A MIDDLE JURASSIC DINOSAUR TRACKWAY SITE FROM OXFORDSHIRE, UK

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ABSTRACT. The Middle Jurassic (Bathonian) Ardley trackway site in Oxfordshire, UK is described in detail. The track site is extensive, containing over 40 more-or-less continuous theropod and sauropod trackways preserved together on a single bedding plane with some trackways up to 180 m in length. The trackways display reasonable preservation, with claw marks discernible. Sauropod trackways are by far the most abundant and are representative of taxa that exhibit both narrow and wide-gauge styles of locomotion. Theropod trackways are represented by large tridactyl prints and claw impressions that display exceptionally low pace angulation values during their walking phase. One theropod trackway is unique in that it reveals a gait transition associated with a temporary increase of speed. These dinosaurs were walking over a lime-mud firmground to hardground that was emergent, or locally very shallowly submerged. GPS (Global Positioning Satellite) data reveal that the tracks, preserved during a short time interval, trend in a north-easterly direction. Multi-herding behaviour is suggested for the sauropods of differing size. The discovery of this site adds significantly to our knowledge of the taxonomic composition of Middle Jurassic ecosystems. Evidence concerning locomotor styles employed by saurischian dinosaurs, footprint identification, potential trackmaker, social interactions and observations concerning estimates of Middle Jurassic faunal diversity, as well as aspects of dinosaur locomotor evolution are discussed.

KEY WORDS: theropod, sauropod, Bathonian, *Megalosaurus*, *Cetiosaurus*, GPS, locomotion.

DINOSAUR trackways have been used as measures of faunal diversity and group behaviour as well as for estimating locomotor posture, gait and speed (Lockley 1998). Trackways have the potential to offer a different approach in elucidating these aspects of dinosaurian biology because they represent a direct interaction of the organism with the substrate. As a consequence, they have been most effectively used to assess the biomechanics of dinosaurian locomotion, and in some cases offer new insights that osteology alone cannot predict (Gatesy *et al.* 1999; Day *et al.* 2002*a*). New dinosaur trackway sites, as with new osteological discoveries, have the potential to add further to our knowledge of this group.

The discovery of the trackway site at Ardley, Oxfordshire, UK is of considerable importance and value because of the age and extensive nature of the site and the ecological, phylogenetic and biomechanical information that it offers (Day *et al.* 2002*a*). Many dinosaur groups radiated during the Middle Jurassic, replacing Late Triassic and Early Jurassic faunas (Weishampel *et al.* 1990; Sereno 1997). The rarity of vertebrate body fossils and tracksites from the Middle Jurassic indicates a poor, or at best incomplete, understanding of vertebrate evolution during this 21-Ma interval of Earth history. Recent discoveries of Middle Jurassic trackway sites in continental Europe and America (dos Santos *et al.* 1994; Lockley *et al.* 1998; Kvale *et al.* 2001), and now in the UK, are therefore important in this regard.

The Middle Jurassic of the Midlands region of England (Text-fig. 1) is yielding considerable information on fossil terrestrial vertebrates during an important period in their evolution. With the exception of Patagonia (e.g. Bonaparte 1979) and some recent finds in China, Middle Jurassic vertebrate localities are not well documented elsewhere in the world (Metcalf and Walker 1994). The vertebrate palaeontology of Ardley Quarry, unlike the nearby Middle Jurassic sites of Stonesfield (UK National Grid Reference SP 387171), Shipton on Cherwell (SP 475178) and Kirtlington (SP 494199) is largely unknown. Stonesfield is historically famous for the discovery of the first described dinosaur, the large theropod *Megalosaurus* (Buckland 1824), as well as a diverse associated fauna, and is generally regarded as one of

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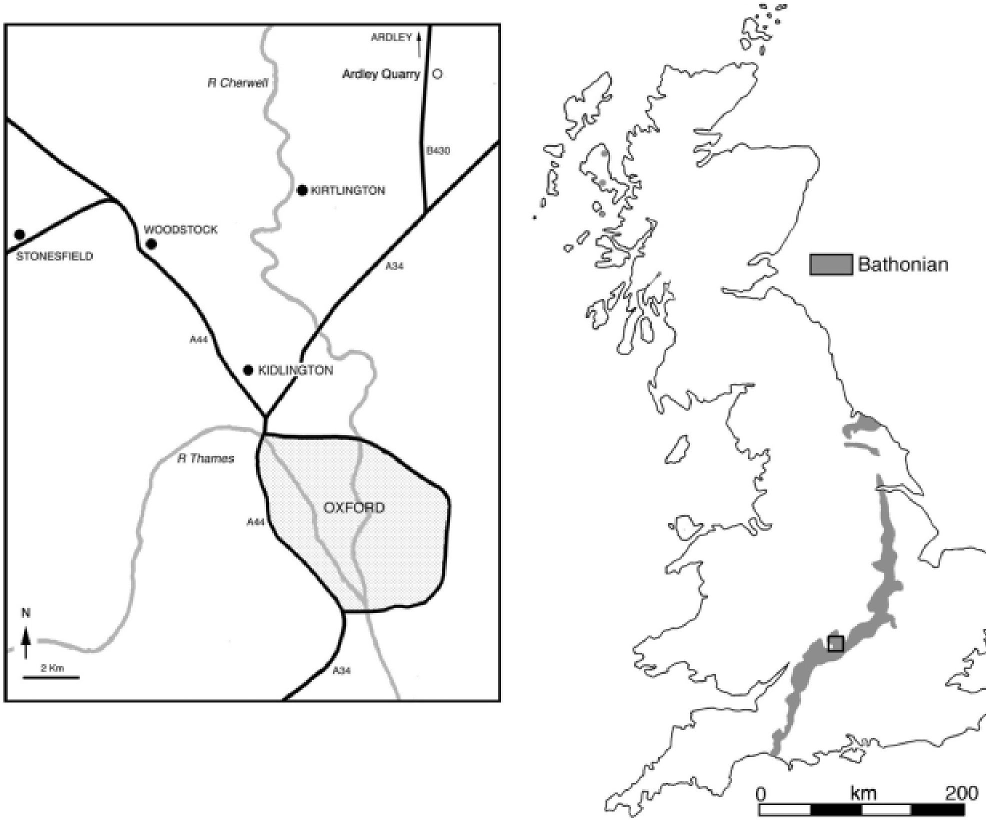


TEXT-FIG. 1. UK map depicting Bathonian rock outcrops (after Benton and Spencer 1995). Inset, map of Oxford and surrounding Middle Jurassic sites.

the best Middle Jurassic terrestrial reptile sites in the world (Benton and Spencer 1995). Kirtlington is of equal importance in terms of its faunal diversity, and is one of the richest known sites for small terrestrial vertebrates, including anurans, caudates, chelonians, lepidosaurians, crocodiles, pterosaurs, tritylodont synapsids and mammals (Evans and Milner 1994). While dinosaur material is rarer at the quarries associated with Shipton-on-Cherwell, this site has yielded significant remains of the crocodile *Steneosaurus*.

Prior to the findings presented here, Ardley Quarry has been mentioned only in the context of comparable late Bathonian fossil localities in Oxfordshire (Benton and Spencer 1995, p. 156), where it was referred to as Ardley Quarries. It has also been discussed as part of wider, regional stratigraphic correlations (Cope *et al.* 1980) and local stratigraphy (Palmer 1973). However, Ardley Quarry is the largest trackway site to have been discovered in the UK, far exceeding all previous discoveries in size and number of tracks (Wright *et al.* 1998). It also appears to contain some of the longest trackways in the world when compared to other sites (e.g. dos Santos *et al.* 1994).

ARDLEY QUARRY

Plan of the quarry and tracks

Ardley Quarry is located in north Oxfordshire (Text-fig. 1), approximately 15 km north of Oxford (SP 542257). The quarry covers an area of approximately 0·5 km^2, although the quarry floor where the footprint bed is exposed is only about half of that area. The footprint horizon is a single layer forming a horizontal and unbroken surface. Work to date at the site has revealed a total of 42 more-or-less continuous trackways, and it is expected that further quarrying will reveal more. Many of the trackways are of considerable length, some measuring up to 180 m. The footprints themselves are reasonably well defined, in that toe and occasionally claw impressions are discernible; however, exceptional morphological details such as digital pads or skin textures have not yet been recorded from any footprint. Trackways are represented by both sauropod and theropod saurischians, but ornithischian tracks have not been recorded from this site so far. Theropod trackways are not nearly as common as those of sauropods, representing only 0·075 per cent of known trackways. Theropod prints appear to be a rare component of previously described Middle Jurassic sites in Europe and are often absent from these assemblages. This is in marked contrast to the comparative abundance of their body fossil remains.

Quarry activities and landfill

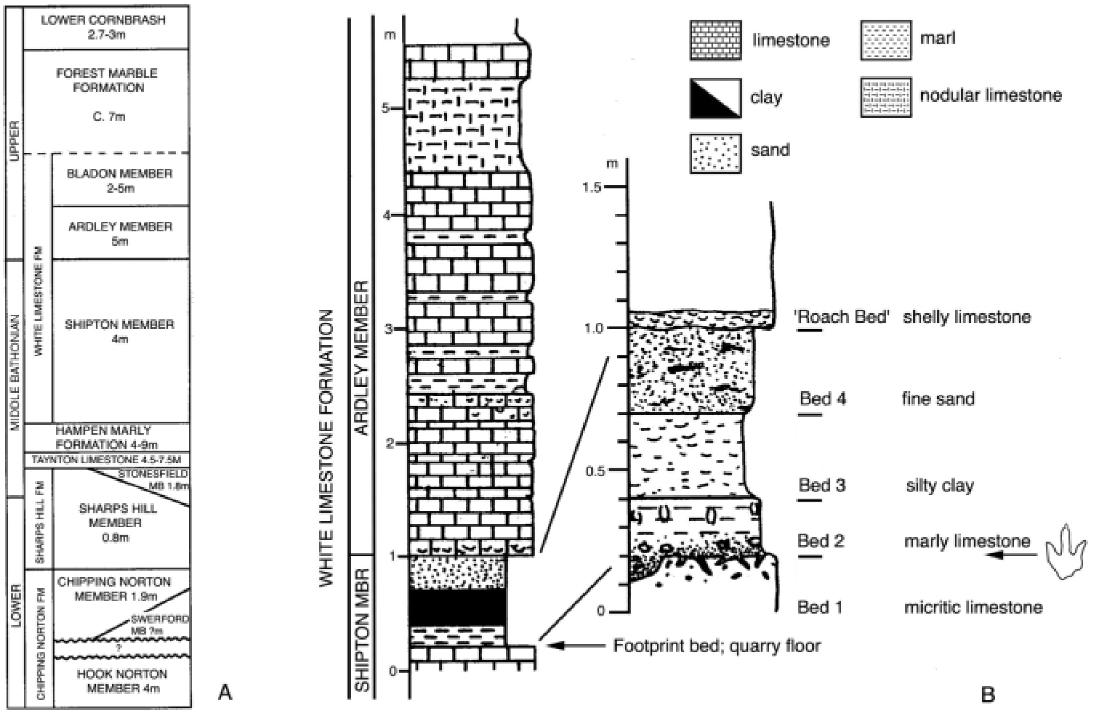
Ardley Quarry is both a working quarry and a landfill site. It is quarried for White Limestone, a micritic limestone used as basal fill for roadways. After quarrying, parts of the quarry floor are then used for landfill. A clay horizon covering the footprint horizon is used to line ‘cells’ making the site ideal for landfill activities. The footprint horizon forms the working floor of the quarry. While quarrying initially exposed the tracks themselves, some have subsequently been damaged by general quarry activity. As the site is used for landfill, many of the initial discoveries recorded here have now been covered and effectively lost to science.

Scientific mission

Prior to the discovery of the trackways, this site already had long-standing consents for quarrying and landfill. The main purpose of this project was the documentation of this site for posterity. This has been achieved by the following: (1) detailed mapping of trackways using GPS data; (2) the creation of a database of trackway and footprint measurements, including footprint and digit length and width, depth of print, pace and stride length and trackway width; (3) the preparation of casts of prints from representative areas of the site and; (4) the generation of a photographic archive of the site referenced with respect to the trackway database outlined in 2. Material and records from this project are held in both the Oxford University Museum of Natural History and the Sedgwick Museum, Cambridge.

Methods

The main method for documenting the trackways within the site was through the utilisation of GPS data. This is the first time GPS has been used for this purpose. Application of GPS greatly facilitates identification of the morphology, number and orientation of trackways. However, GPS was not used during preliminary stages of the survey work, and some trackways initially recorded during manual surveying were subsequently lost through in-filling of the quarry floor towards the north and east of the site. GPS provides an accurate record of topographic features by recording X and Y co-ordinates of each print with respect to a permanent feature of the landscape. Prints were recorded by taking a reading from their centre point. GPS equipment was provided by the Department of Earth Sciences, University of Oxford. Data were subsequently analysed using ArcView software, enabling footprint co-ordinates to be viewed as an entire data set, as individual trackways, or as print triplets. This provided additional data on pace angulation and stride and pace length, as a supplement to the measurements (see Appendix). Each footprint was numbered sequentially, while trackway numbers were not. Trackway data also include measurements of stride length (SL), pace length (PL), trackway width (TW; measured from the lateral margins of the prints), total trackway length, footprint length (FL), footprint width (FW), length and width of digits (theropod trackways) and pace angulation (ANG). These data were not available for all trackways.



TEXT-FIG. 2. A, stratigraphic section of the Bathonian in Oxfordshire (after Cope *et al.* 1980). B, stratigraphy of Ardley Quarry, depicting the footprint horizon. Left: original stratigraphic log from Palmer (1973).

Institutional abbreviations. BMNH, The Natural History Museum, London; OUM, The Oxford University Museum of Natural History.

GEOLOGICAL AGE AND STRATIGRAPHIC CORRELATIONS

The stratigraphic age of the strata exposed at Ardley is Bathonian, a stage that lasted from approximately 166–161 Ma (Harland *et al.* 1990). The Bathonian rocks of Oxfordshire have received much attention (see Arkell 1947; Sellwood and McKerrow 1974; Palmer 1979; Cope *et al.* 1980; Sumbler 1984), although accurate correlations of stratigraphic sections are often problematic owing to the absence of significant fossil evidence (Cope *et al.* 1980).

The succession exposed in Ardley Quarry falls within the Shipton and Ardley members of the White Limestone Formation (Text-fig. 2A; Palmer 1979). The limestones, marls and subordinate sands and clays that comprise this formation were deposited within a south-west–north-east orientated belt of near-shore lagoons that fringed the north-west margin of the London Platform. To the west, the succession becomes progressively more open marine in nature (Palmer 1979), passing into oolitic, spar-cemented limestones in the vicinity of Cirencester. The detailed succession in the lower part of the quarry is shown in Text-figure 2B.

The Ardley succession, previously documented towards the north of the quarry by Palmer (1973), is approximately 6 m in thickness from the base, forming the footprint horizon, to the top, where the White Limestone Formation is overlain by the Forest Marble Formation. The presence of the trackway horizon has not previously been recorded. The footprint horizon is near the top of the Shipton Member, which equates with the top of the *Morrisceras morrisi* Zone of the Middle Bathonian.

The *Cetiosaurus*-bearing beds of the nearby site at Kirtlington (Text-fig. 1) are Late Bathonian in age

(Palmer 1979). Stonesfield (Text-fig. 1) is slightly older, dated as early Middle Bathonian (*Progracilis* Zone; Torrens 1974; Boneham and Wyatt 1993).

LITHOLOGY

Shipton Member

Bed 1, Footprint Bed (0·2–0·3 m exposed). Pale grey micritic limestone containing peloids and bioclastic debris (mostly bivalve shell fragments) and moulds of aragonitic bivalves and gastropods. Comparison with the section formerly exposed in the quarry (approximately 1 km to the north; Palmer 1973) suggests that Bed 1 is probably about 1 m thick in total. The surface has an irregular low hummocky topography and is capped by a strongly burrowed omission surface (*Planolites* burrows) overlain by darker grey contrasting bioclastic arenite which also infills burrows. Bed 1 forms the floor of much of the present Ardley excavation.

Bed 2 (0·2 m). Firm grey coarse bioclastic limestone, passing upwards into marly limestone. At the base, lenses of coarser material containing lignite fragments infill the prints inset into the underlying bed. The bed contains numerous regular echinoids of the genus *Acrosalenia*, some of which retain spines on the surface of the test, and many slightly abraded oysters (*Praeexogyra hebridica*). Brachiopods and vertebrate remains (crocodile teeth, scales and teeth of the fish *Lepidotes* spp., and shark and ray teeth) are also present, but rare. Deep burrowing bivalves of the genus *Pholadomya* are preserved in life position in their burrows.

Bed 3 (0·3 m). Dark grey silty clay, containing abundant oysters (*P. hebridica*) and radioles of *Acrosalenia*.

Bed 4 (0·2–0·3 m). Carbonaceous dark grey fine sand, bioturbated, weathering yellow-brown in the upper part. Contains numerous *P. hebridica* test fragments and spines of *Acrosalenia*, and fragments of lignite.

Ardley Member

4–5 m of bedded bioclastic and micritic limestones of the Ardley Member are exposed in the quarry faces at Ardley (Palmer 1979). The basal limestone of the unit directly overlies the sand of Bed 4 and is 0·5 m thick; it is the 'Roach Bed' of Arkell *et al.* (1933). The lowest 0·15 m of this bed contains abundant moulds of well-preserved gastropods and bivalves.

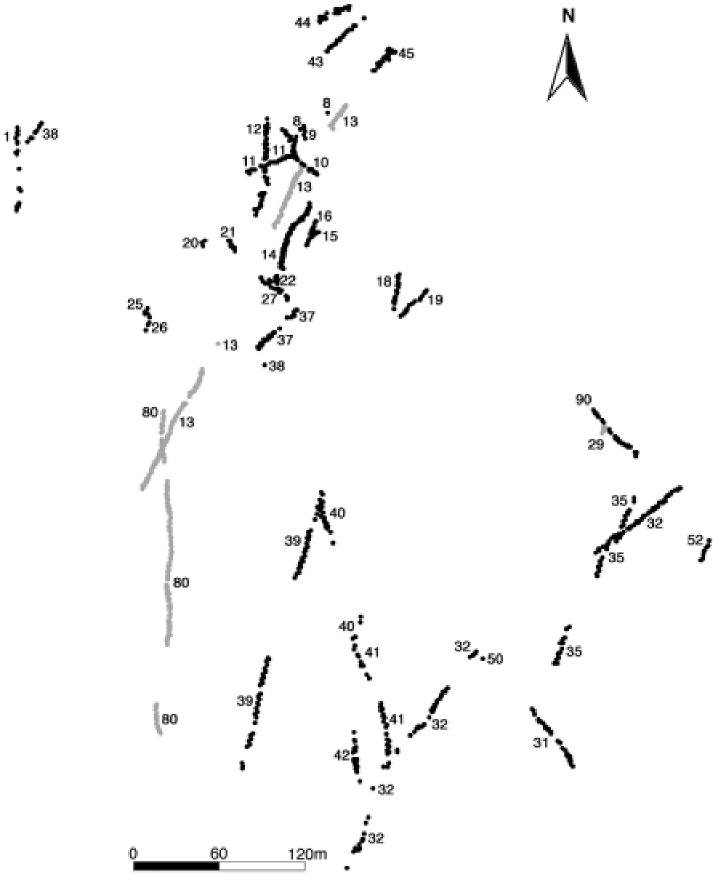
DESCRIPTION OF TRACKWAYS

Orientation of trackways

The GPS data recorded on site (Text-fig. 3) display a distinct trend in trackway orientation, with the majority of trackways bearing north-north-east–south-south-west. Several trackways (T31, 41, 90) are slightly divergent from this general trend, bearing north-west–south-east. The degree of parallelism exhibited by these animals suggests their movements were either constrained by a linear geographical feature, or that they were moving in a herd. A combination of these hypotheses is also possible. The theropod trackways are all oriented in a north-easterly direction (see Text-fig. 3).

Theropod trackways

These are the least common component of the Ardley ichnofauna. However, perhaps the most significant discovery at the site is trackway 13, which provides the first recorded evidence of dual-gauge locomotion in a theropod dinosaur (Day *et al.* 2002*a*). The two longest theropod trackways (T13 and T80) are both in excess of 180 m, comprising approximately 100 prints each. The trackways are orientated in a north-easterly direction (Text-fig. 3), appearing in the southern edge of the quarry and disappearing under landfill

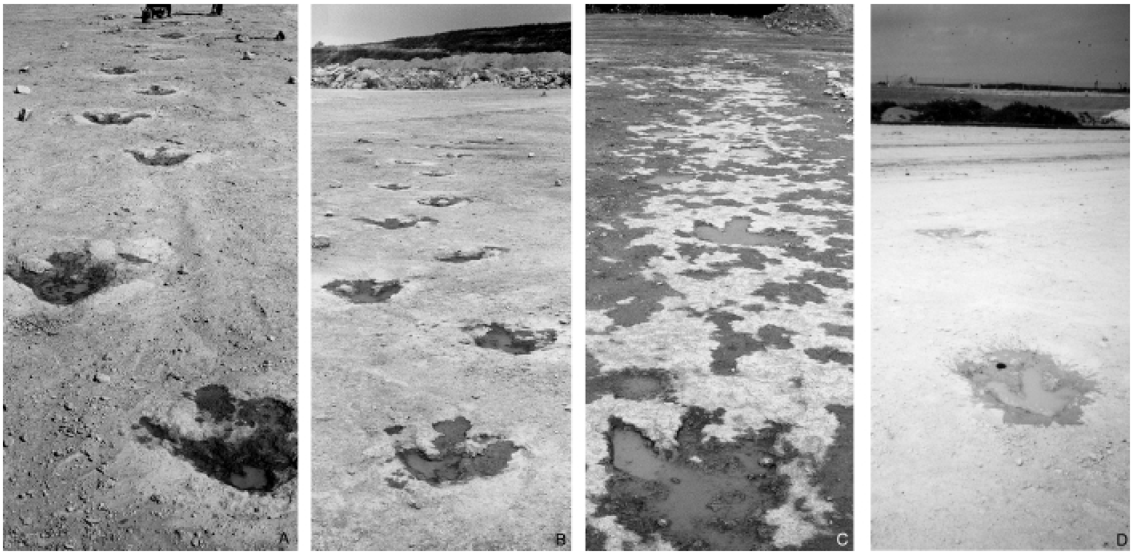


TEXT-FIG. 3. GPS data of the dinosaur trackways at Ardley Quarry. Each point represents a single footprint. Black indicates sauropod trackways, grey indicates theropod trackways.

in the northern part of the site. A third trackway, T29, is considerably less extensive at 30 m long and contains five discernible prints. It is also oriented in the same direction.

There is no obvious interaction or relationship with nearby trackways for much of the length of T13 and T80, until they intersect at a central point in the quarry. A number of sauropod trackways are in close proximity towards the end of T13, which is itself intersected by a single sauropod trackway, T10 (Text-fig. 3). Theropod trackways T13 and T80 are comparatively well preserved, having been recently excavated, while T29 is heavily eroded and is unfortunately not traceable in either direction owing to quarry spoil and a landfill cell. A possible fourth theropod trackway, also oriented northwards, was discovered during the initial investigation of this site, but was not relocated during recent excavations. This is probably a result of the continued movement and displacement of spoil heaps at the quarry.

Pes morphology. The footprints are tridactyl, with pronounced median symmetry (Text-figs 4, 5, 6A–B). The pes is composed of three large, weight-bearing toes (digits II–IV) that are moderately divergent. Print length (measurements excluded spur and claw marks) in trackways 13 and 29 average 0·72 m, while T80 is slightly shorter at 0·66 m. The average widths of the prints from these trackways are 0·51, 0·49 and 0·47 m respectively. Digit III is the longest in the foot, as is usual in theropods. The average measurement for the

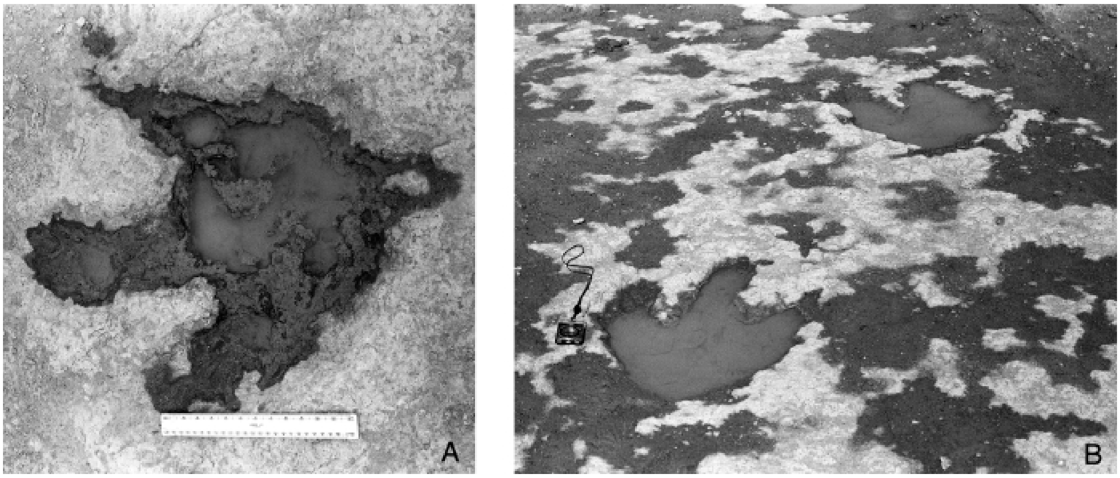


TEXT-FIG. 4. A–B, Ardley theropod trackways 13 and 90 depicting ‘walking’ phase. C–D, Ardley theropod trackway 13 depicting ‘running’ phase.

length of digit III in T13 and T80 is 0·39 m, while the widths are 0·14 and 0·15 m respectively [digit length is measured to the base of the digits (hypex; Thulborn 1990, p. 126, fig. 5·10) and excludes the claw]. Digits II and IV are similar in width and are approximately three-quarters of the length of digit III. Length (L) and width (W) of digit II for T13 and T80 measure 0·32/0·12 m (L/W) and 0·29/0·14 m respectively. Digit III is the most likely to be completely preserved as it forms the main weight-bearing toe. Digits II and IV are often incompletely preserved, but there is no preferential preservation of either digit.

A posteriorly directed furrow associated with some prints may be an impression left by the hallux. Posteromedially orientated hallux prints in some tracks appear to be superficially comparable to the impression of the posteriorly directed hallux of birds. Such trackways have led to speculations concerning undiscovered theropods with a reversed hallux (Nopcsa 1923; Thulborn 1984; Gauthier 1986). However, this does not conform to observations concerning the orientation of the hallux in basal theropods, which currently show no evidence of an avian-like reversed hallux (Gatesy *et al.* 1999). Gatesy *et al.* (1999, p. 142, fig. 1), proposed that a reversed hallux impression is simply the impression left by a hallux that was slightly abducted and flexed, but not reversed. Alternatively, this furrow might represent part of the metatarsus, although trackway evidence substantiates inferences drawn from pedal osteology that theropod dinosaurs were commonly digitigrade. Notable exceptions include trackways where the metatarsus is imprinted along its entire length, suggesting that some theropods were plantigrade (Thulborn and Wade 1984; Kuban 1989; Pérez-Lorente 1993). As the prints at Ardley are relatively shallow and the furrow is narrow and slightly medially directed the interpretation of a hallux impression is more reasonable.

While no clearly defined digital pads are preserved in any of the footprints, the external shape of the print provides some information concerning pedal morphology. The tapering posterior margin seen in most theropod prints, including those at Ardley, represents the impression of a pad beneath the metatarsophalangeal joint of digit IV (Thulborn 1990). A notch along the medial edge of the print (Farlow *et al.* 2000; Text-fig. 6A–B), also found in the Ardley prints, indicates that the joint between the phalanges and the metatarsal of digit II does not extend as far posteriorly as digit IV. Claw impressions are associated with digit III. These are ovoid, with the long axis orientated in the anterioposterior plane of the pes.



TEXT-FIG. 5. A, theropod footprint; scale bar represents 30 cm. B, theropod prints depicting 'walking' phase.

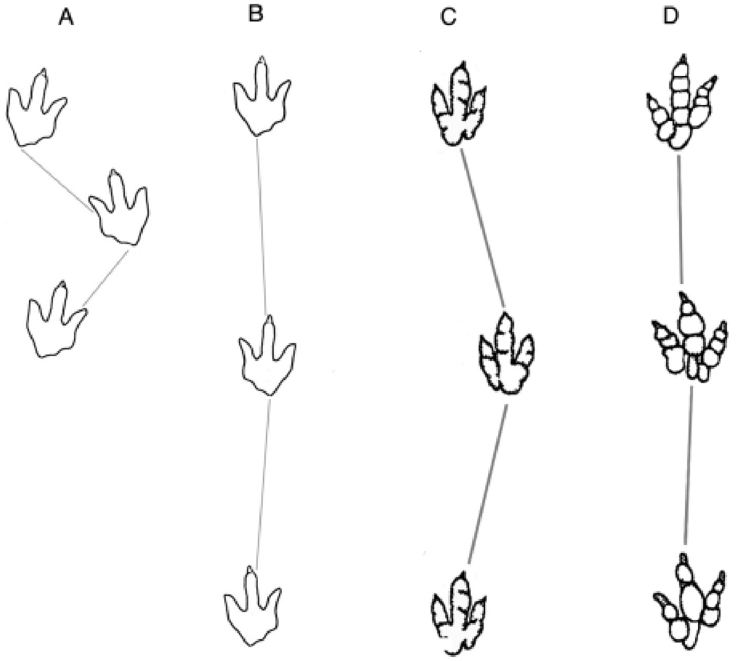
Foot rotation. Theropod footprints tend to show slight positive rotation (Thulborn 1990), i.e. they point inwards. This is particularly apparent in the Ardley prints (Text-figs 4A–B, 5B, 6A). The pes (measured through the midline of digit III) is rotated approximately 10 degrees medially from the midline of the trackway. However, this is significantly less notable in the section of T13 associated with a change in gait. In this series the pes exhibits a slight negative rotation (Text-figs 4C, 6B).

Pace angulation. During the walking phase of the theropod trackways at Ardley, the footprints are positioned lateral to the midline of the track. This positioning of the pes, so that the prints are preserved in a zigzag arrangement, is very unusual in large theropods (see Text-fig. 6C–D of comparative trackways). Typically large theropods have very narrow-gauge tracks in which the prints of the hindfeet are arranged in a single line, with the pace angulation commonly in the range of 160–180 degrees (Thulborn 1990). The pace angulation for the walking phase of trackways 13 and 80 is calculated at 117 and 132 degrees respectively, using the formula of Thulborn (1990, p. 86). Pace angulation is taken as an average from areas of the trackways where pace length is constant.

Gait variation. A section of trackway 13 is unique in that it provides the first evidence of dual-gauge locomotion in a theropod dinosaur (Day *et al.* 2002*a*). The change in gait is associated with a 35-m stretch of trackway. Prints immediately prior to this section are missing, but GPS data reveal this trackway to be a continuation of T13. Decreasing stride length is shown to correlate positively with decreasing pace angulation (Day *et al.* 2002*a*, fig. 1c) and is also associated with a change in foot orientation, from negative to positive rotation. At its maximum stride length, the pes prints are preserved in a single line, rather than the zigzag arrangement of the walking animal (Text-figs 4C–D, 6B) and pace angulation is 173 degrees at its maximum. The significantly higher pace angulation formed in this section of the trackway is more typical of large theropod dinosaurs (see above).

The change in gait from wide- to narrow-gauge implies that these theropods utilised different hind-limb postures during walking and running phases of locomotion. As animals increase their speed, stride length increases and it is more efficient for their legs to be tucked under the body nearer to the midline in order to reduce energy losses and instability caused by pronounced lateral sway.

Stride and pace length. Stride lengths for T80 and T13 are approximately 3·10 and 2·70 m respectively, while the average pace length is 1·70 and 1·58 m. These measurements were taken from the posterior margin of the heel. For the section of T13 associated with a transition in gait, stride length (SL) increases to



TEXT-FIG. 6. A, illustration of the Ardley theropod trackway depicting its 'walking' phase and B, its 'running' phase (after Day *et al.* 2002). C–D, typical narrow-gauge theropod trackways (after Thulborn 1990).

just over double that of its walking phase, to a maximum of 5·65 m, with a maximum pace length of 2·85 m. In this section of the trackway the footprints appear slightly shallower at 10–20 mm deep, whereas they are typically 50–60 mm deep. This may be a consequence of subsequent erosion of this section of the trackway, or of firmer sediment. Trackway evidence of dinosaurs running suggests that they frequently lifted the posterior part of the foot from the ground, such that the footprints reportedly show only the distal parts of the toes (Thulborn 1990). This is not the case in the relevant section of T13, although the posterior margin of the print is less well defined, suggesting that less pressure was applied through this area of the foot. It may also suggest that this animal was not running to the limit of its capabilities.

Speed. Hip height (*h*) is considered to be the most convenient measure of body size in dinosaurs (Thulborn 1990) and is used when estimating speeds from trackways. It can be directly measured from the skeleton, or predicted from measurements of the footprints. There are alternative methods for predicting *h* from trackway evidence but allometric equations are used here following the arguments of Thulborn (1990).

Hip height for both T13 and T80 was calculated using the predictive equations derived initially from dinosaur foot skeletons (Thulborn 1984; Thulborn and Wade 1984), in which the length of the metatarsus (MT) may be substituted by foot length (FL). As the foot length is $>0{\cdot}25$ m, the following predictive equation is used (note that FL and h are expressed in centimetres): $h = 8{\cdot}60\mathrm{FL}^{0{\cdot}85}$.

Foot length should include the total length of digit III and the impression of the metapodium. However, calculating hip height can be difficult owing to the exaggerated length of the foot posterior to digit III. If the entire pes length of T13 and T80 is used (average FL are 0·72 and 0·66 m respectively), the hip heights of these dinosaurs are predicted to be 3·26 and 3·02 m. This is big, even by large theropod dinosaur standards. The hip height of *Tyrannosaurus* is calculated at 3·37 m (Thulborn, 1982). Using only the length of digit III (0·39 m for all trackmakers) the hip height is estimated as 1·93 m. The hip height for *Megalosaurus* is unlikely to have exceeded 1·90 m (JJD, pers. obs). Day *et al* (2002*a*) used the latter estimate on the basis that the size of the metapodium may have been exaggerated owing to a substantial cushion of soft tissue beneath its distal portion.

Dinosaur gaits may be determined on the basis of relative stride length (SL/*h*), that is, the length of the dinosaur's stride (SL) to its height at the hip (*h*) (Thulborn 1984). Living terrestrial vertebrates change from a walking to a trotting or running gait when SL/*h* reaches a value of 2·0 (Alexander 1976). Thulborn (1982) and Thulborn and Wade (1984) have extended this observation to dinosaurian gaits to include a walk (SL/*h* < 2·0), 'trot' (SL/*h* 2·0 to 2·9), and run (SL/*h* > 2·9).

There are several methods of calculating absolute speeds of dinosaurs, most of which are derived from Alexander's (1976) equation: $SL/h = 2{\cdot}3(V^2/gh)^{0{\cdot}3}$ (where SL = stride length, h = height, V = speed, g = acceleration of free fall). A modified equation of this method following Thulborn (1990) was implemented for estimating walking speed. Assuming a hip height of 1·93 m and minimum stride length, the walking speed for T13 and T80 is 1·9 ms^{-1} (6·8 km^{-1}) and 2·4 ms^{-1} (8·5 km^{-1}) respectively. At maximum stride length (recovered from T13), relative stride length is just over the threshold indicated for a running style of locomotion. To calculate absolute speed for this section of the trackway an equation appropriate for a 'running' animal was implemented following Thulborn and Wade (1984) and Thulborn (1990) so that $V = [gh(SL/1{\cdot}8h)^{2{\cdot}56}]^{0{\cdot}5}$. The maximum speed was calculated to be 8·1 ms^{-1} (29·2 km^{-1}), suggesting that large theropods were capable of running (Day *et al.* 2002*a*). If, however, a hip height of 3·26 or 3·02 m for T13 and T80 is used (calculated from total footprint length), the estimated walking speed is 1·1 ms^{-1} (4·0 km^{-1}) and 1·3 ms^{-1} (4·7 km^{-1}) respectively. The maximum speed estimated for the running section of trackway is considerably lower than our previous estimate at 3·6 ms^{-1} (13·0 km^{-1}; Day *et al.* 2002)

Our findings are in agreement with the lower estimates of running speeds for large theropods, which range from around 11 ms^{-1} (e.g. Alexander 1985) to 20 ms^{-1} (Paul 2000). A recent study using the minimum mass of extensor muscle needed for running (Hutchinson and Garcia 2002) showed that for a speed estimate of 11 ms^{-1}, a large theropod such as *Tyrannosaurus* would have been near or above its maximum muscular capacity. Even when the lower estimate of hip height is used, producing a faster speed, these two independent methods of estimating large theropod speed appear congruent. However, the short distance of the running section of the Ardley theropod trackway leaves unanswered questions concerning how long these animals could sustain a running gait (Day *et al.* 2002*a*).

Locomotor capabilities. The trackways of bipedal dinosaurs are often observed to be narrow, with pace angulation commonly in the range of 160–170 degrees, although low pace angulations of approximately 150 degrees have also been recorded (Thulborn 1990). The exceptionally low pace angulation of the Ardley trackways, with minimum values of 117 and 132 degrees, suggests that during their walking phase these animals had a semi-sprawling gait. Wide-gauge theropod trackways have been recorded previously from the Upper Jurassic (Lockley *et al.* 1996), and diagnosed as *Megalosauripus*, although these authors did not provide pace angulation values. Padian and Olsen (1989) suggested that the overall locomotor movements of primitive theropods were more similar to extant birds than to crocodilians. However, the findings presented here suggest that these animals were highly distinctive in their mode of locomotion at low speeds.

Observations of gait change are uncommon in dinosaurs, although they have previously been recorded in ornithopods (Ellenberger 1972). However, unlike the Ardley theropod, the gait change in ornithopods is thought to be a result of their ability to utilise both quadrupedal and bipedal gaits. Pes impressions show a shift in gait from semi-sprawling during quadrupedal locomotion, to one where the pes prints form a single line during bipedal locomotion (Thulborn 1989). Studies in locomotion of extant animals such as the quadrupedal Komodo monitor lizard *(Varanus komodoensis*) indicate a mean pace angulation of 76 degrees (Padian and Olsen 1984), signifying a sprawling gait. Basilisk lizards and crocodiles both have the ability to alternate their gait as required. Crocodiles utilise both sprawling and semi-sprawling gaits whilst on land; in the crocodilian 'high walk', the limbs are held nearly vertically beneath the body, although this is not a true erect gait. It would appear that, as in extant animals, the Ardley theropods had the ability to switch from a bipedal semi-sprawling to upright gait (erect gait).

Theropod trackmakers. Association of tracks with the track-maker has been problematic ever since the earliest discoveries of dinosaur trackways (Hitchcock 1836). This is due to insufficient detail in footprint morphology, and indeed even when prints are well preserved lower level taxonomy may not be possible (Farlow 2001). Nonetheless, inferences from trackways have the potential to be linked to stratigraphy, systematics (Wilson and Carrano 1999; Carrano and Wilson, 2001) and biomechanics. Temporal and spatial coincidence is also relevant in formulating more general conclusions about potential track makers. A combination of evidence is used herein to identify possible candidates.

On the basis of overall morphological similarity of the pes, the Ardley theropod trackways are tentatively assigned to the ichnogenus *Megalosauripus*. This ichnogenus, as currently defined, has been restricted to the Upper Jurassic of Europe, Asia and North America (Lockley *et al.* 1996). Tracks assigned to '*Megalosauripus lusitanicum*' from the Upper Jurassic of Portugal (Lockley *et al.* 1996, p. 114, fig. 2) show elongate metatarsus impressions. This feature may reflect increased sediment hydration, or an animal with an unusually plantigrade stance, although these possibilities were not explored by Lockley and colleagues. However, *in situ* prints do not appear to show a metatarsus impression (see Lockley *et al.* 1996, p. 114, fig. 2). These tracks are up to 0·72 m in total length and all trackways are characterised by an unusually low pace angulation and high trackway width values. Apart from the elongate metatarsus impressions, which may be an artefact of the casts, the tracks at Ardley appear to be similar to those described from Portugal, although the Ardley tracks are in Middle, not Upper Jurassic rocks.

Lockley *et al.* (1996) stated that *Megalosauripus* trackways are characterized by variable gaits, but that a large proportion of these trackways have a low pace angulation. This ichnogenus should then only be considered for those trackways with low pace angulation during their walking phase. Those that do not conform to this diagnosis are rejected and until a more rigorous study is undertaken we remain cautious about assigning the theropod Ardley trackways to this ichnogenus.

Body fossils discovered in Oxfordshire also provide a temporal and spatial perspective as to possible candidates for the trackmakers. The type material of the genus *Megalosaurus* comes from nearby Stonesfield (see Text-fig. 1), and there is also referred material from Kirtlington, Shipton and various other Middle Jurassic sites (see Benton and Spencer 1995).

The type material of *Megalosaurus bucklandi* (Buckland 1824, fig. 6B) consists of an isolated dentary and other dissociated remains. The remains are incomplete and even the syntype series is composed of bones from different localities and individuals (HPP, pers. obs.). Judging by the different morphology of individual femora there may be more than one large theropod present (JJD, pers. obs.). However, some measurements are included here to demonstrate the size of the only known large theropod remains from this area in the Middle Jurassic. The skull was up to 1 m long, with long recurved teeth, each 50–150 mm long (Benton and Spencer 1995). The hind limb skeleton is known from dissociated material, e.g. the pelvis (pubis OUM J.13563; ilium J.13560; ischium J.13564/p) measures 0·76 m anteroposteriorly and 0·27 m dorsoventrally; femora BMNH 31804, 31806, 31808, are *c.* 0·85 m and OUM J.13561, 0·79 m; tibia, OUM J.13562, 0·66 m, and metatarsal III, OUM J.13569, 0·32 m. The hind feet bore large recurved claws.

Megalosaurus bucklandi is speculated to have reached a total length of between 3·5 and 7·0 m (Steel 1970, pp. 33–34). Judging by the size of the hind limb, giving an approximate hip height of approximately 1·9 m (not allowing for ligaments and muscle), *Megalosaurus* would certainly match the proportions of the theropods that made the trackways at Ardley. *Megalosaurus* has also been found in numerous sections of Bathonian age throughout Oxfordshire (see Benton and Spencer 1995, p. 128) as well as reported from other Middle Jurassic sites in Dorset, Wiltshire, Gloucestershire, Northamptonshire, Buckinghamshire, Cambridgeshire and Leicestershire.

Megalosaurus is currently placed within the Tetanurae (Gauthier 1986). Tetanurans are considered not to differ in their locomotor features from more derived theropods (Farlow *et al.* 2000). However, if *Megalosaurus* was the trackmaker of the dual-gauge trackways at Ardley, this raises many questions concerning the biomechanics of locomotion in basal tetanurans.

Sauropod trackways

Sauropod tracks are by far the most common of the two track types preserved at Ardley Quarry. The sauropod trackways, particularly those to the south of the quarry, are very extensive, notably T32 that has a length in excess of 200 m (Text-fig. 4).

Footprint morphology. The footprints of the sauropod trackways fall into three distinct categories, termed type$_1$, type$_2$ and type$_3$ prints. Type$_1$ and type$_3$ prints are considerably smaller than those of type$_2$. It is apparent that one particular size is not more prevalent than another, but the trackways comprising type$_2$ prints are more likely to be found at the southern end of the quarry.

Type$_1$ prints average 0·50 m in width and 0·35 m in length, and have a distinctive D-shaped outline (Text-fig. 7A–B, D). These prints are formed by the manus subtending an arc of approximately 270 degrees, and form reasonably deep impressions (of 40–50 mm). Associated pes prints are rarer, but may be preserved directly behind the manus, within 50 mm, as shallow impressions (Text-fig. 7D). When preserved, the pes prints are notably farther from the midline than the manus print (Text-figs 7D, 8B). They are subcircular in shape and appear to be similar in size to the manus prints. There is a notable absence of any pollex impressions associated with the manus.

Type$_2$ prints are considerably larger than those of type$_1$, the pes is typically in the order of 1·0 m long and approximately 0·50 m deep. Some of these prints, particularly from T34 and T35, tend to be elongate, while the overall morphology is unclear. The deeper, elongate prints were most likely formed in sediments with increased water content. These prints are, therefore, considerably larger than the foot that made them. The elongation of the footprints is similar to the theropod prints described from sites such as Glen Rose (Kuban 1989), albeit on a larger scale.

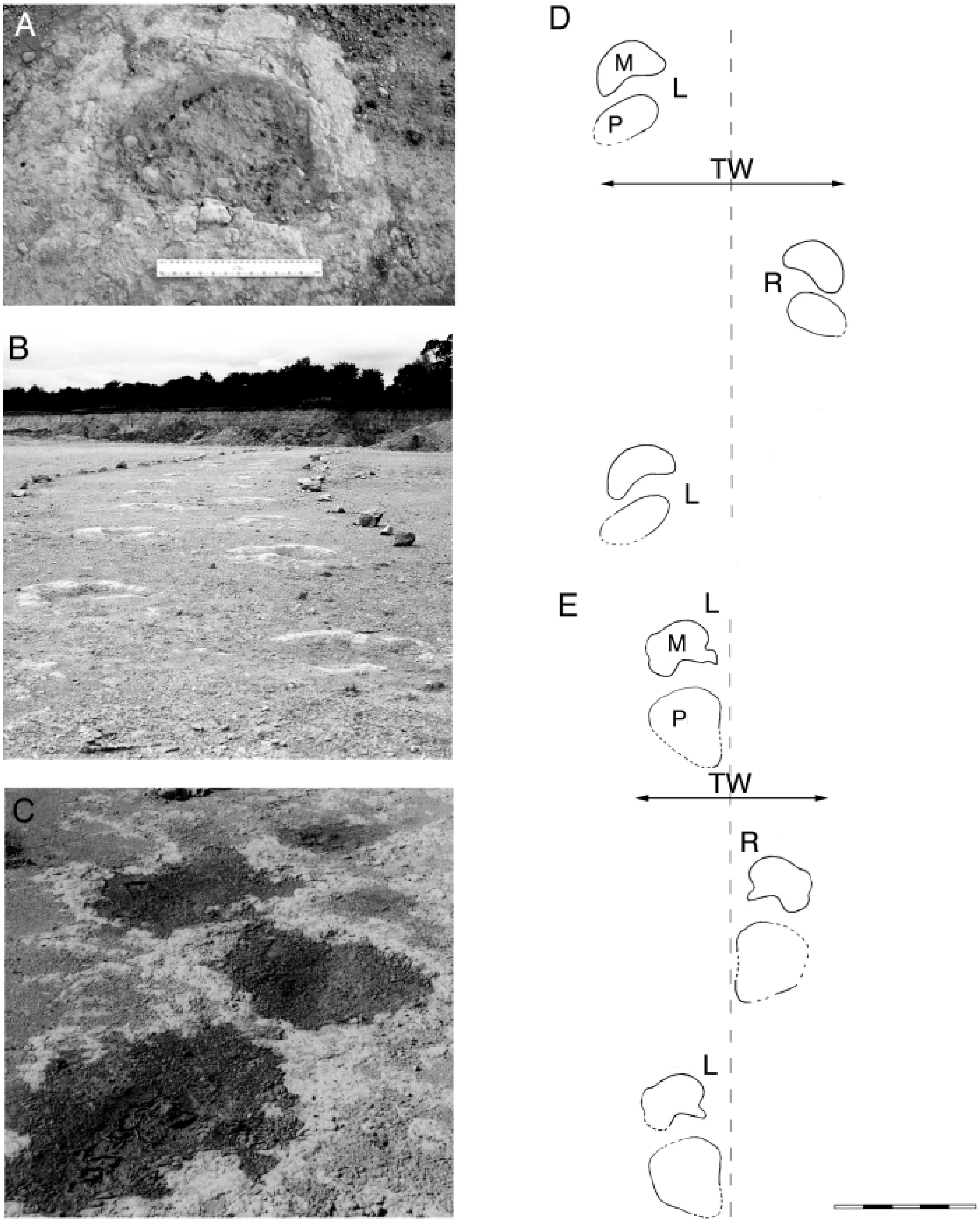
Type$_3$ prints are observed in trackway T90 (Text-fig. 7C). The trackway is not particularly well preserved, but the manus prints are associated with pollex claw marks, directed in a posteromedial direction (Text-fig. 7E). The prints do not have the distinctive D-shaped impressions of type$_1$, being more irregular, a feature that appears to be a consequence of sediment saturation causing ill-formed impressions. These prints are situated close to the track mid-line (Text-figs 7C, E, 8A).

The apparent absence of pes prints from many known sauropod trackways may be explained by the overlapping of the manus print by the pes during normal walking. If this is the case then pes impressions often partially or totally obscure those of the manus. This overlap is common in those animals referred to as short-coupled forms (Leonardi 1987). However, manus dominated trackways are not uncommon (Ishigaki 1989; Lockley and Conrad 1989; dos Santos *et al.* 1994) and can also be explained by under-printing. Under-printing occurs due to the greater weight ratio applied through the front feet of sauropods (see Lockley 1989, p. 442). The presence of partial pes tracks directly behind the manus and clear preservation of the manus suggests this second scenario at Ardley. Heteropody ratios are thus hard to determine for many trackways due to the absence of pes impressions.

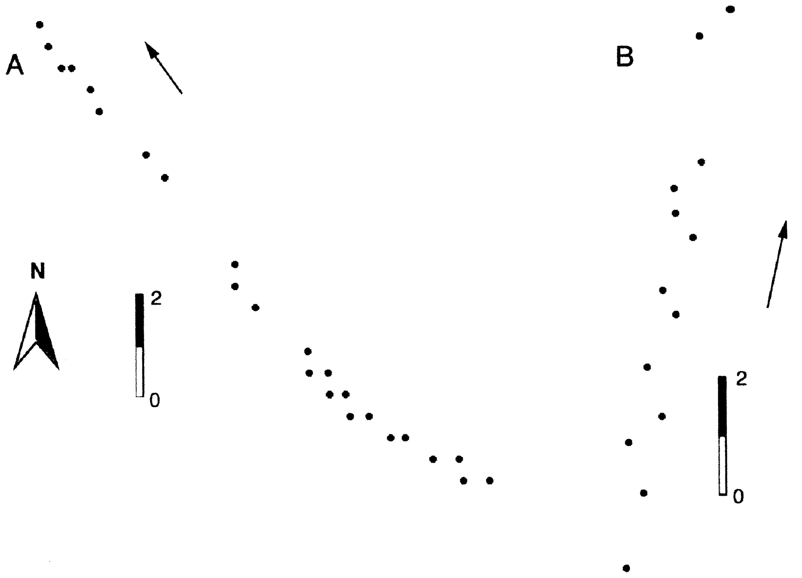
Foot rotation. The sagittal axis of the manus print (passing through digit III) in type$_1$ is orientated anterolaterally relative to the line of travel (see Text-fig. 7D), indicating negative rotation of the manus. Where preserved, pes prints show only slight negative rotation. Those of type$_3$ do not appear to show such marked negative rotation (Text-fig. 7E).

Stride and pace length. The huge disparity in print size between those of type$_{1,3}$ and type$_2$, appears to reflect the saturation of the sediment. However, Text-figure 9 indicates that the individuals that produced T34 and T35 not only have larger footprints, but also considerably longer stride lengths than all other trackmakers, implying that these individuals were particularly large and therefore likely to be adults. Furthermore, the width of T35 is over 2 m, making this trackway the widest at Ardley.

Sauropod trackmakers. Several authors (e.g. Farlow *et al.* 1989; Farlow 1992; Lockley *et al.* 1994) have noted that sauropod trackways fall into the two distinct categories of ‘narrow-gauge’ and ‘wide-gauge’, namely the ichnotaxa *Parabrontopodus* (Lockley *et al.* 1994) and *Brontopodus* (Farlow *et al.* 1989) respectively. *Brontopodus* displays left and right prints widely spaced from the midline, with manus prints positioned closer to the midline than pes prints and no associated pollex claw impressions. Conversely, in *Parabrontopodus* tracks both manus and pes prints fall very close to, or intersect the trackway midline and are associated with pollex claw impressions (Lockley *et al.* 1994). Observations of trackway morphology suggest that these two distinct types of sauropod trackway are also represented at Ardley (Day *et al.* 2002*b*). Trackway gauge disparity could be the result of differences in body size. However, comparison of



TEXT-FIG. 7. A–E, sauropod trackways. A, titanosaur manus. B, wide-gauge trackway 14. C, narrow-gauge trackway 90. D, illustrated wide-gauge trackway 14. E, illustrated narrow-gauge trackway 90. TW indicates trackway width. Scale bar represents 1 m.

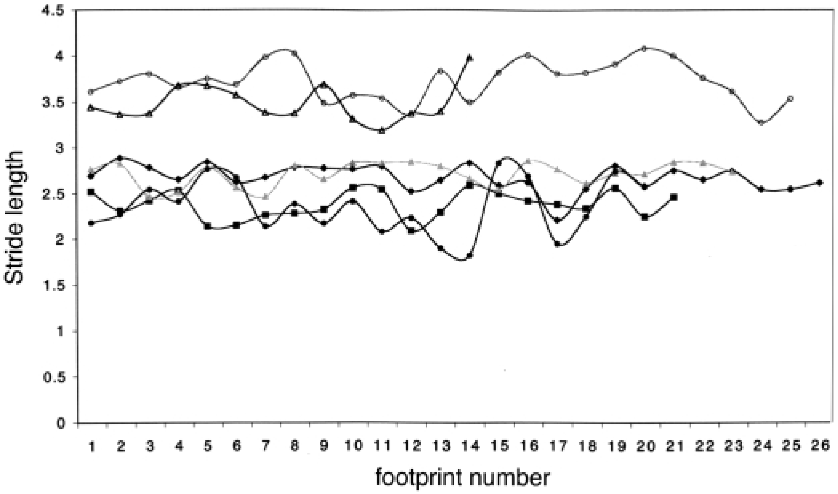


TEXT-FIG. 8. A–B, GPS data of sauropod trackways. A, T90, a narrow-gauge sauropod trackway and B, T35, a wide-gauge sauropod trackway. Each point represents an individual footprint. Arrows indicate direction of travel. Scale bars in metres.

trackways of animals of similar size (e.g. tracks 14 and 90) indicates that the relative width of the Ardley sauropod tracks is not correlated with body size. Sauropods, being a full order of magnitude larger than extant megaherbivores (e.g. the African elephant *Loxodonta africana* and the hippopotamus *Hippopotamus amphibius*), are assumed to be constrained by similar structural limitations that restrict locomotor variation, manoeuvrability and acceleration. It therefore seems unlikely that any one species of sauropod would have been capable of producing both narrow- and wide-gauge trackways (Wilson and Carrano 1999).

Identification of footprints to lower taxonomic levels is exceptionally problematic, as print morphology does not correspond precisely to skeletal morphology. In general, however, biomechanical and systematic information can be used to assign trackways to at least broad taxonomic groupings (Carrano and Wilson 2001). In particular, rigorous trackway identification can be achieved when derived features of the foot skeleton can be recognised in footprint morphologies. Wilson and Carrano (1999) assessed femoral morphological variation in sauropods and found a number of synapomorphies to suggest that titanosaurs were responsible for wide-gauge trackways. For example, the femoral shaft in titanosaurs is more compressed anteroposteriorly than in other sauropods, and the transverse axis through the distal articular condyles is not perpendicular to the long axis of the shaft; together, these and other features allow the lower part of the titanosaur hindlimb to be placed further from the midline than in non-titanosaur sauropods. Day *et al.* (2002*b*) therefore interpreted the wide-gauge Ardley trackways as those of titanosaurs, and supported this with an additional synapomorphy. As mentioned above, the theropod trackways (T13, 29, 80) and the narrow-gauge Ardley sauropod trackways (e.g. T90) preserve claw impressions, whereas the wide-gauge trackways do not. This suggests that the absence of the pollex claw in the latter reflects the true anatomy of the trackmaker, rather than being an artefact of preservation. Salgado *et al.* (1997) noted that the pollex claw, and in fact all manual phalanges, appear to be absent in titanosaurs, and the distal ends of the metacarpals have reduced or lost the well-developed articular surface present in more basal sauropods. Thus, the absence of the pollex claw impression in the wide-gauge Ardley trackways can be regarded as an indication of titanosaur affinities.

The Galinha site near Fátima, Portugal, is comparable in age to Ardley, as it is dated as Middle Jurassic



TEXT-FIG. 9. Graph of stride length from six Ardley sauropod trackways. Open triangle represents T35; open circle represents T39; grey triangle represents T12; black diamond represents T62 (not shown on GPS map); black circle represents T32; grey square represents T14.

(dos Santos *et al.* 1994). The sauropod trackways provide important comparative material in time and space to those at Ardley. The trackways at Galinha appear to fall into two categories, although both were considered 'wide-gauge' by dos Santos *et al.* (1994). Trackways either contain manus and pes tracks with a heteropody ratio of 1:2, and have clear manus claw impressions (dos Santos *et al.* 1994, fig. 3), or are manus dominated (dos Santos *et al.* 1994, fig. 5) with clear D-shaped manus prints. The manus-dominated trackways do not appear to have associated manus-claw impressions, although this is not clearly stated by the authors. These trackways (dos Santos *et al.* 1994, fig. 5), appear to be very similar to the wide-gauge trackways at Ardley. The pes is also often absent from the Ardley trackways, but is distinct enough in some (e.g. T62) to infer a heteropody ratio of 1:2. However, no heteropody ratio is given for Galinha manus-dominated tracks. Judging by the illustrations (dos Santos *et al.* 1994, figs 2–3), the trackways containing the manus-claw impressions also appear to be narrower-gauge than those without.

Recent discoveries, reinterpretations and phylogenetic analyses provide more detail on the evolution of the wide-gauge stance and manus evolution in advanced sauropods. According to Wilson and Carrano (1999) the initial stages of wide-gauge locomotion can be detected in brachiosaurs (the sister-taxon to Titanosauria) and possibly the most basal titanosaur-like sauropods (i.e. *Euhelopus*). Femoral structure suggests that the full development of the wide-gauge stance was present in the most basal true titanosaurs, such as *Phuwiangosaurus* (Martin *et al.* 1999) and *Austrosaurus* (Coombs and Molnar 1981). The distal location and small size of manus elements means that they are frequently lost during preservation, making it difficult to trace the history of phalangeal reduction in sauropod evolution. Relatively large pollex claws (with lengths 75–100 per cent of metacarpal I length) are present in many non-titanosauriform sauropods, such as *Shunosaurus* (Zhang 1988), *Omeisaurus* (He *et al.* 1988), diplodocoids (Gilmore 1936) and *Camarasaurus* (McIntosh *et al.* 1996). In *Brachiosaurus* and the basal titanosaur *Janenschia* (ex '*Tornieria robusta*') the pollex claw is present but somewhat reduced in size (Janensch 1961; Upchurch 1994). *Venenosaurus*, from the Lower Cretaceous of North America, is believed to be a basal titanosaur (Upchurch and Martin 2003) in which the metacarpals retain well-developed distal articular ends (Tidwell *et al.* 2001), suggesting that manual phalanges were still present. It is only in very advanced titanosaurs, such as *Alamosaurus* (Gilmore 1946) and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) that complete loss of all manual phalanges can be confidently established. This brief review of the relative timings of osteological modifications predicts the existence of at least four types of sauropod trackway: (1) narrow-gauge trackways with well-developed manus claw impressions, formed by non-titanosauriform sauropods;

(2) intermediate-gauge trackways with well-developed or reduced manus claw impressions, produced by brachiosaurs and the most basal titanosaurs; (3) fully wide-gauge trackways, with reduction of the manus claw and other manual phalanges, formed by basal titanosaurs; and (4) fully wide-gauge trackways with no indication of the presence of any manual phalanges, produced by advanced titanosaurs. It seems that the Middle Jurassic Ardley and Galinha localities provide evidence for the existence of three of these four categories. The narrow-gauge trackmaker at Ardley represents some form of non-titanosauriform sauropod, but the absence of any other synapomorphies means that it cannot be identified with more precision. The best known non-titanosauriform sauropod from the Middle Jurassic of England is *Cetiosaurus*. Although it is tempting to suggest that this genus formed the narrow-gauge Ardley tracks, recent work by Upchurch and Martin (2003) indicates that a basal diplodocoid may also have existed in the vicinity. The narrower of the 'wide-gauge' Galinha trackways, with claw impressions, were tentatively identified as brachiosaurid by dos Santos *et al.* (1994), based largely on the size of the manus and claw impressions. This remains a possibility, although the analysis above suggests that these trackways are more accurately regarded as those of a basal titanosauriform (i.e. brachiosaur or very basal titanosaur). The truly wide-gauge trackways that lack manus claw impressions imply the presence of more advanced titanosaurs, despite the Middle Jurassic age of the Ardley and Galinha localities. This is a rather unexpected result and has important implications for our understanding of titanosaur evolution.

Day *et al.* (2002*b*) demonstrated that the presence of titanosaurs in the Middle Jurassic extends the ghost range of this lineage back by approximately 12 myr. The ghost range extension would be even more dramatic if the Ardley trackways are accepted as evidence for the presence of advanced titanosaurs in the Middle Jurassic. An earlier origination time for titanosaurs raises interesting questions concerning the scarcity of their remains, relative to those of other sauropod lineages, during the Middle and Late Jurassic. For example, Middle Jurassic deposits in Britain have yielded considerable amounts of fragmentary sauropod material, including several partial skeletons. Many of these specimens cannot be confidently identified, but there is clear evidence for the presence of the basal eusauropod *Cetiosaurus*, a diplodocoid, and perhaps even a brachiosaurid (Upchurch and Martin 2003). However, no material has been recovered from the Middle Jurassic that would be a good candidate for the wide-gauge trackways, indicating considerable missing data for one or more titanosaur lineages. The earliest anatomical record of a titanosaur-like sauropod anywhere in Europe is a partial forelimb from the Lower Cretaceous (Valanginian, approximately 140 Ma) of Sussex, southern England (Upchurch 1995). Were Jurassic titanosaurs simply less diverse, abundant and/or widespread than other sauropods? Or did Jurassic titanosaurs occupy environments with lower preservation potential than those frequented by other sauropod lineages? At present there are insufficient data to answer these questions. However, explanations based on environmental preferences are not supported by the fact that the Ardley trackways demonstrate the presence of titanosaurian and non-titanosaurian sauropods in the same area at the same time. It may simply be that titanosaurs were relatively rare in the Jurassic, but increased in abundance and diversity during the Early and mid Cretaceous as other sauropod lineages declined.

PALAEOENVIRONMENT

The tracks were formed on a single bedding plane that was emergent, or locally very shallowly submerged, and was a lime-mud firmground of variable consistency. The bedding plane is an omission surface, which contains numerous burrows infilled with bioclastic calcarenite. There appears to be a gradation between the far south of the quarried area, where print impressions are deepest (some sauropod prints = W, 0.67 m; L, 1·05 m) and the older workings to the north, described by Palmer (1973), where the correlative bedding surface becomes a true hardground with boring and encrusting organisms (Bromley 1975, 1996). The surface on which most prints are preserved, in the north of the present quarry, probably had the consistency of firm 'cream cheese'. The area over which the dinosaurs were walking was, therefore, one of shallow ephemeral marine lagoons with regions of emergent carbonate mudflats probably comparable to parts of the Florida Keys (Evans and Milner 1994). They were probably a considerable distance from vegetated land, as there is no evidence of palaeosols or roots in the Ardley succession or that exposed in surrounding quarries.

The consistently good preservation of detail on the footprints is evidence that they were formed in a brief interval, and represent essentially a single event. If the trackways had been formed over a much longer timespan, highly variable preservation would be expected as older prints progressively lost their definition through overprinting and erosion. The fine preservation of detail, including theropod claw marks, also supports the idea that these prints are true tracks rather than underprints (Lockley and Meyer 2000). The tracks were made in the pale lime mud of Bed 1, underlying the omission surface, and were subsequently covered by darker carbonate sand, which now infills and overlies the prints.

Preservation of the tracks was brought about through rapid burial that probably occurred as two discrete events. Initially, the individual prints were shallowly filled with rather poorly sorted carbonate sand that contains numerous fragments of lignite; this material could perhaps have been washed in by tidal action. This sediment is not present in the areas between prints, which remained exposed for a somewhat longer period. Subsequently, the entire surface represented in the quarry was covered by a 0·1–0·2 m-thick layer of well-sorted carbonate sand, grading upwards into a silty lime mud (Bed 2). The frequent occurrence within this bed of entire regular echinoids (*Acrosalenia* spp.), some of which retain spines, demonstrates that it was very rapidly deposited and perhaps represents a single storm event. Subsequently, Bed 2 was bioturbated, and specimens of the deep-burrowing bivalve *Pholadomya* in life position are found commonly within it.

Striking similarities exist between the facies, palaeoenvironmental context and preservational style of the Ardley (Bathonian) trackways and certain of those in the Albian (Early Cretaceous) Glen Rose Formation of central Texas (Pittman 1989). This formation was deposited in a vast lagoonal area, adjacent to the Gulf of Mexico, dominated by micritic limestones. One of the best known trackway beds, in the middle of the Glen Rose Formation, is situated immediately beneath the *Salenia texana* Zone (Bergan and Pittman 1990), and was a firmground that lithified locally to form a true hardground (Bromley 1975). The horizon is immediately overlain by clay-rich beds that contains numerous regular echinoids, and is therefore closely comparable to the Ardley situation. The presence of evaporites and stromatolitic algae in the Glen Rose Formation is not paralleled in the Ardley succession and the environment of the latter was probably cooler and less arid. In both the Glen Rose and Ardley successions, trackways were formed and preserved during a transgressive interval of global sea-level rise.

The ichnofaunal component at Ardley is also similar to that described for Glen Rose. The latter site includes a significant proportion of sauropod tracks in association with a large number of tridactyl prints attributed to theropods (Farlow *et al.* 1989), whilst ornithopod tracks are rare (Lockley and Conrad 1989). The reverse of this is true for the ichnofauna of the Dakota Group (Lower Cretaceous, Denver), where ornithopod tracks predominate. For the late Mesozoic Lockley and Conrad (1989) demonstrated that ornithopod tracks predominate in mid–high latitudes characterised by clastic lowland coastal plain deposits, with coals and other evidence of abundant vegetation, in contrast to low-latitude lacustrine and carbonate evaporite settings where sauropod and theropod tracks are more common. However, there are many exceptions, e.g. the co-occurrence of ornithopod and sauropod trackways in the nearshore environments of the Purbeck Limestone Formation (Wright *et al.* 1998). Furthermore, some authors (e.g. Farlow 1992; McIntosh *et al.* 1997) regard the distinct patterns of associated faunal type and palaeoenvironment to be an artefact of sampling and analytic procedure.

PALAEOGEOGRAPHY

During the Bathonian, three main landmasses, separated by a shallow central sea, existed near to the position of the British Isles (Callomon 1979). The Bathonian represented a period of marine transgression, with widespread lagoonal, deltaic and coastal swamps on the European shelf (Evans and Milner, 1994). One of these landmasses, the London-Ardennes in the south-east, may have had a nearby island barrier adjacent to its western coast (Palmer and Jenkyns 1975; Ware and Windle 1981; Ware and Whatley 1983), which is particularly close to the Middle Jurassic localities of Oxfordshire. It has been suggested that in

Bathonian times, Kirtlington lay on or near the south-west shore of this small island barrier, 30 km or so from the coast of the Anglo-Belgian landmass at a subtropical latitude of about 30°N (Evans 1990). The presence of lignite, charophytes and gastropods in the marly sediments suggests a coastal environment of low relief with creeks, lagoons and freshwater lakes (Palmer 1979; Ware and Whatley 1980). The occurrence of a vertebrate fauna including amphibians and aquatic reptiles (choristoderes, crocodilians and turtles) is in agreement with this palaeoenvironmental interpretation (Benton and Spencer, 1995) and the environment as a whole may have been analogous to that of the Florida Everglades, which lie in a similar latitude (Briden *in* McKerrow *et al.* 1969). Since Ardley is close to Kirtlington and of similar age, its palaeoenvironment would no doubt have been comparable.

CONCLUSION

As trackways represent a direct interaction between an organism and the substrate, the discovery of trackways at Ardley bring a dynamic perspective to the faunas of the Middle Jurassic. As such, Ardley, along with the other nearby contemporaneous Middle Jurassic sites of Kirtlington and Stonesfield, presents a more complete picture of life in the Middle Jurassic of Oxfordshire. The site at Ardley represents one of the most extensive and diverse trackway sites in Europe. Furthermore, the Middle Jurassic age of the Ardley site is of considerable interest as dinosaur track sites, and indeed vertebrate fossil sites, of this age are rare world-wide. Comparable Middle Jurassic sites in Europe (dos Santos *et al.* 1994) preserve only monotaxic sauropod trackways. In contrast the trackways at Ardley are represented by three distinct saurischian ichnotaxa. These ichnotaxa represent a large theropod dinosaur and both wide and narrow-gauge sauropods. The findings from this site include new data on behaviour, locomotion and earliest occurrence.

The theropod trackways are here tentatively attributed to *Megalosaurus* on the basis on the relatively abundant fossil material of this large carnivorous dinosaur found in nearby Middle Jurassic sites. The proportions of *Megalosaurus* correspond to the minimum hip height estimations from the Ardley footprints that, while conservative, we consider to be more anatomically reasonable. The trackways include the first record of dual gait locomotion reported in a theropod dinosaur (Day *et al.* 2002*a*). The 'gear change' associated with increasing speed is concurrent with modifications in stride length, pace angulation and foot rotation and has important implications for the biomechanics and the evolution of basal theropods.

Wide and narrow gauge sauropod trackways have not previously been recorded at the same site (Day *et al.* 2002*b*). The findings of Day *et al.* (2002*b*) support the view of Wilson and Carrano (1999) that both narrow and wide-gauge track types have a mixed distribution within the Jurassic, contrary to the clear temporal distribution inferred by Lockley *et al.* (1994). The wide gauge of the trackways at Ardley, and the notable absence of any claw impressions in individual tracks, imply that these were made by titanosaurs. This evidence is important as, prior to these findings, titanosaurs were known only from the Late Jurassic onward. Titanosaurs have often been thought to have originated and radiated in Gondwana during the Cretaceous (Bonaparte and Jaworowska 1987; Lucas and Hunt 1989; Gayet *et al.* 1992; Le Loeuff and Buffetaut 1995). Recent phylogenetic work (Upchurch 1995, 1998; Wilson and Sereno 1998) has identified several Cretaceous Laurasian sauropods as members of the Titanosauria, casting doubt on the 'Gondwana origin' hypothesis. Nevertheless, the possibility that titanosaurs originated in Gondwana during the Late Jurassic, and then dispersed to northern continents during the Cretaceous, remained plausible and has been proposed by several workers (Lucas and Hunt 1989; Le Loeuff and Buffetaut 1995; Upchurch 1995). The discovery of titanosaur trackways in the Middle Jurassic of Europe provides strong counter evidence to the latter biogeographic scenario, since titanosaurs clearly appeared well before the isolation of Gondwana during Callovian times.

Palaeoenvironmental evidence supports the view that these animals were crossing a marginal marine setting analogous to the Florida Everglades. Many theropod/sauropod-dominated sites are found preserved in similar coastal environments. This could plausibly be an artefact of conditions necessary for preservation, but since ornithopod prints are rarely present in this environment, this habitat may have been less favourable for them. Geological data support the view that the trackways were made within the confines of a relatively limited time period. GPS data and the timing of the event suggest that the sauropods were moving in a mixed herd containing both narrow and wide-gauge sauropods of differing ages (Day *et al.* 2002*b*). We are confident in assuming the theropod tracks are from separate individuals based on the temporal disjunction of T13 and T80, size of prints, and common direction of travel. In modern ecosystems it is very unusual for large carnivores to inhabit the same range or territory, unless they are 'communal' animals that hunt in packs. Judging by the size of the theropods inferred from footprint data, it is plausible that these animals were capable of preying on the sauropods, particularly smaller and/or weaker individuals, and may well have been following the sauropod herd. While the inferences of behaviour of extinct animals from trackway evidence is at best tentative, evidence from Ardley may provide new insights into possible pack behaviour in large theropod dinosaurs.

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APPENDIX

Trackway data

Data for trackways T80, 13, 29, 62, 14, 12, 34, 35, 39. TL indicates total length of the trackway. In some instances this length may not correspond to GPS data of trackway length (Text-fig. 3). This is due to changes in the quarry layout causing tracks/prints to disappear as these data were collected after the GPS data. This accounts for why some trackways are documented with both GPS and manual measurements. T62 does not appear on the GPS data as this trackway was discovered only recently.

Measurements. These include: FP *N*, footprint number; L/R, indicates left and right prints; PTL, pes total length; PTW, pes total width; MTL, manus total length; MTW, manus total width; L.II, L.III, L.IV, lengths of digit II, III, IV respectively; W.II, W.III, W.IV, widths of digit II, III, IV; SL, stride length (for sauropod SL and PL 'M' indicates the measurement is taken using the manus); PL, pace length; TW, trackway width; (o), outer width (from lateral edge of prints); (in), inner width (from medial edge of prints). Note footprint numbers are not always continuous (e.g. T13). This is due to breaks in the trackway (either prints are not preserved or have been lost). Measurements in metres (m).

Theropod T80 (TL: 180m)

FP *N*	L/R	PTL	PTW	L.II	L.III	L. IV	W.II	W.III	W.IV	SL(L)	SL(R)	PL(L)	PL(R)	TW
1	L	0·72	0·46		0·39	0·31		0·15	0·18	3·24		1·84		1·1
2	R	0·71	0·55		0·37			0·16			3·18		1·76	
3	L		0·5							3·31		1·77		1·2
4	R		0·47								3·32		1·7	
5	L	0·69	0·5							3·11		1·72		1·1
6	R	0·72	0·53								2·97		1·55	
7	L	0·69	0·49		0·38					2·78		1·56		1·15
8	R	0·72	0·44		0·41	0·28		0·15	0·16		3·11		1·76	
9	L	0·76	0·5							3·13		1·76		1·15
10	R		0·47			0·32			0·15		3·21		1·76	
11	L	0·68	0·52		0·4	0·38		0·13	0·21	3·23		1·78		1·15
12	R		0·47								3·09		1·68	
13	L	0·72	0·49		0·38			0·17		3·08		1·7		1·1
14	R	0·71	0·42								2·98		1·66	
15	L	0·75	0·52		0·38					3·01		1·52		1·1
16	R	0·73	0·48		0·41	0·31		0·14	0·14		2·93		1·6	
17	L	0·72	0·48	0·25	0·42		0·15	0·15		3·05		1·57		1·2
18	R	0·77	0·46								4·12		1·7	
19	L	0·82	0·54							4·34		2·81		1·2
20	R	0·73	0·52		0·39			0·15			3·29		1·71	
21	L	0·75	0·51	0·23	0·43	0·29	0·16	0·19	0·17	3·37		1·78		1·15
22	R	0·71	0·51	0·28	0·4	0·25	0·16	0·14	0·17		3·21		1·79	
23	L	0·7	0·52	0·19	0·39	0·29	0·14	0·15	0·16	3·24		1·76		1·1
24	R		0·49				0·16				3·31		1·81	
25	L	0·7	0·45						0·16	3·18		1·8		1·1
26	R	0·7	0·45								3·09		1·78	
27	L		0·47					0·13		3·21		1·75		1·1
28	R	0·7	0·48								3·16		1·69	
29	L	0·72	0·54		0·36	0·24		0·15	0·16	2·12		1·58		1·1
30	R	0·76	0·53								3·11		1·76	
31	L	0·68	0·52							2·89		1·56		1·15
32	R	0·7	0·51		0·42		0·12	0·14			3·05		1·66	
33	L	0·72	0·5							3·14		1·71		1·2
34	R	0·7	0·53	0·28	0·4		0·14	0·14	0·14		3·16		1·62	
35	L	0·72	0·52		0·43					3·17		1·77		1·2
36	R	0·68	0·53		0·38						3·19		1·65	
37	L	0·7	0·53		0·35	0·28		0·17	0·17	3·16		1·73		1·15
38	R	0·64	0·45	0·35	0·4	0·2	0·15	0·16	0·14		3·16		1·76	
39	L	0·7	0·45	0·2	0·35	0·25	0·15	0·15	0·14	3·09		1·68		1·15
40	R	0·68	0·45	0·28	0·38	0·28	0·16	0·14			3·1		1·69	
41	L	0·71	0·5		0·36		0·15		0·15	3·18		1·76		1·15

Theropod T80 (TL: 180m) (Cont.)

FP *N*	L/R	PTL	PTW	L.II	L.III	L. IV	W.II	W.III	W.IV	SL(L)	SL(R)	PL(L)	PL(R)	TW
42	R	0·74	0·5	0·28			0·16				3·07		1·7	
43	L	0·7	0·5		0·38			0·14		3·17		1·72		1·15
44	R	0·71	0·45		0·4						3·19		1·73	
45	L	0·72	0·5		0·38			0·14		3·12		1·73		1·1
46	R	0·7	0·48								3·24		1·74	
47	L	0·71	0·5		0·41			0·15	0·15	4		1·71		1·1
48	R	0·7	0·54								2·41		1·26	
49	L	0·7	0·45	0·32	0·42	0·25	0·15	0·15		2·5		1·27		1·1
50	R		0·48								2·97		1·63	
51	L	0·7		0·2	0·4		0·15	0·16	0·15	2·84		1·6		1·1
52	R		0·5			0·3			0·16		2·81		1·46	
53	L	0·73	0·49	0·23	0·39		0·14	0·15	0·15	3·1		1·61		1·15
54	R	0·71	0·49		0·39		0·14				2·91		1·75	
55	L	0·7	0·48		0·38		0·15	0·15	0·15	2·92		1·54		1·15
56	R	0·7	0·5		0·38						3·02		1·69	
57	L	0·7	0·5									1·58		1·15
58	R		0·48				0·15				3·1		2·1	
59	L			0·27	0·42					2·7		1·2		1·15
60	R	0·68	0·52	0·3	0·4	0·32	0·15	0·16					1·67	
61	L	0·65	0·52	0·33		0·34				3·14		1·73		1·1
62	R	0·69	0·46											
63	L													1·15
64	R			0·36										
65	L	0·65	0·5		0·45		0·15			3·13				1·15
66	R			0·26										
67	L	0·7	0·5	0·3	0·44	0·25		0·15		3·26		1·68		1·15
68	R	0·68	0·48		0·38		0·16				3·11		1·78	
69	L	0·7	0·48							2·71		1·73		1·1
70	R			0·32							2·87		1·68	
71	L	0·67	0·48	0·28	0·41	0·3	0·14	0·14	0·14	3·11		1·68		1·1
72	R	0·68	0·45	0·32	0·39	0·29			0·15		3·06		1·72	
73	L	0·65	0·48		0·4					3·07		1·67		1·1
74	R	0·66	0·44	0·3	0·36	0·29	0·15	0·15			3·24		1·73	
75	L	0·69	0·48		0·4		0·15	0·16	0·15	3·19		1·81		1·1
76	R		0·48					0·16			2·94		1·78	
77	L	0·66	0·48		0·36	0·27				3·08		1·46		1·15
78	R	0·67	0·44								2·68			
79	L									2·7				1·15
80	R	0·7	0·51		0·39						3·19		1·66	
81	L									3·14		1·72		1·15
82	R										3·16		1·77	
83	L	0·67	0·49	0·34	0·38	0·33		0·15		3·11		1·61		1·15
84	R										3·19		1·68	
85	L	0·63	0·47	0·31	0·38	0·33	0·14	0·15	0·14	3·17		1·72		1·15
86	R	0·68	0·48	0·33	0·4	0·35			0·14		3·18		1·71	
87	L	0·69	0·49		0·4	0·32			0·14	3·05		1·73		1·15
88	R	0·65	0·47	0·31	0·37						3·21		1·72	
89	L	0·69	0·47		0·41	0·32		0·16		3·13		1·64		1·15
90	R	0·7	0·46		0·41	0·31			0·14		3·19		1·69	
91	L	0·66	0·46	0·36	0·42	0·34	0·14	0·15				1·64		1·15
92	R	0·69	0·49	0·31	0·39	0·33	0·15	0·15	0·15					

Theropod T13 (TL: 180 m)

FP *N*	L/R	PTL	PTW	L.II	L.III	L. IV	W.II	W.III	W.IV	SL(L)	SL(R)	PL(L)	PL(R)	TW
1	R													
2	L													
3	R	0·8	0·54		0·43						3·04		1·75	
4	L	0·78	0·59	0·32	0·49					3		1·72		
5	R	0·68	0·55		0·5	0·24		0·19			2·98		1·62	
6	L	0·78	0·59							2·72		1·7		
7	R	0·72	0·5	0·3	0·5						2·65		1·54	
8	L	0·75	0·52	0·29	0·45	0·28	0·15	0·16	0·13	2·93		1·66		
9	R	0·7	0·51	0·27	0·38		0·14	0·14			2·97		1·67	
10	L	0·67	0·48	0·32	0·41			0·15		2·86		1·62		
11	R	0·64	0·5								2·92		1·54	
12	L	0·65	0·54	0·4			0·14			3·08		1·7		
13	R	0·69	0·51		0·46			0·15					1·66	
14	L	0·66	0·48	0·33	0·35			0·16		2·21		1·62		
15	R	0·74	0·48	0·35	0·39	0·27	0·14	0·14	0·13		2·6		1·59	
16	L	0·67	0·47	0·36	0·49	0·26				2·85		1·52		
17	R	0·64	0·47	0·33	0·4						2·61		1·61	
18	L									2·59		1·7		
19	R	0·66	0·49								2·84		1·66	
20	L	0·65	0·49	0·34	0·41	0·26		0·14		2·93		1·59		
21	R	0·65	0·5	0·34	0·38			0·13			2·87		1·7	
22	L	0·65	0·49		0·45	0·34		0·14	0·13	2·91		1·56		
23	R	0·7	0·51	0·53	0·43		0·14	0·16			2·74		1·57	
24	L		0·44							2·7		1·52		
25	R	0·73	0·51	0·35	0·45	0·34					2·78		1·63	
26	L	0·75	0·49		0·46	0·33	0·15	0·15		2·76		1·5		
27	R										2·69			
28	L											1·65		
29	R										2·44		1·34	
30	L											1·59		
31	R										2·12		1·59	
32	L	0·74	0·49							2·88				
33	R	0·7	0·49	0·36	0·39						3·06			
34	L	0·72	0·49		0·37			0·15						
35	R										2·78			
36	L	0·69	0·5	0·34	0·43		0·17	0·15						
37	R													
38	L													
39	R												1·65	
40	L	0·67	0·51	0·35	0·44							1·56		
41	R													
42	L		0·49		0·33				0·14		2·75			
43	R												1·44	
44	L	0·65	0·49							2·76	2·49	1·62		
45	R	0·67	0·49										1·58	
46	L	0·7	0·46									1·57		
47	R	0·69		0·33										
48	L	0·68												
49	R													
50	L											1·63		
51	R												1·62	
52	L									3		1·54		
53	R	0·66	0·5								2·59		1·61	

Theropod T13 (TL: 180 m) (Cont.)

FP *N*	L/R	PTL	PTW	L.II	L.III	L. IV	W.II	W.III	W.IV	SL(L)	SL(R)	PL(L)	PL(R)	TW
54	L	0·65								2·65		1·41		
55	R	0·69	0·51	0·33	0·43			0·15			2·44		1·6	
56	L	0·68	0·52							2·42		1·51		
57	R	0·65	0·52		0·45						2·79		1·42	
58	L	0·69	0·5				0·17			2·37		1·51		
59	R	0·7	0·52								2·59		1·67	
60	L									2·8		1·44		
61	R	0·65	0·51								2·51		1·49	
62	L			0·27	0·39		0·15	0·15		2·43		1·54		
63	R	0·69	0·49								2·83		1·63	
64	L	0·7	0·42	0·27	0·4		0·15	0·15	0·15	2·89		1·42		
65	R	0·67	0·43								2·54			
66	L	0·68	0·45	0·3	0·4		0·16	0·15						
67	R	0·65	0·47											
68	L													
69	R													
−2	L									5·3		2·76		1·1
−1	R										5·41		2·63	1·
0	L									5·65		2·81		1·1
1	R	0·81	0·6	0·42			0·18				5·63		2·85	1·05
2	L	0·68	0·6		0·49	0·4		0·15	0·2	5·39		2·81		1·05
3	R	0·7		0·37							5·27		2·63	1·05
4	L	0·65	0·43		0·44			0·15		4·1		2·69		1·1
5	R	0·64	0·52	0·4	0·45		0·16	0·18			2·9		1·54	1·1
6	L	0·65	0·5		0·46			0·14		2·92		1·52		1·1
7	R	0·54	0·45		0·4			0·13			2·78		1·57	1·1
8	L									2·57		1·47		1·1
9	R	0·6	0·5	0·38	0·46						2·55		1·43	1·05
10	L	0·69	0·5									1·45		1·1
11	R	0·65	0·52	0·36	0·44								1·45	1·05
12	L	0·65	0·52	0·36	0·33									1·1
13	R													
14	L													
15	R													
16	L	0·68	0·55		0·44									1·1
17	R													1·1
18	L	0·53	0·45			0·36			0·15	2·67		1·55		1·1
19	R												1·62	1·1
20	L									2·77		1·4		1·1
21	R										2·55		1·48	1·1
22	L	0·57	0·45		0·35			0·14		2·52				1·1
23	R	0·7	0·47	0·47	0·38			0·16						1·1
24	L	0·68	0·45		0·51	0·36		0·14	0·16					1·1

Theropod T29 (TL: 30 m)

FP *N*	L/R	PTL	PTW	L.II	L.III	L. IV	W.II	W.III	W.IV	SL(L)	SL(R)	PL(L)	PL(R)	TW
1	L	0·8	0·46							2·3		1·2		
2	R		0·51								3		1·35	
3	L	0·72	0·47							3·3		1·65		1·1
4	R	0·7	0·53										1·6	1·1
5	L	0·75	0·51											

Sauropod T62 (TL: 70 m)

FP *N*	L/R	MTL	MTW	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)	TW(in)
1	L	0·39	0·31	2·69		1·62		1·4	0·3
2	R	0·52	0·35		2·88		1·59	1·55	0·6
3	L	0·52	0·35	2·78		1·81		1·6	0·6
4	R	0·52	0·32		2·65		1·55	1·6	0·6
5	L	0·49	0·31	2·84		1·56		1·5	0·65
6	R	0·52	0·32		2·62		1·56	1·35	0·45
7	L	0·5	0·28	2·67		1·51		1·55	0·7
8	R	0·53	0·36		2·78		1·81	1·3	0·4
9	L	0·46	0·27	2·77		1·64		1·5	0·65
10	R	0·47	0·3		2·76		1·7	1·35	0·5
11	L	0·52	0·23	2·79		1·75		1·5	0·55
12	R	0·57	0·34		2·52		1·63	1·45	0·5
13	L	0·58	0·31	2·64		1·6		1·61	0·65
14	R	0·58	0·31		2·83		1·68	1·3	0·55
15	L	0·53	0·37	2·59		1·67		1·6	0·6
16	R	0·55	0·34		2·62		1·56	1·3	0·5
17	L	0·48	0·29	2·21		1·69		1·65	0·5
18	R	0·53	0·35		2·55		1·19	1·45	0·55
19	L			3·37		2·21		1·4	0·6
20	R	0·53	0·35		2·58		1·77	1·6	0·7
21	L	0·54	0·33	2·75		1·58		1·53	0·5
22	R	0·5	0·33		3·02		1·87	1·3	0·5
23	L	0·47	0·25	2·74		1·62		1·35	0·4
24	R	0·57	0·37		2·54		1·64	1·4	0·55
25	L	0·56	0·36	2·54		1·48		1·35	0·45
26	R	0·54	0·32		2·61		1·54	1·45	0·6
27	L	0·51	0·34	2·64		1·59		1·5	0·5
28	R	0·56	0·4		3·6		1·72	1·45	0·55
29	L	0·52	0·34	2·19		1·46		1·55	0·6
30	R	0·49	0·32		2·23		1·51	1·6	0·65
31	L	0·52	0·3	2·57		1·56		1·55	0·5
32	R	0·56	0·32		2·71		1·64	1·6	0·6
33	L	0·55	0·3	2·68		1·72		1·5	0·45
34	R	0·55	0·35		2·29		1·34		
35	L			2·75		1·71			
36	R				3·06		1·67		
37	L			2·9		2·04			
38	R				3·12		1·05		
39	L			3·15		2·25			
40	R	0·55	0·31		2·98		1·76		
41	L	0·49	0·29	2·84		1·82			
42	R	0·53	0·34		2·5		1·45		
43	L	0·52	0·33	2·9		1·47			
44	R				2·72		1·67		
45	L			2·67		1·63			
46	R						1·65		

Sauropod T14 (TL: 27 m)

FP *N*	L/R	MTL	MTW	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)	TW(in)
1	R	0·34	0·5		2·52	1·71		1·65	0·75
2	L	0·3	0·52	2·31			1·45	1·55	0·7
3	R	0·33	0·52		2·42	1·54		1·5	0·5
4	L	0·31	0·52	2·53			1·66	1·55	0·6
5	R	0·32	0·51		2·14	1·56		1·65	0·65
6	L	0·31	0·52	2·15			1·48	1·6	0·65
7	R	0·34	0·52		2·26	1·57		1·7	0·75
8	L	0·33	0·53	2·28			1·53	1·6	0·7
9	R	0·33	0·52		2·32	1·51		1·6	0·75
10	L	0·31	0·48	2·56			1·59	1·65	0·7
11	R	0·32	0·52		2·54	1·71		1·75	0·7
12	L	0·31	0·52	2·09			1·49	1·65	0·65
13	R	0·32	0·56		2·29	1·38		1·6	0·75
14	L	0·33	0·54	2·59			1·76	1·55	0·65
15	R	0·33	0·52		2·5	1·69		1·7	0·65
16	L	0·31	0·55	2·42			1·51	1·6	0·7
17	R	0·32	0·51		2·38	1·67		1·65	0·75
18	L	0·33	0·5	2·34			1·54	1·7	0·75
19	R	0·32	0·5		2·56	1·68		1·75	0·7
20	L	0·34	0·52	2·25			1·62	1·55	0·75
21	R	0·24	0·44		2·46	1·47		1·6	0·7
22	L	0·31	0·47				1·71	1·65	0·7
23	R	0·27	0·49					1·65	0·7

Sauropod T12 (TL: 38 m)

FP *N*	L/R	MTL	MTL	PTL	PTL	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)	TW(in)
1	R	0·29	0·48				2·76		1·37	1·4	0·5
2	L	0·29	0·51			2·82		1·73		1·45	0·5
3	R	0·28	0·48				2·46		1·71	1·55	0·55
4	L	0·27	0·48			2·51		1·53		1·5	0·55
5	R	0·29	0·48				2·78		1·72	1·5	0·5
6	L	0·33	0·51			2·56		1·7		1·55	0·5
7	R	0·33	0·48				2·46		1·67	1·5	0·6
8	L	0·27	0·48			2·8		1·78		1·55	0·55
9	R	0·28	0·46				2·65		1·68	1·5	0·55
10	L	0·3	0·47	0·35	0·45	2·83		1·66		1·5	0·55
11	R	0·24	0·46	0·25	0·35		2·83		1·76	1·5	0·6
12	L	0·29	0·48	0·35	0·45	2·84		1·64		1·55	0·55
13	R	0·22	0·46				2·79		1·71	1·55	0·6
14	L	0·28	0·48	0·3	0·47	2·66		1·71		1·5	0·55
15	R	0·28	0·47				2·54		1·58	1·4	0·5
16	L	0·26	0·48	0·25	0·45	2·85		1·55		1·4	0·5
17	R	0·25	0·47	0·3	0·4		2·76		1·85	1·45	0·5
18	L	0·29	0·47	0·3	0·4	2·61		1·49		1·45	0·5
19	R	0·3	0·49	0·35	0·47		2·72		1·77	1·5	0·55
20	L	0·24	0·48			2·71		1·59		1·5	0·5
21	R	0·25	0·49	0·3	0·5		2·84		1·76	1·5	0·55
22	L	0·27	0·49			2·83		1·74		1·45	0·55
23	R	0·26	0·48				2·73		1·69	1·45	0·55
24	L	0·25	0·48	0·35	0·45			1·66		1·5	0·5
25	R	0·26	0·49	0·29	0·5					1·5	0·5

Sauropod T34 (TL: 82 m)

FP *N*	L/R	MTL	MTW	TLP	TWP	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)
1	R	0·98	0·69				3·61		1·77	1·6
2	L	0·99	0·73			3·72		2·04		1·6
3	R	1·14	0·75				3·8		2	1·65
4	L	1·16	0·66			3·66		1·95		1·7
5	R	1·14	0·8				3·75		1·88	1·65
6	L	0·91	0·64			3·69		1·94		1·65
7	R	1·19	0·68				3·98		1·99	1·65
8	L	1·03	0·54			4·02		2·17		1·65
9	R	0·96	0·62				3·48		2·17	1·7
10	L	1·16	0·78			3·57		1·89		1·7
11	R	1·29	0·71				3·54		2·14	1·7
12	L	1·14	0·53			3·36		1·8		1·65
13	R	1·2	0·76				3·83		2·15	1·6
14	L	1·01	0·57			3·49		1·78		1·6
15	R	1·05	0·52				3·82		1·92	1·6
16	L	1·21	0·67			4·01		2·12		1·6
17	R	1·14	0·65				3·81		2·1	1·6
18	L	1·09	0·73			3·82		2·02		1·65
19	R	1·12	0·75				3·91		1·99	1·65
20	L	1·08	0·68			4·08		2·16		1·65
21	R	1·22	0·64				4		2·13	1·6
22	L	1·24	0·79			3·76		2·08		1·6
23	R	1·11	0·74				3·61		1·92	1·65
24	L	1·04	0·7			3·27		1·9		1·65
25	R	1·01	0·71				3·53		1·68	1·6
26	L	1·08	0·82					2·05		1·6
27	R	1·22	0·72							1·6

Sauropod T35 (TL: 24 m)

FP *N*	L/R	MTL	MTW	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)
1	L	1	0·76	3·44		1·99		2·2
2	R	0·89	0·68		3·36		1·88	2·2
3	L	0·97	0·76	3·37		2·05		2·2
4	R	1·02	0·74		3·67		1·87	2·1
5	L	0·97	0·76	3·67		2·28		2·3
6	R	0·97	0·71		3·57		1·87	2·25
7	L	0·99	0·82	3·38		2·03		2·25
8	R	1·09	0·76		3·37		1·9	2·2
9	L	0·96	0·74	3·68		2·24		2·3
10	R	1·14	0·86		3·31		1·62	2·3
11	L	0·96	0·75	3·19		1·78		2·25
12	R	1·13	0·7		3·37		1·96	2·2
13	L	1·02	0·71	3·39		2·06		2·2
14	R	1·1	0·8		3·98		2·29	2·3
15	L	1·11	0·73					

Sauropod T39 (TL: 31 m)

FP *N*	L/R	MTL	MTW	SLM(L)	SLM(R)	PLM(L)	PLM(R)	TW(o)
1	L			2·18		1·45		
2	R				2·27		1·4	1·35
3	L			2·54		1·53		1·2
4	R	0·57	0·52		2·41		1·57	1·15
5	L			2·76		1·46		1·2
6	R	0·54	0·54		2·67		1·85	1·3
7	L			2·14		1·22		1·35
8	R	0·4	0·35		2·38		1·52	1·25
9	L	0·46	0·44	2·17		1·2		1·2
10	R	0·44	0·31		2·41		1·44	1·2
11	L	0·47	0·4	2·08		1·36		1·2
12	R	0·46	0·35		2·23		1·25	1·2
13	L	0·5	0·39	1·9		1·35		1·25
14	R	0·48	0·33		1·82		1·17	1·3
15	L	0·44	0·4	2·83		1·41		1·3
16	R				2·69		1·9	1·35
17	L	0·52	0·34	1·95		1·21		1·35
18	R				2·25		1·46	1·3
19	L	0·47	0·48	2·74		1·55		1·3
20	R	0·52			2·57		1·58	1·3
21	L					1·48		1·25
22	R	0·44	0·33				1·49	1·25
23	L							1·3
24	R							1·25
25	L	0·41	0·38	2·23		1·92		1·25
26	R	0·42	0·3		1·89		1·2	1·25
27	L					1·33		1·3
28	R							