TECHNICAL COMMENT

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

Our recent study on the nature of the ascent of the dinosaurs (1) argued three main points: (i) that a major terrestrial tetrapod mass extinction is concentrated at the palynologically identified Triassic-Jurassic boundary in eastern North America (based on footprints and bones); (ii) that truly large predatory dinosaurs appear immediately after the boundary (based on footprints); and (iii) that both the boundary and the mass extinction level are associated with a modest Ir anomaly and fern spike, plausibly of asteroid or comet impact origin.

Although the comment of Thulborn (2) addresses a number of paleontological issues in (1), his only point salient to the conclusions of our paper is his extraordinary claim that very large theropod dinosaurs were already present in the Carnian, some 20 million years or so before the Triassic-Jurassic boundary [in contrast to our assertion in point (ii), above]. His claim is extraordinary because the evidence cited by Thulborn is an isolated and probably incomplete plaster cast of a footprint from strata dated by floral data as Carnian-yet there are no other osteological or footprint data anywhere in the world of large Carnian dinosaurs, let alone very large theropod footprints. Here, we will not address the age of the track-bearing strata, which we take at face value as Triassic (3). Instead, we concentrate on the claim that the supposed track maker was a theropod dinosaur.

Superficially, the photograph of a plaster mold provided by Thulborn [previously published in (4)] would seem to represent a very large (43 cm) tridactyl footprint that, apart from its age, would normally be assumed to be dinosaurian, probably theropod, in origin. However, assessment of the footprint is hampered by the truncation of the rear of the track, a lack of pad impressions, and the general blotchy coloration of the artificial mold, as well as the very superficial documentation of the material. The track is certainly not, contrary to the assertion of Thulborn (2), "identical to . . . [the] ichnogenus Eubrontes," the type material of which was redescribed by one of us (5). Indeed, visible in the photograph [figure 1 in (2)] are a depression lateral to digit II that could be

interpreted as an impression of a large digit I,and an apparent metatarso-phalangeal impression behind the phalangeal pads. If thisinterpretation is correct, this minimally tetradactyl track would unquestionably not belong to the ichnogenus Eubrontes, and would probably not be interpreted as theropod in origin. Pentadactyl footprints of a size comparable to this Australian ichnite have been described from strata rather more securely dated as Carnian in North Carolina, USA (6) (Fig. 1). Were the rear of these tracks to be truncated artificially, as is the track in the figure produced by Thulborn, the result would look superficially Eubrontes-like, although not directly assignable to that ichnogenus. Indeed, many other putatively tridactyl early dinosaur footprints have upon rigorous examination proved to be pentadactyl and nondinosaurian (7). In any case, until the Australian material is properly described and illustrated, it will be difficult to assess its relevance to theropod dinosaur evolution. We regard the North Carolina material as being most similar to *Parachirotherium* as described by Haubold (ϑ), albeit without manus impressions, and suggest a similar assignment is possible for the material cited by Thulborn (2). These types of tracks have been interpreted as dinosauroid (ϑ), if not dinosaurian, but given our current state of knowledge, they could just as well be crurotarsan in origin. The line drawing of the trackway provided in (ϑ) provides no additional information pertinent to this discussion, because it is far too diagrammatic to be reliable.

Our study (1) proffered two scenarios that might explain the increase in size in theropod dinosaurs across the Triassic-Jurassic boundary in eastern North America. (i) The appearance of the much larger theropods could represent a dispersal event from some unknown location. (ii) It could represent an evolutionary event triggered by the elimination of competitors. We favor the second hypothesis, but if the tracks Thuborn cites prove to be both of theropod origin and Carnian in age, we would be more favorably inclined to our first scenario. Indeed, we are well aware that the terrestrial tetrapod records of Triassic extra-tropical regions are extremely poorly known and surely will have many surprises, and we look forward to the full documentation and description of track assemblages from the higher latitudes from both hemispheres.

On the other hand, Thulborn argues that "[t]he Carnian biota of Gondwana was fundamentally different from the contemporary biota of Laurasia," an assessment that



Fig. 1. (A) Medium-sized and **(B)** very large examples of cf. *Parachirotherium* sp. from Carnian age strata of the Peking Formation of the Deep River basin, North Carolina [images from (6); reprinted with permission of *Southeastern Geology*]. Middle digits are superficially similar to theropod footprints. (A) shows impression of left pes; (B) shows natural cast of right pes, with much smaller superimposed trackway of *Apatopus lineatus*.

TECHNICAL COMMENT

may be correct (pending better correlation tools) but that is not strongly supported by the current faunal evidence. What we can say is that the Carnian of eastern North America does not have "a flora dominated by conifers and an insect fauna depauperate in beetles and cockroaches, but rich in flies," as stated by Thulborn. These eastern North American Carnian floras are dominated by ferns and cycadeoids (10, 11) as well as by conifers, and only one locality has produced flies. Even at the latter Lagerstätte, flies are third in abundance after true bugs and beetles (11). All other Triassic insect localities in eastern North America are dominated by beetles and roaches and lack flies (12).

Contrary to Thulborn's assertion that "it is not particularly surprising that large theropod dinosaurs should appear in one faunal assemblage but not in the other," we argue that it is surprising, indeed startling, because large, highly mobile animals such as theropods could easily have walked from Brisbane to New York during a single lifetime in Triassic Pangea. If they did not do so, something must have prevented them. Even if climatic or ecological processes maintained a strong terrestrial provinciality during the Late Triassic, as we have maintained elsewhere (13), perhaps excluding large theropods in regions of Pangea, the abrupt breakdown of that provinciality at the Triassic-Jurassic boundary would still signal a global biological event of immense importance, rather than a "local" event.

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References and Notes

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