PALEONTOLOGY

Sauropod Trackways, Evolution, and Behavior

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We report the discovery and analysis of sauropod trackways exposed on a bedding surface of the White-Limestone formation (*1*) at Ardley Quarry, Oxfordshire, United Kingdom. The tracks are dated as Middle Jurassic [Middle Bathonian, 163 million years ago (Ma)] (*1*) and are found in association with large theropod trackways (*2*). These trackways were formed as the dinosaurs crossed an emergent or shallowly submerged coastal plain. Forty more or less continuous sauropod trackways were mapped, some in excess of 180 m in length. The prints are identified as sauropod on the basis of a number of derived features—e.g., the manus impressions indicate that the metacarpals were held in the characteristic semicircular arrangement (*3*, *4*). The trackways can be divided into two distinct types. In some cases (e.g., track number 14), the manus print is D-shaped and shows negative rotation (i.e., toes directed outward), with no impression of the large claw normally present on the first digit (Fig. 1A). Pes prints are not as deeply imprinted and are often not preserved. The prints are widely spaced from the track midline (Fig. 1A), with the manus prints slightly closer to the midline than the pes prints. In the second type (e.g., track number 90; Fig. 1B), the footprints lie close to, or even intersect, the midline of the trackway. The manus prints are more elliptical in outline and include impressions of the large claw on digit I.

Comparison of "wide-" and "narrow-gauge" trackways from similar sized individuals (e.g., tracks 14 and 90) indicates that gauge is not a function of body size. Narrow-gauge limb posture, acquired early in sauropod evolution, was retained by all basal sauropods, diplodocoids, and basal macronarians (*2*). However, absence of synapomorphies from the narrow-gauge Ardley trackways does not allow them to be assigned to any particular clade within the Sauropoda. The Titanosauria, in contrast, developed a number of derived skeletal features indicating that their limbs were held further from the midline of the animal, suggesting that this advanced clade of largely Cretaceous sauropods was responsible for wide-gauge trackways (*3*). Both the narrow-gauge sauropod tracks and those belonging to the theropods (*2*) include claw impressions. This implies that the consistent absence of the manus claw impression in the wide-gauge trackways does not reflect poor preservation. The large manus claw on digit I is found in diplodocoids and basal macronarians. In brachiosaurs [the sister group to titanosaurs (*4*)], the claw is somewhat reduced, and in titanosaurs, it is believed to have been entirely lost (*4*). The loss of the manus claw is a derived state that supports the view that the wide-gauge trackways were made by titanosaurs.

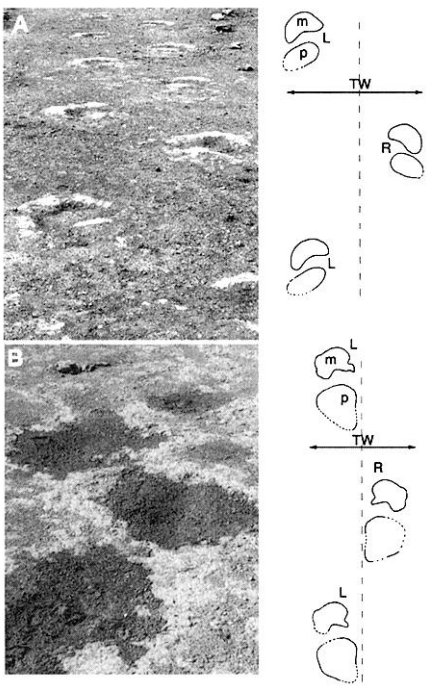

Fig. 1. Sauropod trackways from Ardley Quarry: **(A)** wide-gauge trackway, number 14, and **(B)** narrow-gauge trackway, number 90. Footprints are identified as left (L), right (R), manus (front foot, m), and pes (hindfoot, p). TW, trackway width. Scale: manus width = ~0.50 m in all trackways.

Several Middle Jurassic localities are reported as putative wide-gauge tracks (*5*, *6*); however, there is no evidence that these trackways were formed by titanosaurs, because they are associated with manus claw marks and in some cases are not truly wide gauge. Therefore, the previous earliest substantiated "titanosaur" tracks are from the Late Jurassic (*3*). The earliest known skeletal remains of titanosaurs belong to *Janenschia* from the Late Jurassic (Kimmeridgian) of Tendaguru, Tanzania (*7*). Recent studies of sauropod diversity also place the divergence between brachiosaurs and titanosaurs in the Late Jurassic (*8*). Thus, the wide-gauge sauropod tracks from Ardley provide direct evidence that titanosaurs had diverged from other sauropods by the Bathonian (a range extension of at least 12 Ma).

Virtually all of the trackways trend in a northeasterly direction and are subparallel to each other to within a few degrees. This signal strongly suggests that the sauropods formed a single herd. The footprints are consistently well preserved and do not show overprinting or erosion. They are preserved on a single bedding plane that was probably only exposed for a few hours between two high tides. The Ardley trackways indicate that sauropod herds may have contained more than one species. As with extant mammals, sauropods may have formed multispecies herds as part of a defense against predation and/or as a by-product of shared migration routes. The Ardley locality provides a powerful illustration of the contribution that trackway data can make to our understanding of evolutionary history, preservation biases, and paleoecology.

References and Notes

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