TECHNICAL COMMENT

Comment on "Ascent of Dinosaurs Linked to an Iridium Anomaly at the Triassic-Jurassic Boundary"

Olsen *et al.* (1), in a detailed study of skeletal remains and fossil footprints in the Newark Supergroup of eastern North America, found that Triassic theropods there were all of small to moderate size, whereas large theropod bones and footprints such as Eubrontes giganteus $(\sim 35 \text{ cm long})$ did not appear until the earliest Jurassic. From that evidence, they inferred that the maximum body size of theropods increased significantly at the start of the Jurassic, perhaps in response to the elimination of nondinosaurian competitors in a mass extinction at the close of the Triassic. An alternative explanation-that big theropods had immigrated to eastern North America at the start of the Jurassic-was discounted but is actually supported by footprint evidence from the Gondwana continents.

The Molteno Formation of southern Africa and the contemporaneous Ipswich Coal Measures of southeastern Queensland, Australia, are equivalent to the Triassic fraction of the Newark Supergroup in northeastern North America (2) and contain footprints representing the earliest evidence of dinosaurs in



Fig. 1. Large theropod dinosaur footprint (compare Eubrontes), from the Blackstone Formation of the Ipswich Coal Measures (Carnian) in Queensland, Australia (specimen F5474; Queensland Museum, Brisbane). An artificial mold of right pes print originally preserved as natural cast; scale bar indicates 5 cm. [Image from (8); reprinted with permission of Association of Australasian Palaeontologists]

Gondwana (3-6). Despite their wide geographic separation, the African and Australian dinosaur occurrences are strikingly similar: in both cases, tridactyl dinosaur footprints resembling the ichnogenus Grallator are found in association with a Dicroidium flora, occasional remains of paleoniscoid fishes, and a variety of invertebrates dominated by insects. More significant is that the Ipswich Coal Measures have also yielded the world's earliest examples of large theropod footprints (5).

The most compelling evidence of big Triassic theropods is a trackway sequence of three footprints preserved as natural casts (convex hyopreliefs) in roof shales of the Striped Bacon Seam at Rhondda colliery, near Ipswich, in southeast Queensland (5). The Striped Bacon Seam lies within the basal 20 m of the Ipswich Coal Measures, a thick $(\sim 1000 \text{ m})$ sedimentary unit that accumulated in a remote intermontane basin at the extreme eastern margin of East Gondwana and is securely dated as Late Triassic (Carnian) on the basis of palynological data and its prolific and long-studied macroflora (7).

The best-preserved print from Rhondda colliery was 43 cm long-i.e., 20% bigger than the North American Eubrontes giganteus (1)-and the length of stride was measured at 1.91 m. One print (Fig. 1) was recorded in the form of an artificial mold (8-10) and is very similar to, or even identical to, North American examples of the "classic" theropod ichnogenus Eubrontes. Using morphometric relationships (11), it may be estimated that a theropod dinosaur producing footprints 43 cm long would have stood more than 2 m high at the hip. By any standards, that is a large theropod; for example, it is bigger than the type specimen of the familiar Jurassic predator Allosaurus fragilis, which stood at about 1.8 m high at the hip (12).

From the distribution of their fossil footprints (6), it is evident that theropod dinosaurs had achieved a global distribution as early as the Carnian, and evidence from the Ipswich Coal Measures indicates that these animals had already undergone some diversification into large Allosaurus-sized forms by the time of their first appearance in the fossil record-at least 20 My before the

faunal turnover marking the Triassic-Jurassic boundary. The seeming absence of large theropods from the Triassic sediments of the Newark Supergroup is probably a local peculiarity of ecology, rather than a feature of continental tetrapod faunas worldwide. Those Newark sediments accumulated in a tropical environment at a paleolatitude about 10° N, with a flora dominated by conifers and an insect fauna depauperate in beetles and cockroaches, but rich in flies. By contrast, the Molteno Formation and Ipswich Coal Measures accumulated at a paleolatitude of about 50 to 60° S, with floras dominated by the seed-fern Dicroidium and insect faunas that lacked flies but included many and diverse beetles, cockroaches, and bugs (2). The Carnian biota of Gondwana was fundamentally different from the contemporary biota of Laurasia, and it is not particularly surprising that large theropod dinosaurs should appear in one faunal assemblage but not in the other.

In short, the emergence of big predatory dinosaurs was not the consequence of mass extinction at the Triassic-Jurassic boundary, and the footprint assemblages of the Newark Supergroup likely reflect local (Laurasian) events in dinosaurian history, rather than events of global significance.

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