AUSTRALIA'S EARLIEST THEROPODS: FOOTPRINT EVIDENCE IN THE IPSWICH COAL MEASURES (UPPER TRIASSIC) OF QUEENSLAND

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ABSTRACT: Small tridactyl footprints are reported from the Blackstone Formation of the Ipswich Coal Measures near Dinmore, in southeast Queensland, Australia. These Upper Triassic (Carnian) footprints are attributed to small theropod dinosaurs and are assigned to the ichnogenus *Grallator* Hitchcock, 1858 (*sensu stricto*). Their discovery constitutes only the second definite report of Triassic dinosaurs in Australia, and it reveals that small theropods had dispersed into the remote intermontane basins of East Gondwana as early as the Carnian. These footprints are among the earliest dinosaurian fossils yet discovered in Gondwana, and they confirm that theropods have an extremely long history in the Australasian region.

RESUME: Petites empreintes de pas proviennent de la Formation Blackstone (Triassique supérieur, Carnien) des houillers d’Ipswich près de Dinmore, à sud-est de Queensland, Australie. Les empreintes sont attribuées aux dinosaures théropodes d’une taille petite et sont rapportées à l’ichnogénre *Grallator* Hitchcock, 1858 (*sensu stricto*). La découverte est même la deuxième des dinosaures triassiques en Australie, révélant que les petites théropodes étaient distribuées aux bassins de l’Est du Gondwana depuis l’étage Carnien. Les empreintes sont parmi les fossiles dinosauriens les plus anciennes dans le Gondwana - évidence d’une histoire très longue pour les théropodes en Australie.

INTRODUCTION

In October 1983 a group of students from the Queensland Institute of Technology, Brisbane, discovered some small fossil footprints while searching for plant remains in Upper Triassic coal measures near Dinmore, southeast Queensland. The footprints were briefly mentioned in field-guides to the geology and palaeontology of the Brisbane area (THULBORN, 1986; SIMPSON, 1992) and are described here in detail for the first time. They are a substantial addition to the extremely poor fossil record of Triassic dinosaurs in Australia and their discovery implies that small theropods were probably distributed worldwide as early as the Carnian.

PROVENANCE

The footprints were found in spoil-heaps on the northern edge of Rylance No. 5 Opencut Colliery, about 300 m to the south of a prominent clay-pit in the Tertiary Redbank Plains Formation (Ipswich 1:10,000 map, grid reference 829465). The Rylance Colliery exploits coal resources of the Blackstone Formation which, together with the underlying Tivoli Formation, forms the coal-bearing fraction (Brassall Subgroup) of the Ipswich Coal Measures (Fig. 1). The interbedded sediments and volcanics of the Ipswich Coal Measures accumulated in an intermontane basin which experienced uplift and erosion towards the close of the Triassic (Norian). Subsequently the eroded upper parts of the Ipswich Coal Measures were overlain unconformably by sediments of the Bundamba Group, dated from Rhaetian through Early Jurassic (CRANFIELD, SCHWARZBOCK & DAY, 1976). The Ipswich Coal Measures yield miospores (DE JERSEY, 1949, 1982, 1970, 1971, 1975; HELBY, MORGAN & PARTRIDGE, 1987) and abundant plant macrofossils representing a *Dicroidium* flora of Triassic aspect (WALKOM, 1915, 1917a, 1917b; JONES & DE JERSEY, 1947; DENMEAD, 1955; HOUSTON, 1967; RETALLACK, 1977; WEBB, 1986; PLAYFORD & Rigby, 1988). The associated fauna comprises rare freshwater bivalves (HILL, PLAYFORD & WOODS, 1965; GOULD, 1967), conchostracans (MITCHELL, 1927; WEBB, 1986), a great variety of insects (TILLYARD, 1923; TILLYARD & DUNSTAN, 1924; RIEK, 1956; EVANS, 1961; HILL, PLAYFORD & WOODS, 1965; ROZEFELDS, 1985; MALEWICZ & PARTRIDGE, 1988).
theropod dinosaur tracks from the originat.ed near the base of the Woods. Footprints reported here (cf. *Eubrontes Hitchcock*, 1845) previously reported by STAINES & WOODS (1964). Dinosaur tracks are not known from Upper Triassic coal measures of the other intermontane basins, though Lower Jurassic sandstones of the Callide Basin have yielded small ornithopod tracks identified as *Anomoepus Hitchcock*, 1846 (THULBORN, 1994).

1986), and some poorly preserved fish scales (FLEMMING, 1966), presumably derived from palaeoniscoids. Trace fossils comprise insect leaf-mines (ROZEFELDS, 1985; ROZEFELDS & SOBBE, 1987) and a few vertebrate footprints (STAINES & WOODS, 1964; MOLNAR, 1982; THULBORN, 1986).

Palynological evidence, summarized by BALME & FOSTER (1996), indicates that the Ipswich Coal Measures range in age from late Middle Triassic (end-Ladinian) through Late Triassic (Late Carnian). As the Rylance Colliery operates near the base of the Blackstone Formation (DENMEAD, 1955; CRANFIELD, SCHWARZBOCK & DAY, 1976), the footprints described here probably originated near the Rob Roy seam (at the base of the formation) or the Striped Bacon seam (between 15 m and 33 m higher in the succession). They are most likely Mid-Carnian to Late Carnian in age.

DESCRIPTION

The footprints occur in extremely fragile pieces of siltstone and shale, most of which may be reassembled into a single slab (Fig. 2). There are at least six footprints, here identified by arbitrary code-letters A to F (Fig. 4). Three prints are fairly obvious (A, B, D), whereas the others (C, E, F) are so faint or incomplete that they are easily overlooked. All the footprints are preserved as shallow natural moulds (concave epireliefs), less than 2 mm deep. Two of them (A, B) are also represented as incomplete natural casts (convex hyporeliefs) on a small block of the overlying siltstone. The largest footprint (A) is little more than 7 cm long.

Evidently the footprints were impressed in a firm and unyielding substrate, now represented by a paper-thin sheet of dark grey shale overlying finely laminated siltstone of paler blue-grey colour. The shale parting has an uneven surface, with extensive desiccation cracks and irregular swellings, hollows and dimples.

The better-preserved footprints are clearly those of small bipedal dinosaurs with functionally tridactyl hindfeet comprising digits II, III and IV. None of them shows any trace of the hallux (digit I). Footprint measurements are summarised in Table I. All measurements were taken directly from the specimens and were checked on enlarged photocopies of latex peels which had been gently rubbed with powdered graphite. This “quick and dirty” technique is useful for revealing morphological details in even the faintest footprints.

FOOTPRINT A

The best-preserved and most complete footprint (A) shows three slender, tapering and sharply pointed digits (Fig. 2, 3, 4A). It has an overall length of 7.2
cm and is identified as a print of the right pes for several reasons. First, digit IV extends slightly further to the rear than digits II and III, which is frequently the case in tridactyl dinosaur tracks. Second, the body of digit III (excluding its large claw impression) is weakly curved, and such curvature is typically convex to the lateral side in the footprints of small bipedal dinosaurs. And, third, a faint smear at the tip of digit III confirms that the track-maker's foot was lifted forwards and laterally from the substrate, which appears to have been the usual direction of foot movement in bipedal dinosaurs.

There are faint, but definite, indications of long and slender digital nodes in digit III, both in the cast and the mould. The indentations defining these nodes are better defined along the lateral edge of the digit than along the medial edge - a distinction that is matched in many other small dinosaurian footprints (e.g. LULL, 1953: fig. 37-40).

Digit III shows a distinct claw-impression which is shaped like a tear-drop, about 8.0 mm long and 4.9 mm wide. It extends directly forwards into a slit, about 2 mm long, which presumably resulted from forwards dragging of the claw-tip. The impression of digit III grows progressively more shallow towards the rear and eventually fades out entirely.

Much of the mould of digit III is still filled with siltstone broken away from the cast; however, the rear part of the mould is cleanly exposed and reveals a surface marked with tiny longitudinal wrinkles. This wrinkled texture does not resemble the tuberculate skin impressions reported in various other dinosaur tracks (e.g. HITCHCOCK, 1858: 63; CURRIE, NADON & LOCKLEY, 1991). It may have resulted from slight slippage of the track-maker's foot as it was applied to (or lifted from) the substrate, or it might represent small-scale slickensides developed along the shale interface between cast and mould.

The distal part of digit II is a small almond-shaped impression comprising a narrow claw and its adjoining node. The claw is roughly similar in size to that in digit III, but is not quite so sharply pointed. Some 3 cm behind the tip of the claw a faint circular dimple, about 9 mm in diameter, represents the hindmost node in digit II. This faint impression is more readily visible on the cast than on the mould, and it provides a useful indication to the total length of digit II.

On the mould digit IV is represented only by its distal end, plugged with siltstone broken away from the overlying cast. The cast is more complete and reveals that digit IV extends slightly further back than the rear end of digit III. In other respects digit IV resembles digit III, though it is slightly smaller overall. It shows equally faint indications of digital nodes, and a similar claw-impression - though this does not extend into a slit made by the dragging claw-tip.
FOOTPRINT A

A second and incomplete right footprint (B) is partly overtrodden by footprint A (Fig. 2, 3, 4B). It shares the same orientation as footprint A, but lies about 3 cm behind it and slightly off to one side (laterally). Digit III is virtually a duplicate of that in footprint A, but is not so deeply impressed; it shows a comparable claw-impression, with a similar drag-mark at the tip of the claw. The cast shows almost the full extent of digit III and reveals two clearly defined nodes towards its rear end. Digit II also resembles its equivalent in footprint A but is somewhat foreshortened and less deeply impressed. It is represented on both cast and mould by a short scratch-like trace of its claw and, a few centimetres behind, by an irregular oval impression. Digit IV would have lain beyond the broken edge of the slab.

FOOTPRINT C

Example C is a very incomplete print from the left pes, showing only the tips of the three digits (Fig. 2, 4C). It lies about 32 cm in front of print A and is aligned transversely in relation to it. The tip of digit II is represented by a small oval impression which extends medially and slightly forwards into a curved groove incised by the claw-tip. Digit III is represented by a shallow pear-shaped impression, with its anterior third narrowing into a groove made by the underside of the claw. Digit IV is a long and somewhat irregular scratch-like impression which lacks very clear indications of the claw or digital nodes.

FOOTPRINT D

This fourth footprint (D) lies about 20 cm in front of footprint A and has the same orientation (Fig. 2, 4D). Although it is about as deeply impressed as footprint A, it shows only two digits - apparently digits III and IV of a left pes. Digit III resembles that in footprints A and B, though the claw-impression is poorly defined. Digit IV is somewhat irregular in outline, but generally comparable to its equivalent in footprint A. From the sharply-pointed tip of its narrow triangular claw a prominent scratch-like marking extends forwards and laterally for a distance of nearly 6 mm. The shale substrate reveals no impression whatsoever from digit II.

FOOTPRINT E

The fifth example (E) is so faintly impressed that it was initially overlooked (Fig. 2, 4E). It shares the same orientation as prints A, B and D, and lies approximately 22 cm in front of the latter. It comprises impressions of only two digits. The larger of these, evidently digit III, is a weak furrow 43 mm long. Despite the poor preservation, low-angle lighting reveals a definite impression of the claw, again shaped like a tear-drop. Behind this claw-impression a string of three tiny dimples may represent the very faintest indications of digital nodes. A second digit (II?) is represented by an equally shallow impression, 30 mm long, which includes the ill-defined trace of a somewhat smaller claw. There is no indication of the remaining digit (presumably digit IV).

FOOTPRINT F

A sixth footprint (F) is represented by the impression of a single digit extending transversely between the tips of digits II and III in footprint C (Fig. 2). This impression is virtually a mirror-image of digit III in the presumed left footprint D, though slightly smaller overall; for that reason it is tentatively identified as
digit III of a right footprint. Whatever its exact identity, this digital impression has an unusual location - in the midline of a broad desiccation crack. The adjoining shale surfaces are undisturbed, with no trace of the other digits.

**DISCUSSION**

**PRESERVATION**

Before discussing the identity and significance of the footprints it is useful to consider how far their morphology might have been affected by accidents of preservation. This precaution is important when dealing with rare and fragmentary material. Such accidental variations are known to result from the physical properties of the substrate and the manner in which the track-maker's foot interacted with that substrate (Thulborn & Wade, 1989). First, it may be noted that the footprints are oriented randomly with respect to desiccation cracks on the same slab. Evidently the distribution of shrinkage cracks was not controlled by lines of weakness along the digits of existing footprints (see Hitchcock, 1858: 170; Thulborn, 1990: 139). In other words, the shrinkage cracks were formed before the footprints. Any substrate that had dried to the point of developing shrinkage cracks must, surely, have had a rather firm surface. This conclusion is supported by the fact that none of the footprints shows evidence of slumping or collapse after withdrawal of the track-maker's foot. However, the firm surface of the substrate was merely an impermeable skin of mud, beneath which the slightly coarser and more porous silt may still have been moist and plastic. Such a laminated substrate may have been sufficiently elastic for small and lightweight animals to traverse it without trace. Elsewhere shallow footprints might be formed only where the sharp claws of track-makers penetrated the muddy skin, permitting water to bleed through from the underlying silt.

Prints A and B are nearly identical, and in both cases it seems likely that the sharp claws of all three digits punctured the muddy skin of the substrate and sank a few millimetres into the underlying silt. The rear parts of the digits did not break through the muddy surface and produced very shallow impressions, sometimes little more than vague saucer-like dimples (as at the rear of digit II in footprint A). Print C shows only the distal parts of the three digits; these are so widely spread as to suggest that the track-maker's weight was supported largely on the outer side of the foot, so that the lightly-loaded inner toe (II) failed to leave any impression. Similar faintness or absence of digit II appears to be fairly common among small tridactyl dinosaur tracks in general. Print E shows extremely faint, yet seemingly unweathered, claw-impres­

**TABLE II.**

Comparison of three aspects of footprint shape. Small theropod footprints, cf. *Grallator* Hitchcock, 1858, from the Blackstone Formation of southeast Queensland, Australia, exemplified by specimen A (Fig. 4A). Comparative data for

<table>
<thead>
<tr>
<th>Sample of Small Theropod Footprints</th>
<th>Sample of Small Ornithopod Footprints</th>
</tr>
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<tbody>
<tr>
<td>0.73 +/- 0.19 (N = 40)</td>
<td>0.91 +/- 0.018 (N = 43)</td>
</tr>
<tr>
<td>0.32 +/- 0.03 (N = 12)</td>
<td>0.44 +/- 0.01 (N = 13)</td>
</tr>
<tr>
<td>49° +/- 23° (N = 15)</td>
<td>62° +/- 9° (N = 15)</td>
</tr>
</tbody>
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...
Above transverse fracture at centre right, prominent V-shaped structure comprises sediment-filled digit IV of print A (to right) overlying tip of digit III in print B (to left). Small depression at lower left represents digit II of print B. Scale bar, 1 cm.

Fig. 3 - Small theropod footprints, cf. Grallator Hitchcock, 1858, from the Ipswich Coal Measures, southeast Queensland, Australia. Showing overlapping natural moulds of two prints (examples A and B in Fig. 2). Above transverse fracture at centre right, prominent V-shaped structure comprises sediment-filled digit IV of print A (to right) overlying tip of digit III in print B (to left). Small depression at lower left represents digit II of print B. Scale bar, 1 cm.

STATUS AND AFFINITIES

The most distinctive and consistent features of the Rylance footprints are as follows: the functionally tridactyl pes is V-shaped in outline, narrow at the rear, with slim tapering digits; there are definite indications of digital nodes and impressions of long and sharply pointed claws, each shaped like a tear-drop; the claw on digit IV is deflected laterally (most obviously in print D, but also in examples A and C); footprint length is noticeably greater than footprint width (x 1.2 in footprint A), and the interdigital angles are narrow (with total divarication of digits II-IV at 55° in print A). Nearly all these features are matched in footprints conventionally attributed to theropod dinosaurs (THULBORN, 1990: 219-223).

TABLE II shows that the ratio of footprint width to footprint length (0.82 in example A) is intermediate between that in samples of small theropod tracks (mean 0.73) and small ornithopod tracks (mean 0.91). So, too, is the total divarication of digits II-IV (55° in print A, as opposed to mean values of 49° in small theropods and 62° in small ornithopods). These slight differences from other theropod tracks probably resulted from spreading of the trackmaker's toes on the exceptionally firm substrate, a feature shown to an exaggerated degree in print C. The impressions of the digits are comparatively narrow - far more so than in ornithopod tracks and even in typical theropod tracks. Exceptional narrowness of the digital impressions is probably correlated with their extreme shallowness which, once again, reflects the firmness of the substrate.

The Rylance footprints are generally similar to examples of the ichnogenus Grallator Hitchcock, 1858, often grouped with other presumed theropod tracks in the ichnofamily Grallatoridae Lull, 1904. Tracks similar or identical to Grallator are widespread in continental sediments of the Upper Triassic and Lower Jurassic, having been reported from North and South America, Europe, Africa and Asia (see HAUBOLD, 1971, 1984, 1986). Even so, their classification remains a matter of debate. At one extreme, for example, HAUBOLD (1984) listed no fewer than 37 ichnogenera under the heading "Grallatoriden" sensu lato (though, admittedly, with the plain implication that many of them might prove to be synonyms). Elsewhere, OLSEN & GALTON (1984) recommended that the widely accepted ichnogenera Eubrontes Hitchcock, 1845 and Anchisauripus Lull, 1904 should be relegated to the synonymy of Grallator Hitchcock, 1858 - along with nearly a dozen of the many dinosaurian ichnogenera identified by ELLENBERGER (1971, 1974) in the Stormberg Series of southern Africa. More recently LEONARDI & LOCKLEY (1995) considered the ichnogenus Coelurosaurichnus von Huene 1941 to be a synonym of Grallator Hitchcock, 1858, and IRBY (1996) suggested that Dilophosauripus Welles, 1971 might prove to be a preservational variant of Eubrontes Hitchcock, 1845. Despite much discussion of these possibilities, and others (e.g. WEEMS, 1992; GIERLINKSI, 1996), the classification of grallatorid tracks remains in a state of confusion. In these circumstances it is neither meaningful nor informative to seek a very precise ichnotaxonomic label for the Rylance footprints, particularly as they are represented by such fragmentary material. For the present at least these footprints may be identified no more closely than small theropod tracks, cf. Grallator.

The near-coincident and almost identical footprints A and B might, conceivably, be two impressions from the right foot of a single animal. Their near-coincidence may indicate that the animal had adjusted the placement of its foot while standing or moving slowly. It is also conceivable that the sequence of
footprints A (or B), D and E represents the trackway of the same animal (Fig. 2). According to that interpretation, pace lengths A-D and D-E would be 23.8 cm and 21.0 cm respectively; the length of stride would be 43.2 cm and the pace angulation approximately 162 degrees. From the length of the best-preserved footprint (A) it may be estimated that the track-maker was about 31 cm high at the hip (using methods of THULBORN, 1990: 250-254). Relative stride length would be about 1.41, indicative of a walking gait and close to the average value for bipedal dinosaurs in general (THULBORN, 1994). From these data the track-maker may be estimated to have been walking at a speed of about 0.95 m.s\(^{-1}\) (3.4 km.h\(^{-1}\)). According to these interpretations, the material comprises footprints of three (or four) animals, two (or three) of which are represented by single footprints (C, F and, possibly, A or B). Other interpretations are feasible: for example, footprints B and D might represent a pace, with the succeeding pace being completed by a print that lay beyond the broken edge of the slab. This would imply that footprint E was produced by another individual - an interpretation consistent with the obvious differences in depth and preservation of footprints A (or B) and E. At the other extreme, the material might represent the tracks of as many as five or six animals, with two or three of them sharing a common direction of travel. However, the material is really so fragmentary that it is difficult to choose among these several interpretations.

**SIGNIFICANCE FOR THEROPOD DISTRIBUTION**

There is very little evidence of dinosaurs in the Triassic rocks of Australia. The only skeletal remains are those of an anchisaurid prosauropod, *Agrosaurus macgillivrayi* SEELEY, 1891, which is closely related or identical to *Thecodontosaurus* RILEY & STUTCHBURY, 1836 (e.g. VON HUENE, 1906; GALTON & CLUVER, 1976). It has usually been assumed, following SEELEY (1891), that *Agrosaurus* was collected from Upper Triassic rocks somewhere along the north-eastern coast of Australia (e.g. LONG, 1990; WEISHAMPEL, 1990; MOLNAR, 1991). In fact, *Agrosaurus* might equally well be of Early Jurassic age (MOLNAR, 1982), and there is no incontrovertible evidence that it originated from Australia: the type and only material was purchased at auction and lacked any definite indication of its original source. Uncertainties surrounding the provenance of *Agrosaurus* may be resolved by work in progress elsewhere (T.H. Rich, pers. comm., 1997).

More definite evidence of Triassic dinosaurs is a sequence of three footprints reported from the Ipswich Coal Measures by STAINES & WOODS (1964; see also HILL, PLAYFORD & WOODS, 1965: pl. T13, item 5; BARTHOLOMAI, 1966: 148, unnumbered fig; MOLNAR, 1991: 659, fig. 37P). These footprints were found as natural casts (convex hyporeliefs) in roof shales of the Striped Bacon seam at Rhondda colliery, roughly 2 km west of the Rylance colliery. The best-preserved footprint was 46 cm long, and the length of stride was about 2 m. STAINES & WOODS (1964) referred these tracks to the ichnogenus *Eubrontes* HITCHCOCK, 1845 - which, as mentioned above, is invariably attributed to theropod dinosaurs and sometimes regarded as a size-variant of *Grallator* HITCHCOCK, 1858.

Reports of Upper Triassic dinosaur tracks in the Callide Basin, near Biloela, in eastern Queensland (THULBORN, 1990; MOLNAR, 1991), are erroneous. On investigation, these tracks proved to originate not from the Callide Coal Measures, but from overburden of Precipice Sandstone, which is Early Jurassic in age. Most of the tracks so far identified in the Precipice Sandstone, both in the Callide Basin and elsewhere, appear to be those of ornithopod dinosaurs. Some at least are referable to the ichnogenus *Anomoepus* HITCHCOCK, 1848 (THULBORN, 1994).
Finally, the Blackstone Formation of the Ipswich Basin has also yielded an example of *Plectoptera Hitchcock, 1858* (MOLNAR, 1982, 1991), an ichnogenus originally established on material from the Newark Supergroup of the Connecticut Valley. The identity of the *Plectoptera* track-makers is unclear. MOLNAR (1982) dismissed a suggestion that the example from the Blackstone Formation might be the track of a flying reptile (WILLIAMS, 1966), and later considered that it might represent a rauisuchian (MOLNAR, 1991). By contrast, LEES (1986: 282) listed the same specimen under the heading of "paleopod tracks, F. Anchisauridae". Elsewhere, HAUBOLD (1971, 1984) has classified *Plectoptera* among "laceroid" tracks of uncertain affinities. Some examples of *Plectoptera* might, perhaps, be dinosaur tracks affected by secondary narrowing of the digital impressions (an effect described by THULBORN & WADE, 1989; THULBORN, 1990), but this possibility remains to be investigated.

In summary, there are only two definite reports of dinosaurian fossils in the Triassic rocks of Australia - both from the Blackstone Formation of the Ipswich Basin. The first report, by STAINES & WOODS (1964), concerns large theropod tracks (*Eubrontes Hitchcock, 1845*); the second, given here, concerns small theropod tracks (cf. *Grallator Hitchcock, 1858*). The existence of these tracks in a remote intermontane basin of East Gondwana indicates that theropod dinosaurs had achieved very extensive, and possibly global, distribution as early as the Middle to Late Carnian.

The theropod tracks of the Blackstone Formation are the earliest indications to the existence of dinosaurs in Australia and are, indeed, among the earliest examples of dinosaur tracks anywhere in the world. Reports of dinosaur tracks in the Lower and Middle Triassic of the English Midlands appear to be erroneous (see KING & BENTON, 1996; SARJEANT, 1996), and suspected theropod tracks, *Coelurosaurichnus ratumensis* DEMATHIEU & OOSTERINK, 1988, from the Muschelkalk (Middle Triassic) of Winterwijk, in the Netherlands, should be regarded with some caution. The pes of *C. ratumensis* is not complete in any single specimen and is not demonstrably of dinosaurian form. Moreover, the associated manus prints are pentadactyl and strongly reminiscent of those in chirotheriod tracks. In fact, the presence of a five-fingered manus rules out any possibility that *C. ratumensis* could comprise the tracks of theropods (THULBORN, 1993).

The earliest convincing examples of theropod tracks (or, indeed, of any dinosaurian tracks) are from Triassic sandstones flanking the eastern border of the French Massif Central (e.g. DEMATHIEU, 1970, 1971, 1989; DEMATHIEU & GAND, 1972; GAND, 1976; GAND, PELLIER & PELLIER, 1976a, 1976b). Casual inspection of ichnological literature gives the impression that these tracks are firmly assigned to the Middle Triassic (e.g. HAUBOLD, 1971; DEMATHIEU & HAUBOLD, 1972, 1974). However, the footprints occur only a few metres below the presumed Muschelkalk-Keuper boundary (COUREL, 1973), and it appears that this lithostratigraphic boundary has been widely interpreted in chronostratigraphic terms (cf. WARRINGTON et al., 1980, on analogous problems in the Triassic of Britain). In fact, that boundary is probably diachronous. After noting that "...the advance [transgression] of the Upper Muschelkalk is fairly regular in all western Europe..." and that "...it took place, probably earlier to the East than to the west, but always in the Ladinian...", COUREL & GALL (1977: 190) went on to review the work of VIRGILI (1977) - which revealed that the base of the Muschelkalk transgresses the Ladinian-Carnian boundary when traced westwards across northern Spain. In Provence, southern France, a depauperate microfauna (foraminifera, conodonts, crustacean coprolites) gives only an imprecise indication to the age of the local "Muschelkalk supérieur" (ZANINETTI, 1977): here it seems that the top of the Muschelkalk is probably Upper Ladinian or possibly Lower Carnian. These scattered pieces of evidence lead me to suspect that ichnological literature has tended to exaggerate the age of vertebrate tracks from the northeastern border of the Massif Central: those tracks might perhaps be Late Ladinian, or even Early Carnian, rather than Late Anisian to Early Ladinian.

In this context, two other points deserve note. First, the stratigraphic and ichnological literature contains an element of circularity: fossil tracks from the borders of the Massif Central have themselves been used as evidence for dating the parent sediments (e.g. DEMATHIEU, COUREL & DURAND, 1984; DEMATHIEU, 1989). Indeed, Courel (in DEMATHIEU, COUREL & DURAND, 1984: 63) regarded those tracks as biostratigraphic data providing "...les résultats les plus spectaculaires et les plus fiables..." Second, the tracks attributed to dinosaurs are most abundant in younger (presumed Late Ladinian) sandstones in the region of Autun, along the northeastern border of the Massif Central; such tracks are "very scarce" in older sandstones (presumed Middle Anisian) to the south, in the region of Alès (DEMATHIEU, 1989: 202). In other words, the most numerous and most convincing of these French dinosaur tracks might better be regarded as Late Ladinian, or even Early Carnian, rather than Early Ladinian. Most of them have been assigned to various ichnospecies in the grallatorial ichnogenera *Coelurosaurichnus von Huene, 1941*, Anchisauripus Lull, 1904 and *Grallator Hitchcock, 1858* (see COUREL & DEMATHIEU, 1976; DEMATHIEU, 1970, 1971, 1989; DEMATHIEU & GAND, 1972; GAND, 1976; GAND, PELLIER & PELLIER,
1976a, 1976b). Though a few examples were initially likened to small ornithopod tracks in the ichnospecies *Anomoepus Hitchcock*, 1848, these were subsequently re-identified as *Coelurosaurichnus* (GAND, PELLIER & PELLIER, 1976a, 1976b).

Grallatorid tracks in the Ipswich Coal Measures of Queensland are probably somewhat younger than those from the borders of the French Massif Central, though it is currently impossible to assess very precisely their difference in age. A more illuminating comparison may be made with grallatorid tracks (cf. *Grallator Hitchcock*, 1858) reported by RAATH (1996) from the Molteno Formation of South Africa. In their age and ecological context these African tracks appear to be remarkably similar to those of the Ipswich Coal Measures: they are also found in beds of Carnian age, in association with a *Dicroidium* flora, occasional remains of palaeoniscoid fishes, and a variety of invertebrates dominated by insects (RAATH et al., 1990). The grallatorid tracks of the Molteno Formation have been regarded as the earliest evidence for the existence of dinosaurs in Gondwana (RAATH, 1996) - a description that might justifiably be extended to encompass the dinosaur tracks of the Ipswich Coal Measures.

The tracks of the Ipswich Coal Measures reveal that theropods were widely distributed across Gondwana in the Late Triassic, and that these animals may already have undergone some diversification into large forms (represented by the ichnogenus *Eu­brontes Hitchcock*, 1845) and small (represented by *Grallator Hitchcock*, 1858). In addition the tracks confirm that theropod dinosaurs do have an extremely long history on the Australian continent, even though their skeletal remains have not yet been discovered in sediments older than Early Cretaceous (MOLNAR, 1991). Finally, the existence of theropod footprints in Upper Triassic coal measure, both in eastern Australia and in southern Africa, is consistent with the notion that early theropod dinosaurs may have been forest-dwellers (COLBERT, 1951).

NOTE ADDED IN PROOF

A detailed study of *Agrosaurus macgillivrayi* SEELEY, 1891, has concluded that this prosauropod dinosaur is more likely to have originated from England than from Australia (VICKERS-RICH et al., 1999). Consequently footprints from the Ipswich Coal Measures may constitute the entire fossil record of Triassic dinosaurs in Australia.

Preservational variation in a series of dinosaur tracks from the Upper Triassic of Greenland (GATESY et al., 1999, fig. 1e, f) reinforces my suspicion that *Plectopterana Hitchcock*, 1858, may be a dinosaur footprint that collapsed on withdrawal of the track-maker's foot. In that case, MOLNAR'S (1982) report of *Plectopterana* would be additional evidence of dinosaurs in the Ipswich Coal Measures.

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REFERENCES


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