Review and analysis of African sauropodomorph dinosaur diversity

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Introduction

Sauropodomorphs were a major Mesozoic terrestrial radiation of gigantic, herbivorous dinosaurs. Their remains have been discovered on all continents and by the close of the Triassic they had achieved a global distribution (Galton & Upchurch 2004). African sauropodomorphs are known from the Carnian (Late Triassic; Raath 1996), right through to the Maastrichtian (Late Cretaceous; Curry Rogers & Forster 2001), thus spanning the entire known temporal range of dinosaurs. In addition, their remains have been recovered from 16 different African countries, ranging across the entire continent (Fig. 1). Here, the sauropodomorph diversity from each geological Epoch will be summarized, with a concluding analysis of African sauropodomorph diversity through time.

Late Triassic

The Late Triassic of Africa is almost entirely dominated by remains from South Africa. These include numerous basal sauropodomorphs (Eucnemesaurus and Plateosaurus, as well as undiagnostic remains; Van Hoepen 1920; Haughton 1924; Yates 2003, 2007a; Galton et al. 2005), several indeterminate prosauropods (including remains from Zimbabwe; Raath 1996), as well as Azendohsaurus from Morocco (originally described as an ornithischian and then reinterpreted as a prosauropod; Dutuit 1972; Gauffre 1993a), which is now considered a non-dinosaurian archosauriform (Irmis et al. 2007). Additionally, two South African taxa originally considered as prosauropods (Melanorosaurus and Blikanasaurus; Haughton 1924; Galton & van Heerden 1985) have more recently been resolved as basal sauropods (Upchurch et al. 2004, 2007; Yates 2007b). A third South African Triassic sauropod (Antetonitrus) was named by Yates & Kitching (2003).

Early Jurassic

The Early Jurassic is dominated by the South African and Zimbabwean prosauropod Massospondylus (Owen 1854), which is known from over 80 skeletons (Galton & Upchurch 2004). Barrett (2004) noted the presence of another diagnostic Early Jurassic South African sauropodomorph, though this is considered a new species of Massospondylus (Barrett, in press) and is not included as a distinct taxon in the diversity analysis. As well as various indeterminate sauropodomorph remains, there are also recently excavated skeletons from South Africa that have been suggested to represent three new sauropodomorph taxa, including a basal sauropod (Yates et al. 2007). The Zimbabwean taxon Vulcanodon was originally identified as a prosauropod (Raath 1972) but has subsequently been demonstrated to be a basal sauropod (Cruickshank 1975; Upchurch et al. 2004). Gauffre (1993b) named a second species of Melanorosaurus (M. thabanensis) based on an isolated femur from Lesotho; however, Yates (2007b) recently expressed doubt as to the validity of this species and it is here considered a nomen dubium. Another basal sauropod, Tazoudasaurus, is known from the Toarcian of Morocco (Allain et al. 2004).

Middle Jurassic

By the Middle Jurassic, African sauropodomorphs were composed entirely of sauropods, with prosauropods seemingly having become extinct. The first Madagascar remains are known from this time period, with the basal eusauropod Archaeodontosaurus (Buffetaut 2005) and the titanosauriform Lapparentosaurus (Bonaparte 1986; Upchurch et al. 2004) roughly contemporaneous alongside material described by Lydekker (1895) as ‘Bothriospondylus madagascariensis’. This latter material represents a derived non-neosauropod eusauropod which is distinct from the other named Madagascar taxa (Mannion, in press). The basal macronarian Atlásaurus is known from Morocco (Monbaron et al. 1999), as are also remains originally described as ‘Cetiosaurus mogrebiensis’ (Lapparent 1955), which are in need of revision and are currently considered undiagnostic. Most recently, Mahammed et al. (2005) described a basal eusauropod, Chebsaurus, from Algeria.

Late Jurassic

Currently known Late Jurassic African sauropods are restricted to Tanzania and Zimbabwe. Most remains were collected during the German Tendaguru expeditions of 1909–1913. Diplodocoids (Australodocus, Dicraeosaurus and Tornieria), Brachiosaurus, the putative titanosaur Janenschia and a taxon of unknown affinities (Tendaguria) are all known from Tanzania (Fraas 1908; Janensch 1914; Wild 1991; Bonaparte et al. 2000; Remes 2007). Material...
from Zimbabwe has also been referred to several of these genera (Raath & McIntosh 1987).

Early Cretaceous

The first sauropod material known from Malawi is preserved in Early Cretaceous deposits. This is represented by the titanosaurs *Malawisaurus* and *Karongasaurus* (Haughton 1928; Jacobs *et al.* 1993; Gomani 2005). *Rebbachisaurus* is known from Morocco (Lavocat 1954) and another rebbachisaurid (*Nigersaurus*) has been described from Niger (Sereno *et al.* 1999). Also described from Niger is the eusauropod (or basal macronarian; Upchurch *et al.* 2004) *Jobaria* (Sereno *et al.* 1999). Material described from Niger, Tunisia and Algeria as *Rebbachisaurus tamesnensis* (Lapparent 1960) may be a mixture of *Nigersaurus* and *Jobaria*. A brachiosaurid ("Brachiosaurus nougaredi") was also named by Lapparent (1960) based on Algerian remains, but is not here considered valid. Lastly, indeterminate sauropod material is known from South Africa, Cameroon and Kenya (Weishampel *et al.* 2004, and references therein; Sertich *et al.* 2005; De Klerk 2008).

Late Cretaceous

Valid, named Late Cretaceous taxa are composed entirely of titanosaurans, with *Aegyptosaurus* and *Paralititan* both described from the Cenomanian of Egypt (Stromer 1932; Smith *et al.* 2001), and *Rapetosaurus* known from the late Maastrichtian of Madagascar (Curry Rogers & Forster 2001). Indeterminate remains (predominantly of titanosaurans, but also including some possible diplodocoids) are also known from Morocco, Niger, Sudan, Swaziland and Tanzania (Weishampel *et al.* 2004, and references therein; Pereda Suberbiola *et al.* 2004; Jacobs *et al.* 2006; O’Connor *et al.* 2006).

Discussion and conclusions

Thirty-one African sauropodomorphs are considered generically distinct, spanning the full temporal interval that dinosaurs existed and including representatives of all the main sauropodomorph clades. An African sauropodomorph taxic diversity curve (Fig. 2) shows peaks in the Norian (Late Triassic), Hettangian-Sinemurian (Early Jurassic), Bathonian (Middle Jurassic) and Kimmeridgian-Tithonian (Late Jurassic), as well as a shallower peak in the mid-Cretaceous. The curve also suggests that the Pliensbachian-Bajocian (Early-Mid Jurassic), Oxfordian (Late Jurassic), and much of the Cretaceous were periods of apparent lower diversity.

In general, this matches quite closely with diversity curves based on global taxic and phylogenetic diversity estimates (i.e. Barrett & Upchurch 2005; Upchurch & Barrett 2005; Fig. 2), although the African diversity curve unsurprisingly shows lower diversity levels based on only sampling from one continent. The main difference is the lack of any known African taxa for much of the Late Cretaceous, in comparison to global values. Upchurch & Barrett (2005) used dinosaur-bearing formations (DBFs) to help tease apart genuine global diversity signals from preservational biases. During the Cretaceous, DBFs were at their highest; however, the number of DBFs for the African Late Cretaceous (based on Weishampel *et al.* 2004) is extremely low, thus this low diversity may be an artefact of a poor African Late Cretaceous rock record. The overall closeness in fit suggests that African sauropodomorphs were at least as diverse as in other areas of the world, and followed similar fluctuations temporally.

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