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The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania

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The rise of dinosaurs was a major event in vertebrate history, but the timing of the origin and early diversification of the group remain poorly constrained. Here, we describe *Nyasasaurus parringtoni* gen. et sp. nov., which is identified as either the earliest known member of, or the sister-taxon to, Dinosauria. *Nyasasaurus* possesses a unique combination of dinosaur character states and an elevated growth rate similar to that of definitive early dinosaurs. It demonstrates that the initial dinosaur radiation occurred over a longer timescale than previously thought (possibly 15 Myr earlier), and that dinosaurs and their immediate relatives are better understood as part of a larger Middle Triassic archosauriform radiation. The African provenance of *Nyasasaurus* supports a southern Pangaean origin for Dinosauria.

1. Introduction

The appearance of dinosaurs in the Triassic was an important event in the history of life because it marked the onset of a faunal diversification that has dominated terrestrial ecosystems for almost 230 Myr. The exact timing of dinosaur origins and the pace of early dinosaur diversification remain unclear [1,2], but a growing consensus suggests that dinosaurs were initially rare components of Early–Late Triassic terrestrial ecosystems and that their ascent was gradual and regionally diachronous [3]. The oldest well-dated and unambiguously identified dinosaurs are from the late Carnian (approx. 230 Ma) of Argentina [4], and by the end of the Carnian, all three major dinosaur lineages were present (Ornithischia, Sauropodomorpha, Theropoda) [5,6]. The surprising early diversity and morphological disparity of early dinosaurs occurring together in the oldest dinosaur-bearing strata indicate that either (i) dinosaurs experienced an ‘early burst’ of diversification in the Carnian, or (ii) dinosaurs had a deeper, cryptic origination in the Triassic and that their diversification occurred more slowly than shown by current knowledge of their fossil record. The closest relatives of dinosaurs, silesaurids, are known from the late Anisian (Middle Triassic); ghost lineages inferred from phylogenetic analyses of ornithomirans predict that Dinosauria and its immediate stem lineage should be at least as old if these topologies are correct [7].

To date, every reported pre-late Carnian dinosaur body-fossil or footprint(s) has proved to be non-dinosaurian, referable to taxa with convergent morphology, or ambiguously identified [1,8]. Here, we present the best available evidence for a Middle Triassic dinosaur (or at least the closest dinosaur relative yet found) from the late Anisian of Tanzania.

2. Systematic palaeontology

Archosauria Cope 1869 (*sensu* Gauthier & Padian 1985)

Dinosauriformes Novas 1992

Dinosauria Owen 1842 (*sensu* Padian & May 1993)

Nyasasaurus parringtoni gen. et sp. nov.

(a) Etymology

Nyasa, from Lake Nyasa near the type locality, and *sauros*, Greek for lizard; *parringtoni*, in honour of Francis Rex Parrington, collector of the holotype.

(b) Holotype and referred material

Holotype: NHMUK R6856 (The Natural History Museum, London, UK); right humerus, three partial presacral vertebrae and three sacral vertebrae. Referred specimen: SAM-PK-K10654 (Iziko South African Museum, Cape Town, South Africa) (= *Thecodontosaurus alophos*); three cervical vertebrae and two posterior presacral vertebrae.

(c) Locality and age

The holotype was collected from a single locality (Parrington's locality B36) from the Lifua Member of the Manda beds, Ruhuhu Basin, southern Tanzania. The Lifua Member is late Anisian (Middle Triassic) in age, on the basis of biostratigraphic comparisons with the tetrapod fauna of the *Cynognathus* Assemblage Zone (subzone C) of South Africa [9]. Cynodonts (*Aleodon brachyrhamphus* and *Scalenodon angustifrons*), dicynodonts (*Sangusaurus edentatus* and *Angonisaurus cruickshanki*) and the rhynchosaur *Stenaulorhynchus stockleyi* co-occur at the same horizon in the immediate vicinity.

(d) Diagnosis

Nyasaosaurus parringtoni was a 2–3 metre long (estimated from vertebral dimensions) dinosauriform with the following unique combination of humeral character states: ventrally elongated deltopectoral crest; laterally deflected apex of the deltopectoral crest; distinct notch central to the apex of the deltopectoral crest; pointed expansion on the proximal surface near the dorsal extent of the deltopectoral crest; proximal surface of the humerus continuous with the lateral surface of the deltopectoral crest; and distinct fossa present on the posterodorsal surface, just ventral to the proximal surface. Humeral histology indicates rapid growth characterized by complex vascularization, highly woven bone tissue and the absence of any lines of arrested growth. The vertebrae also have a distinct combination of character states, including: at least three sacral vertebrae; dorsoventrally tall sacral ribs; and hyposphene–hypantrum intervertebral articulations in the presacral vertebrae (last character also present in the referred specimen; see the electronic supplementary material for additional information).

3. Description

The humerus of *Nyasaosaurus parringtoni* bears a subrectangular, distally elongated deltopectoral crest that extends down the shaft for more than 30 per cent of its estimated total length, an unambiguously optimized dinosaur character state in all recent phylogenies [1,2]. The apex of the deltopectoral crest is deflected laterally at its anterior tip, a feature present exclusively in dinosaurs (e.g. *Tawa*, *Saturnalia*, *Heterodontosaurus*) as found in our phylogenetic analysis. The humerus does not share any synapomorphies exclusively with any other Triassic archosaur clade.

The preserved axial column consists of partial posterior presacral vertebrae and elements of the sacrum. The presacral

vertebrae bear hypantrum intervertebral articulations as indicated by a clear gap between the prezygapophyses, as in some pseudosuchians (e.g. *Batrachotomus*), silesaurids (e.g. *Silesaurus*) and dinosaurs (e.g. *Dilophosaurus*). The sacrum consists of three partial vertebrae: two primordial/ancestral vertebrae frame an additional vertebra between the two (see the electronic supplementary material). Parts of each sacral rib are preserved, and the articular facet on the first sacral rib indicates that the ilium was nearly vertical and the sacral rib was dorsoventrally elongated like that of all early dinosaurs [10].

The referred specimen (SAM-PK-K10654) consists of presacral vertebrae, three of which are anteroposteriorly elongated cervical vertebrae with significant vertical offset between the anterior and posterior articular faces. One specimen (figure 1j) preserves the bases of epiphyses immediately dorsal to the postzygapophyses, a character state present in, but not exclusive to, Dinosauriformes. The cervical vertebrae bear deep fossae (i) lateral to the neural canal in anterior view, and (ii) on the posterolateral surface of the neural arch just anteroventral to the prezygapophyses. Both of these character states are present in *Silesaurus* [11], but not in the earlier diverging silesaurid *Asilisaurus*, and in early theropod dinosaurs [10] and have been interpreted as possibly homologous with features that represent unambiguous postcranial pneumaticity in theropod dinosaurs [12].

The histology of the holotypic humerus (figure 1c–e) suggests sustained, elevated growth rates similar to those of dinosaurs (e.g. *Megapnosaurus (Syntarsus) rhodesiensis*, *Herreasaurus*) and higher than those of most other archosauriforms with the exception of pterosauroforms [13,14]. Unaltered, primary, woven-fibred bone comprises much of the humeral cortex, and all vascular canals are primary osteons. Many of these canals are longitudinal canals, but at least half of these anastomose with other canals (in all directions), and locally, short radial canals may dominate. The outermost cortex shows a decrease in osteocytes and a temporary transition from woven-fibred to parallel-fibred bone (figure 1e), which we tentatively identify as an annulus (see the electronic supplementary material for further details).

This condition differs from that of *Silesaurus*, which shows low levels of vascular connectivity and lacks the complex vascular patterns seen in *Nyasaosaurus* [15], and is histologically more similar to *Megapnosaurus rhodesiensis* (see the electronic supplementary material).

4. Relationships

Nyasaosaurus bears two character states that are considered autapomorphic for dinosaurs in the holotype (elongated and laterally deflected deltopectoral crest) and one character state that could represent a dinosaur plesiomorphy, but which has a complex distribution among dinosauriforms (three sacral vertebrae). Additionally, the referred specimen bears two character states in the cervical vertebrae consistent with, but not exclusive to, theropod dinosaurs (deep fossae lateral to the neural canal in anterior view, deep lateral fossae). Together with all other aspects of the morphology, this combination of character states is unique for any dinosaur or close relative; so we scored the holotype and the

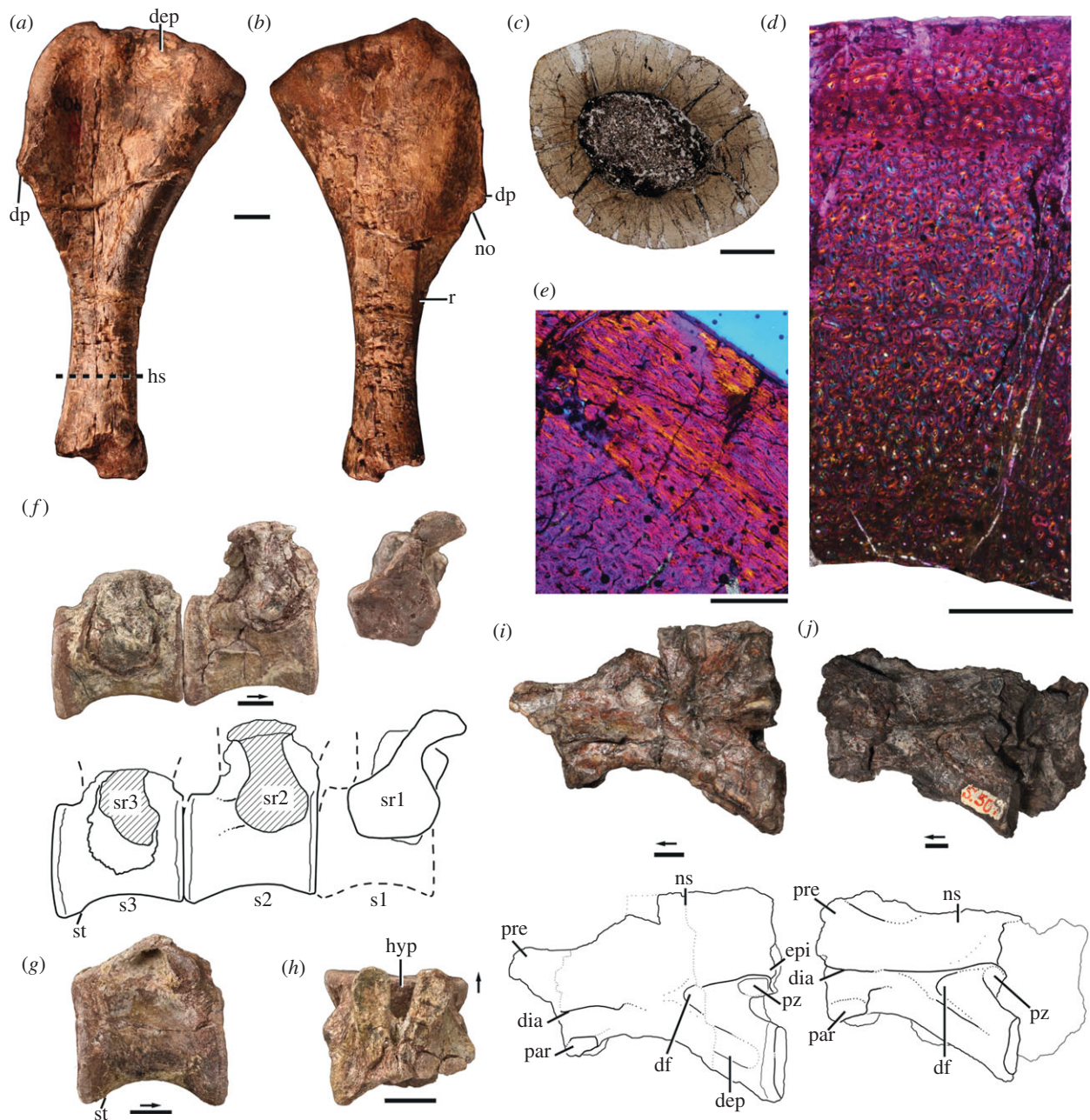


Figure 1. Holotype (*a–h*; NHMUK R6856) and referred (*i–j*; SAM-PK-K10654) specimens of *Nyasasaurus parringtoni* gen. et sp. nov. Right humerus in (*a*) anterior and (*b*) posterior views. Histological section of humerus in (*c*) complete cross-section in transmitted light, (*d*) cross-section through the entire cortex in crossed Nicols, and (*e*) cross-section through the outer portion of cortex in crossed Nicols. (*f*) Rearticulated sacrum in right lateral view with interpretive drawing (below). (*g*) Posterior presacral vertebra in right lateral view. (*h*) Partial posterior presacral vertebra in dorsal view. (*i*) Anterior cervical vertebra in left lateral view with interpretive drawing (below). (*j*) Anterior cervical vertebra in left lateral view with interpretive drawing (below). Arrows point anteriorly. Scale bars, (*a,b,f–j*) 1 cm, (*c*) 4 mm, (*d*) 1 mm, (*e*) 500 nm. Dep, depression; df, deep fossa; dia, diapophysis; dp, deltopectoral crest; epi, epiphysis; hs, histology section; hyp, hypantrum; no, notch; ns, neural spine; par, parapophysis; pre, prezygapophysis; pz, postzygapophysis; r, ridge; s1–3, sacral vertebra number; sr1–3, sacral rib number; st, striations.

referred specimen independently in a comprehensive early archosauriform phylogeny [16], but then combined their scorings in a second analysis. The methods of the phylogenetic analysis were identical to those of Butler *et al.* [17] and the Nexus file, and high-resolution histological and osteological images are deposited online at <http://morphobank.org/permalink/?P485> (see the electronic supplementary material for accession numbers). The holotype was found in a polytomy with all members of Dinosauria included in the analysis in the strict consensus tree, but was found as the sister-taxon of Dinosauria or within Dinosauria in the various most parsimonious trees. The referred specimen was

recovered within Dinosauria as a theropod, and when the scores of the holotype and referred specimen were combined, *Nyasasaurus* was found as either the sister taxon of Dinosauria or to lie within the clade.

The shared synapomorphies of *Nyasasaurus* and Dinosauria are present in axial and appendicular elements, thus demonstrating that the characters are spread across the skeleton rather than restricted to a single element. We interpret these results as supporting our identification of *Nyasasaurus* as either the sister-taxon to, or the earliest-known member of, Dinosauria, but do not consider the phylogenetic positions within Dinosauria as a robust portrayal of

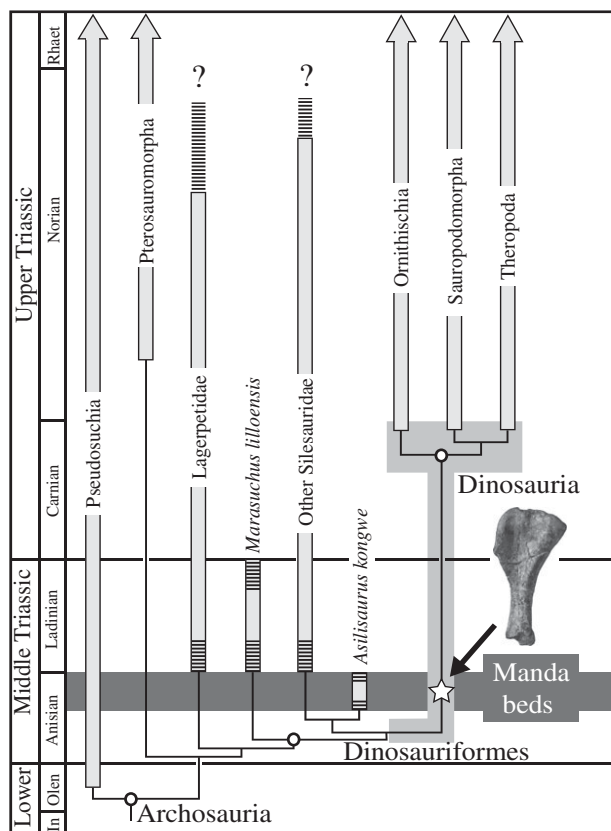


Figure 2. Possible phylogenetic position of *Nyasasaurus parringtoni* gen. et sp. nov. as either within, or the sister-taxon of, Dinosauria (indicated by the medium grey box), illustrating the decrease in the dinosaurian ghost lineage. Dashed bars represent uncertainty. In, Induan; Olen, Olenekian.

the available evidence. The unique character combination of *Nyasasaurus* may represent the plesiomorphic states present just outside or within Dinosauria given its age, but there are considerable uncertainties about (i) the plesiomorphic character states of early ornithischians [17], (ii) character optimizations of vertebral fossae interpreted as pneumatic-like [18], and (iii) the phylogenetic position of early saurischians such as *Herrerasaurus* [1].

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5. Discussion

All of the available morphological, phylogenetic and histological evidence indicates that *Nyasasaurus* represents either the sister-taxon to, or the earliest member of, Dinosauria (figure 2). The occurrence of a late Anisian 'stem' dinosaur or true dinosaur has previously been predicted by the sister-taxon relationship with the Middle–Late Triassic silesaurids [7]. It is noteworthy that the oldest known silesaurid, *Asilisaurus kongwe*, also occurs in the Lifua Member. This co-occurrence indicates (i) that dinosaurs and their nearest relatives coexisted in the same terrestrial environments, and (ii) if *Nyasasaurus* belongs to Dinosauria or the dinosaurian stem lineage, the current 10–15 Myr ghost lineage separating these taxa is immediately eliminated (figure 2).

The relationships of *Nyasasaurus* and its age have important implications regardless of whether this taxon is a dinosaur or 'near-dinosaur.' The late Anisian age demonstrates that essentially dinosaur-like dinosauriforms (or the earliest dinosaurs) were just another component of an extensive archosauriform radiation that existed in the aftermath of the end-Permian mass extinction. Moreover, if *Nyasasaurus* is a dinosaur, it establishes that dinosaurs evolved earlier than previously expected and that the dinosaurs from the Ischigualasto Formation and elsewhere do not necessarily record an 'early burst' of diversification in the Late Triassic. The limited material available for *Nyasasaurus* in comparison with that for other members of the same assemblages (e.g. synapsids, rhynchosaurs; [19]) also suggests that dinosaurs or 'near-dinosaurs' were rare in Middle Triassic vertebrate assemblages. Finally, the occurrence of *Nyasasaurus parringtoni* in Tanzania supports a southern Pangaeian origin for dinosaurs, as predicted by the distributions of the earliest unambiguous dinosaur taxa from southern South America [2].

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