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THE TRIASSIC OF VIRGINIA

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ABSTRACT

Banisterobates boisseau ichnogen. et ichnosp. nov. is described from Triassic (Carnian) sediments of the Danville Basin, Virginia. The type, and only, specimen is represented by three pedal and two manual impressions preserved in part and counterpart. Although four digit imprints are preserved, the pedal print is mesaxonic, with digit I very much reduced. The trackway is remarkable for its very small size (pes 18 mm long) yet finely preserved pad impressions. The evidence strongly supports a dinosauromorph maker of the trackway. Evidence for a more specific referral is inconclusive, but if the trackmaker was a true dinosaurian, on balance an ornithischian is favored over a theropod.

INTRODUCTION

The Newark Supergroup of eastern North America is famed for its assemblages of reptile footprints. The dinosaur trackways from the Hartford and Deerfield basins of the Connecticut Valley are particularly well-known, and have been studied since the early 1800s (Hitchcock, 1836, 1843, 1847, 1858, 1865; Lull 1904, 1915, 1953). Originally considered to be Triassic, all the documented footprints of the Connecticut Valley occur in sediments above the oldest extrusive basalt flows, and are now generally considered to be Early Jurassic in age (Olsen & Baird, 1986).

The past few years have seen dinosaur trace fossils develop into a major research field which has generated a wealth of new data and new perspectives (e.g., Gillette & Lockley, 1989; Thulborn, 1990; Lockley,

1991; Lockley & Hunt, 1995). As a consequence, the descriptions of the Connecticut Valley assemblages are urgently in need of revision. Similar Early Jurassic footprint assemblages have since been identified elsewhere in the Newark Supergroup (Olsen et al., 1982; Olsen & Baird, 1982), including localities in Virginia. By contrast, both collections and descriptions of footprint assemblages from the Triassic strata of the Newark Supergroup have been relatively neglected. The literature tends to generate a somewhat false impression of a general lack of ichnofossils within the Late Triassic sequences.

At least one very significant Triassic footprint locality occurs within Virginia. Weems (1987) first described the occurrence of numerous footprints in the Culpeper Stone Quarry of the Culpeper basin. The sediments exposed in the quarry have not been precisely dated, but they are considered to be Norian in age (Olsen & Johansson, 1994). The track-bearing horizon initially described by Weems contains very poorly defined trackways, and the six taxa he erected (including a putative sauropod) must be regarded as equivocal. However, a second bedding plane at the same locality was more recently shown to contain numerous, clearly defined theropod dinosaur tracks complete with pad impressions (Weems, 1993). The majority of these Weems assigned to the ichnogenus *Kayentapus* on the basis of some similarity to *Kayentapus hopii* from the Kayenta Formation of Arizona. However, we would suggest that because the skeletal morphology of the theropod foot was quite conservative, at least among some of the early Mesozoic forms, all we know presently is that the Culpeper tracks were made by a moderate-sized theropod that was similar in size to the maker of the *Kayentapus* tracks. Weems arbitrarily distinguished between tridactyl footprints on the basis of size so that he assigned tracks less than 230 mm to *Grallator*. Additional footprints at Culpeper indicate the presence of phytosaurs and a few trackways of quadrupedal animals which Weems attributed to aetosaurs (Weems, 1993).

Triassic strata of the Danville/Dan River basin have also produced reptile footprints. Olsen et al. (1978) discussed the occurrence of some of the tracks in this basin, and additional descriptions (Olsen & Baird, 1986; Olsen et al., 1989) indicate the abundance of relatively well defined tracks in the Triassic of the Newark Supergroup. As well as providing some measure of the diversity of terrestrial tetrapods, certain trackways have been shown to have potential biostratigraphic significance. For example, in describing the ichnogenus *Atreipus* Olsen & Baird (1986) showed that it had a relatively limited range, from the late Carnian to the late Norian.

The purpose of the present paper is to describe a completely new ichnotaxon from the Danville/Dan River basin.

GEOLOGY

The Dan River/Danville basin is a particularly narrow one (some 175 km long and with a maximum width of 13 km), which extends across the Virginia-North Carolina border. Originally the sediments in each state were described separately, with the state line being almost regarded as some kind of natural break! This obviously resulted in a confusing dual system of nomenclature. Meyertons (1963) recognized three formations in Virginia, which were differentiated to some extent on grain size: the Leaksville (principally claystones, siltstones and sandstones), Dry Fork (mostly graywackes, arkoses), and Cedar Forest (shales and conglomerates) formations. Meyertons (1963) divided the Leaksville Formation into two members based principally on color: the red Cascade Station member and the gray to black Cow Branch Member. Although Meyertons regarded the Leaksville and Dry Fork formations to be time equivalent, he considered the Cedar Forest to be younger.

In North Carolina the Dan River Group was also seen to comprise three formations (Thayer, 1970); the fluvial Pine Hall Formation, the lacustrine Cow Branch Formation, and the fluvial Stoneville Formation, with the Pine Hall Formation being regarded as the oldest and the Stoneville Formation the youngest.

Thayer (op. cit.) recognized that the rocks of the Danville basin were not time stratigraphic units, but intertonguing lithologic facies (Fig. 1). Consequently, he (1970, 1980) proposed a single scheme, extending the North Carolina system into Virginia, and this has been accepted into general usage (Luttrell, 1989). In the southwest part of the basin the Cow Branch Formation forms the reference beds for the division of the rocks into the Stoneville and Pine Hall formations (Fig. 1). However, where it is absent in the central part of the basin there is no basis for distinguishing more than a single unit and the Dry Fork Formation has been retained (equivalent to the sandstone facies of the Pine Hall and Stoneville formations). The Leaksville and Cedar Forest formations have been abandoned, with the rocks of the Cedar Forest Formation having been assigned to the Dry Fork, and the Cow Branch Member of the Leaksville revised as the Cow Branch Formation and the Cascade Station Member recognized as equivalent to the siltstone facies of the Pine Hall and Stoneville formations.

On the basis of pollen and spore assemblages Robbins (1982) considered the Cow Branch Formation to be late middle to late Carnian in age, noting that the underlying Pine Hall Formation is most probably middle Carnian. She considered the Stoneville Formation to be late Carnian in age, since it overlies the dateable Cow Branch, with deposition possibly extending into the early Norian (based on

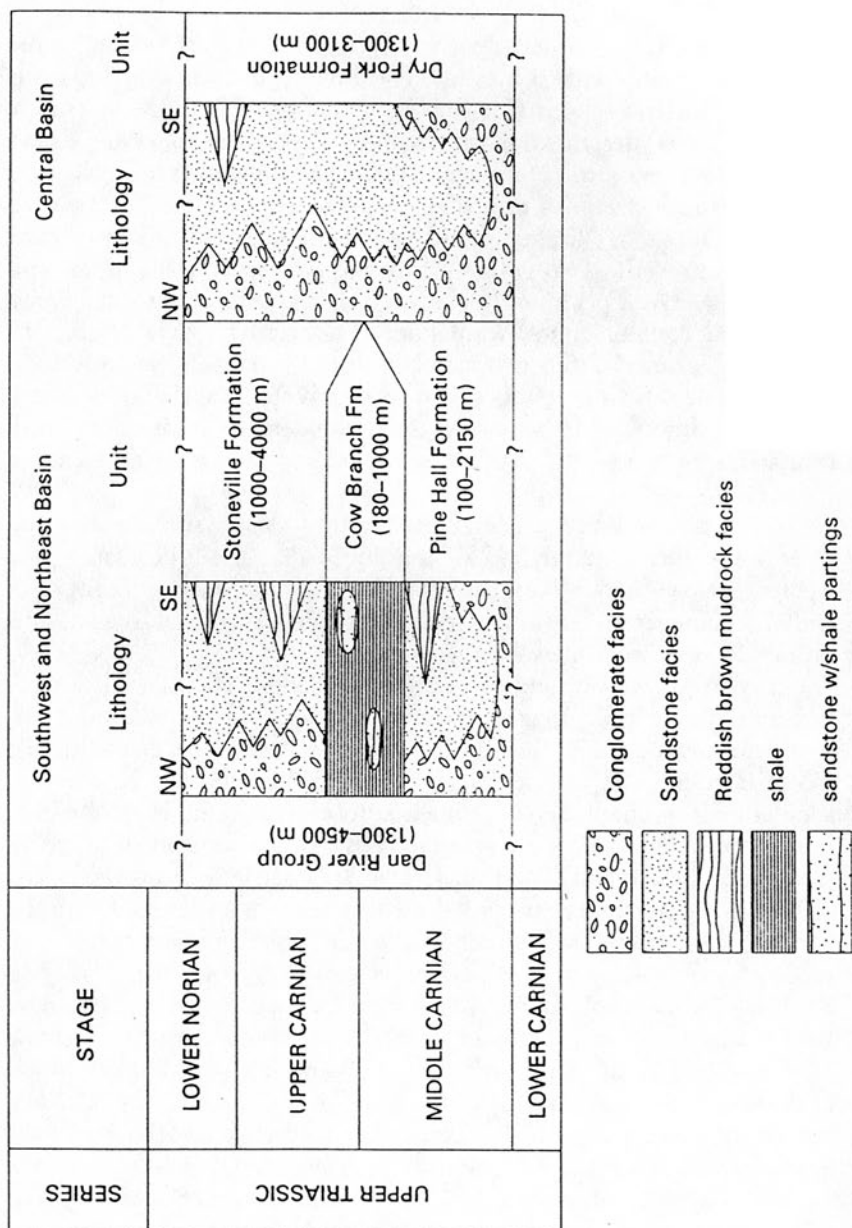


Fig. 1. Stratigraphic relations of the sediments of the Dan River/Danville basin

palynomorph assemblages comparable with those from the Passaic Formation).

Without doubt the most significant outcrops of the Dan River Group occur in the Virginia Solite Corporation Quarry at Cascade, Pittsylvania County. The quarry straddles the North Carolina state line and contains outcrops in a series of cyclical lacustrine shales of the Cow Branch Formation. Some of the oldest true flies (Krzeminski, 1992), thysanopterans (thrips), trichopterans (caddis flies), and water bugs (Fraser et al., 1996), together with angiosperm-like plant remains (Cornet, 1993) make the site one of the most important in North America. Vertebrate fossils include abundant articulated remains of the amphibious reptile, *Tanytrachelos*, various fish as well as a diversity of footprints (e.g., Olsen & Johansson, 1994). Dinosaurian footprints are represented by the ichnogenera *Grallator* and *Atreipus*. Two other archosauromorph ichnogenera, *Apatopus* and *Gwyneddichnium*, also occur at the site.

Baird (1957) suggested that *Apatopus* might have been made by a phytosaur such as *Rutiodon*, a suggestion which has been generally accepted by later workers (e.g., Olsen 1980). For instance, Olsen noted the similar ranges of phytosaurs and *Apatopus* in the Newark Super-group. However, more recently, Parrish (1986) has shown that the pedal morphology of phytosaurs, such as *Rutiodon*, is inconsistent with *Apatopus*, and he suggests that a rhynchosaur or trilophosaur is a more probable candidate for the trackmaker. The much smaller *Gwyneddichnium* trackways frequently show traces of webbing between the digits and they are consistent with the pedal morphology of *Tanytrachelos*.

Further north, to the southeast of Gretna, good exposures of the Dry Fork and Cow Branch formations occur along Virginia Rt. 683. Footprints have been recorded and collected in this area by various amateur collectors, particularly from the silty and sandy facies of the Dry Fork Formation, which outcrop in a cliff on the northeast side of Rt. 683 about 1.1 miles north of the junction with Rt. 938. Here some 90 feet of exposure occurs, consisting of well-laminated maroon, brown and brown-green siltstones and sandstones. Cross-bedding, ripple marks, and raindrop impressions are common. Worm-trails occur throughout, but otherwise the beds are generally unfossiliferous. Typically the tetrapod tracks are rather poorly defined *Grallator*-type prints. A notable exception is a small tetrapod trackway that was found by Bill Hathaway in 1978. It consists of three well-defined hindfoot impressions and also the rather more poorly defined manus prints. Both part and counterpart are preserved and the specimen is now housed in the collections of the Virginia Museum of Natural History.

SYSTEMATIC ICHNOLOGY

Banisterobates ichnogen. nov.

Type species: *Banisterobates boisseaui*

Etymology: For the Banister River and "bates" meaning walker.

Diagnosis: Ichnite of quadruped; tetradactyl pes, but with first digit very much reduced so that pes is essentially mesaxonitic; digit III markedly longer than II and IV, digit II slightly longer than IV; manus poorly defined, but with three very short digit impressions.

Banisterobates boisseaui ichnosp. nov.

Holotype: VMNH 202, part and counterpart of a short trackway bearing three pedal and two manual impressions.

Type locality and horizon: On Virginia Route 683, 1.1 miles north of the junction with Rt. 938, Pittsylvania County, Virginia; silty facies of the Dry Fork Formation.

Etymology: In honor of Peter Boisseau, former chairman of the VMNH board of trustees, for his part in bringing the natural history of Virginia to the people of the Commonwealth.

Diagnosis: Same as for the genus diagnosed above.

Description: Although only one example of this type of footprint has been documented to date, it is so unlike any other footprint described from the Newark Supergroup, or elsewhere, that it is appropriate to designate it as a new ichnogenus. One of the most striking features of the new form is its unusually small size, and since limulid tracks have frequently been mistaken for those of small vertebrates (Caster, 1939, 1941, 1944), the possibility of a limulid as the maker will be considered first.

The new form lacks any evidence of a "median" groove that commonly occurs in limulid trackways as a result of the dragging tailspine. More importantly there is no evidence whatsoever for the impressions of the three or four walking legs typically found in addition to the "footprint-like" impressions of limulids. Finally the asymmetry of the trackway, with clear alternate left and right impressions, clearly distinguishes the new track as that of a vertebrate and distinct from that of a limulid.

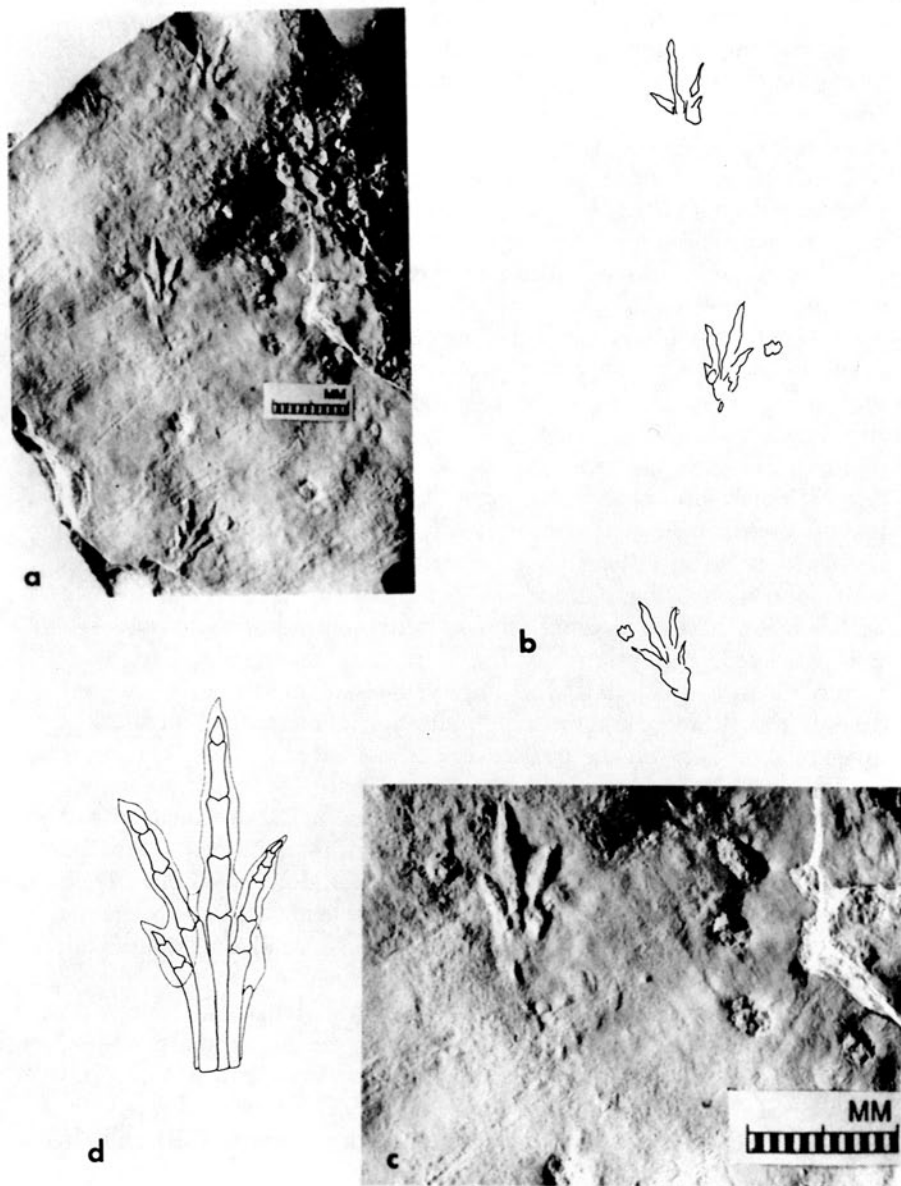


Fig. 2. Holotype, VMNH 202 of *Banisterobates boisseaui* gen. et sp. nov., natural cast of the trackway and (b), camera lucida of the natural mold. (c), single manual and pedal natural cast showing details of the pads and claws. (d), restoration of the pedal skeleton.

A particularly valuable feature of this short trackway is that at least partial pad impressions are exhibited despite the exceptionally small size of the footprints. Three pes and two manus impressions are preserved both as natural molds and natural casts (Fig. 2a). The third manus impression was presumably broken off when the specimen was recovered from the outcrop; there is certainly no evidence that its absence reflects a change to a fully bipedal gait. Further excavation at the site was carried out in 1991, but no more *Banisterobates* tracks were found, although tracks of other ichnotaxa were recovered and will be described elsewhere.

Two left and one right pedal impressions are preserved, and the details of the pads are most clearly seen in the right pes, particularly in the natural cast. As preserved the right pes is 2.5 cm long. It is tetradactyl, with all four digits pointing forwards, but I is very much reduced (Fig. 2b). The print is mesaxonic with III being the principal digit. The new form is unusual in that digit II is a little longer than IV; it is more common in similar functionally tridactyl pedal impressions for digit IV to be equal in length to or slightly longer than digit II. There is a faint impression of the metapodium in the first two pedal prints, but the well-defined "heel" sometimes seen in certain ornithopod trackways is not preserved, and essentially the prints are digitigrade. Each digit terminates in a small claw. Pad impressions are most clearly seen on digits II and III and they give some indication of the bone structure, but differentiation between the pads of digit IV is blurred.

The manus impressions are small, almost undifferentiated, depressions (Fig. 2b). The left manus is positioned above digit IV and just lateral to digit III. The right manus imprint is positioned just to the right of the distal end of digit IV. There is some indication of three digits that are best seen in the right print, but they are equivocal, and certainly there are no convincing claw impressions. No trail drag marks are preserved.

The pace angulation (PA) is 146° , the stride length (SL) measures 122.0 mm, and the foot length (FL), including the metapodium, is 24.0 mm, but excluding the weakly defined metapodium it is 18.0 mm. This gives an SL/FL ratio in the range of 5/1 to 7/1. The total divarication between the digits measures 54° with the interdigital angles II-III and III-IV practically equal at 27° and 26° respectively.

DISCUSSION

Baird (1954) raised the issue that within Triassic sediments it might prove difficult to differentiate between dinosaur trackways and those of certain "thecodontians" with an "advanced" locomotor anatomy. For instance, the high pace angle which characterizes many dinosaurian

trackways may also occur in some Triassic "thecondontians." In a discussion of the ichnogenus *Rotodactylus*, Thulborn (1990) drew attention to the presence of the impression of a backwardly-turned digit V. He noted that reduction of digit V would leave a digitigrade print of a dinosaurian type. Thulborn recognized three criteria to distinguish between dinosaurian and "thecondontian" prints in Triassic sediments: 1) the tracks are mesaxonic, 2) digit V is strongly reduced or absent, and 3) the track-maker was consistently digitigrade when walking. With respect to the *Banisterobates* pedal print it is certainly conceivable that the apparent metapodium impression could be interpreted as the impression of a backwardly turned digit V. However, this is considered unlikely as there is no suggestion of a terminal claw impression. Furthermore, the metapodium impression, if present, is clearly very weak, so that the print can be considered to be essentially digitigrade. More importantly the foot is mesaxonic, a condition which is typical of dinosaurian trackways. Thus, with respect to Thulborn's criteria, *Banisterobates* would seem to be attributable to a small dinosaur. However it should be noted that certain Dinosauromorpha also possess a mesaxonic footprint. Although the pes of *Lagerpeton* (Fig. 3a) would clearly produce an ectaxonic print, the general shape and gracile build of the pes of *Marasuchus* (Fig. 3b) is much more consistent with the *Banisterobates* trackway. However digit IV is again slightly longer than digit II in *Marasuchus*. It is also worth noting here that what is known of the pes of *Herrerasaurus* is not inconsistent with the *Banisterobates* pedal impression, although *Herrerasaurus* was a much larger and more robust animal than the maker of the *Banisterobates* trackway. Sereno & Novas (1992) consider *Herrerasaurus* to be a true dinosaur, in particular a basal theropod (Novas, 1993; Sereno, 1993; Sereno & Novas, 1993). On the other hand Padian & May (1994) and Fraser & Padian (1995) consider the herrerasaurs to lie outside the Dinosauria. Further discussion of the constitution of the Dinosauria is outside the scope of the current paper.

If *Banisterobates* is accepted as a dinosaurian ichnogenus, there remains the difficulty of making the distinction between a theropod or an ornithopod.

The prominent digit III impression is more suggestive of a theropod than an ornithopod (in which the three main digit impressions are typically more subequal). The small claw prints on the pes are also perhaps more consistent with a theropod since the digits of ornithopods typically terminate in a blunt "nail" or "hoof-like" claw. However, it should be noted that gracile and small ornithopods such as *Heterodontosaurus*, *Hypsilophodon*, and *Fabrosaurus* possess narrow claws that are not dissimilar to those of theropods and, furthermore, these genera also possess a relatively long third pedal digit.

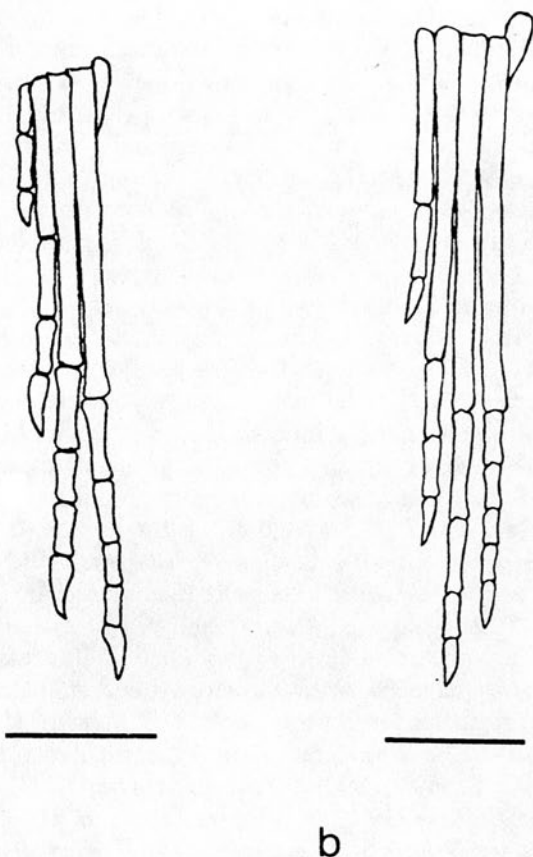


Fig. 3. Restoration of the pes in anterior view of (a), *Lagerpeton* (scale bar = 2 cm) and (b), *Marasuchus* (scale bar = 1 cm). (a, based on Sereno & Arcucci, 1993; b, based on Romer, 1971, and Sereno & Arcucci, 1994.

The presence of an impression of digit I which points forwards, rather than backwards, is indicative of an ornithopod. However, many of the early theropods, such as *Syntarsus*, had the hallux directed forward alongside digit II, and thus could produce a print similar to some of the early ornithopods—particularly those with slender feet such as the “fabrosaurs.” Perhaps more importantly, manus prints are not typically

found in theropod trackways. While a few trackways, which are generally referred to theropods, do show manus prints, such as *Atreipus metzneri* (Heller 1952), Thulborn (1990) noted that in theropod trackways that preserved a manus print, the pes lacked any impression of the metapodium. Indeed, Thulborn cited this factor as one of the reasons that he considered *Atreipus* to be a theropod ichnotaxon rather than an ornithopod as had been tentatively proposed by Olsen & Baird (1986).

A comparison of the lengths of digits II and IV offers no further insight. For example, in ceratosaurs, such as *Syntarsus*, and "coelurosaurs", such as *Compsognathus*, although digits II and IV are of a comparable length, digit IV is typically slightly longer. Although in *Fabrosaurus* the reverse is true, it does not seem to be a general rule amongst small ornithopods.

The pace angulation, stride length, total digit divarication and SL/FL ratio are consistent with ranges given by Thulborn (1990) for both small ornithopods and "coelurosaurs." Small ornithopods often have subequal interdigital angles II-II and III-IV, but certainly by itself this is not a convincing argument for regarding *Banisterobates* as a theropod.

The lack of any fine detail on the manus impression is intriguing. In view of the rather clear impressions of claws in the pedal prints, their absence in the manus is perhaps somewhat surprising. It is, therefore, postulated that the trackway may represent a quadruped that "knuckle-walked." Knuckle-walking has been previously proposed for sauropods (Beaumont & Demathieu, 1980), but this has not been widely accepted (Thulborn, 1990). The forelimbs may have been supported by the metacarpals with the digits curled up behind, thus failing to leave an impression. Equally if the forelimbs bore considerably more weight than the hindlimbs, then the manual impressions may well be weak.

The size of the *Banisterobates* pes print is comparable with some examples of *Wintonopus* from the mid-Cretaceous of Queensland (Thulborn & Wade, 1984), and they rank amongst the smallest dinosaur ichnites known. As such, it is quite possible that the *Banisterobates* trackway was made by a juvenile, but in the absence of any other comparable tracks it is clearly impossible to comment further on this.

The evidence for either a basal dinosauromorph or a true dinosaurian is inconclusive. If a member of the Dinosauria was the maker of the *Banisterobates* trackway then, on balance, the occurrence of a partial metapodium impression, the forward-pointing hallux (although this is primitive for Ornithodira) and the presence of manus prints are considered to favor an ornithopod.

EARLY MESOZOIC FAUNAS AND THE BIOSTRATIGRAPHIC
IMPLICATIONS OF ICHNITES

The Early Mesozoic is a key period in the evolution of terrestrial vertebrates. During Triassic times the pterosaurs and non-avian dinosaurs came to prominence. In addition, Triassic rocks have yielded the first mammals, crocodiles, lissamphibians, turtles and possibly even the first birds (Chatterjee, 1991). At the same time a number of major tetrapod taxa became extinct, including the rhynchosaurs, dicynodonts, procolophonids and a variety of "thecodontian" groups such as the phytosaurs and stagonolepids. In the last decade attention has focused on this change from what might be termed faunas of "paleo-tetrapods", or primitive terrestrial vertebrates, to Early Jurassic faunas comprising "neotetrapods", or terrestrial vertebrates of essentially modern aspect. It has been variously argued that this faunal turnover was gradual (e.g., Bonaparte, 1982; Charig, 1984) or, at least in part, catastrophic (e.g., Benton, 1983). Where arguments have been made for catastrophic extinctions, two alternative patterns are frequently debated. One school of thought argues for a single event at the very end of the Norian (e.g., Olsen et al., 1987), while the second proposes a major end-Carnian event, which in turn may have been followed by a smaller end-Norian extinction (e.g., Benton 1991, 1994).

The lack of any unequivocally dated fossiliferous sequences documenting the entire Late Triassic-Early Jurassic period has fueled the debate concerning the timing of these putative mass extinctions. The sediments of the Newark Supergroup can potentially be of tremendous importance in resolving some of the arguments, since collectively they unquestionably provide a continuous sequence across the boundary. However, there is a gap in the fossil record due to the apparent paucity of skeletal remains in the Norian sections. Benton (1991) has implied that this gap may be a real phenomenon reflecting an end-Carnian mass extinction. However, we contend that many of the Norian sections of the Newark Supergroup are indeed fossiliferous, but unfortunately they remain undescribed in the literature. It is equally important to recognize that parts of the Late Triassic sequences represent sedimentary environments that typically lack body fossils. Nevertheless, it is becoming increasingly apparent that many such horizons contain an abundance and diversity of ichnofossils, and a number of authors have recognized the biostratigraphic potential of trackway assemblages. For example Olsen & Galton (1984), in assessing the footprint assemblages from the Stormberg Group of southern Africa, developed a generalized global correlation scheme for Late Triassic-Early Jurassic trackway assemblages.

In broad terms, according to this scheme, Late Triassic assemblages seem to be dominated by chirothere trackways together with *Grallator*-types, and distinct forms such as *Rhynchosauroides*, *Gwyneddichnium*, and *Atreipus*. On the other hand the *Grallator* type footprints become markedly more dominant in Early Jurassic assemblages, and forms such as *Anomoepus* and *Batrachopus* are apparently entirely restricted to the Jurassic. Haubold (1986) and Lockley & Hunt (1995) attempted to refine Olsen and Galton's scheme to the stage level. However, it is felt that at present the diversity of tetrapod trackways described from Early Mesozoic sediments is too limited to offer a reliable biostratigraphic framework at this level. For instance, some of the distinctions between one stage and the next reflect little more than size differences in grallatorid-type trackways. That is not to say that we believe that clear distinctions are necessarily absent, but that presently there is insufficient published information to be able to evaluate whether tetrapod tracks and trackways might offer useful additional biostratigraphic data, which in turn could help resolve the issue of end Triassic extinction patterns.

It is hoped that awareness of the potential value of Early Mesozoic trackways will encourage descriptions of the nature and distribution of both new forms such as *Banisterobates*, as well as such well-established ichnotaxa such as *Grallator*. Only when the abundant trackway assemblages from the Carnian, Norian, and Hettangian of the Newark Supergroup are fully described will it be possible to comment on claims for a depauperate Norian fauna.

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