palaeontology, 34: 487–501.

Kuhn, O., 1958. Die Fährten des vorzeitlichen Amphibien und Reptilien. Meisenbach, Bamberg, pp. 1–64.

Leonardi, G. (Editor), 1987. Glossary and manual of tetrapod footprint palaeoichnology. Dep. Nac. Prod. Mineral, Brasilia, pp. 1–75.

Lockley, M.G., 1991. Tracking Dinosaurs; a New Look at an Ancient World. Cambridge Univ. Press, pp. 1–238.

Lockley, M.G. and Hunt, A.P., 1995. Dinosaur tracks and other fossil footprints of the western United States. Columbia Univ. Press, New York, pp. 1–338.

Novas, F.E., 1994. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. J. Vertebr. Paleontol., 13: 400–423.

Pollard, J.E., 1985. *Isopodichnus*, related arthropod trace fossils and notostracans from Triassic fluvial sediments. Trans. R. Soc. Edinb. Earth Sci., 76: 273–285.

Rogers, R.R., Swisher III, C.C., Sereno, P.C., Forster, C.A. and Monetta, A.M., 1993. The Ischigualasto tetrapod assemblage (Late Triassic) and $^{40}Ar/^{39}Ar$ calibration of dinosaur origins. Science, 260: 794–797.

Romer, A.S., 1966. Vertebrate Paleontology. Univ. Chicago Press, 3rd ed.

Romer, A.S., 1970. The Triassic faunal succession and the Gondwanaland problem. In: IUGS Symp., Buenos Aires, 1967. UNESCO, Paris, pp. 273–400.

Sarjeant, W.A.S., 1967. Fossil footprints from the Middle Triassic of Nottinghamshire and Derbyshire. Mercian Geol., 2: 327–341.

Sarjeant, W.A.S., 1970. Fossil footprints from the Middle Triassic of Nottingham and the Middle Jurassic of Yorkshire. Mercian Geol., 3: 269–282.

Sarjeant, W.A.S., 1974. A history and bibliography of the study of fossil vertebrate footprints in the British Isles. Palaeogeogr. Palaeoclimatol. Palaeoecol., 16: 265–378.

Sereno, P.C., 1994. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. J. Vertebr. Paleontol., 13: 425–450.

Sereno, P.C., Forster, C.A., Rogers, R.R. and Monetta, A.M., 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. Nature, 361: 64–66.

Sereno, P.C. and Novas, F.E., 1992. The complete skull and skeleton of an early dinosaur. Science, 258: 1137–1140.

Sereno, P.C. and Novas, F.E., 1994. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. J. Vertebr. Paleontol., 13: 451–476.

Sollas, W.J., 1879. On some three-toed footprints from the Triassic Conglomerate of South Wales. Q. J. Geol. Soc. Lond., 35: 511–516.

Swinnerton, H.H., 1912. The palmistry of the rocks. Rep. Trans. Notts. Nat. Soc., 60: 65–68.

Swinnerton, H.H., 1960. Fossils. Collins, London, pp. 1–274.

Thomas, T.H., 1879. Tridactyl uniserial ichnolites in the Trias at Newton Nottage, near Porthcawl, Glamorgan. Rep. Trans. Cardiff Nat. Soc., 10: 77–91.

Thulborn, R.A. 1989. The gaits of dinosaurs. In: D.D. Gillette and M.G. Lockley (Editors), Dinosaur Tracks and Traces. Cambridge Univ. Press, New York, pp. 39–50.

Thulborn, R.A., 1990. Dinosaur Tracks. Chapman and Hall, London, pp. 1–410.

Tresise, G.R., 1993. Triassic vertebrate footprints from Cheshire, England: localities and lithologies. Mod. Geol., 18: 407–417.

Tucker, M.E. and Burchette, T.P., 1977. Triassic dinosaur footprints from South Wales: Their context and preservation. Palaeogeogr. Palaeoclimatol. Palaeoecol., 22: 195–208.

Von Huene, F., 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Monogr. Geol. Paläontol., 4 (1): 1–361.

Warrington, G., Audley-Charles, M.G., Elliott, R.E., Evans, W.B., Ivimey-Cook, H.C., Kent, P.E., Robinson, P.L., Shotton, F.W. and Taylor, F.M., 1980. A correlation of Triassic rocks in the British Isles. Spec. Rep. Geol. Soc. Lond., 13: 1–78.

Weems, R.E., 1987. A Late Triassic footprint fauna from the Culpepper Basin, Northern Virginia (U.S.A.). Trans. Am. Philos. Soc., 77: 1–79.

Wild, R., 1973. Die Triasfauna der Tessiner Kalkalpen. 23. *Tanystropheus longobardicus* (Bassani) (neue Ergebnisse). Schweiz. Paläontol. Abh., 95: 1–162.

Wills, L.J., 1970. The Bunter Formation at the Bellington pumping station of the East Worcestershire Waterworks Company. Mercian Geol., 3: 387–397.

Wills, L.J. and Sarjeant, W.A.S., 1970. Fossil vertebrate and invertebrate tracks from boreholes through the Bunter series (Triassic) of Worcestershire. Mercian Geol., 3: 399–414.