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A Triassic Fauna from Madagascar, Including Early Dinosaurs

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The discovery of a Middle to Late Triassic (~225 to 230 million years old) terrestrial vertebrate fauna from Madagascar is reported. This fauna documents a temporal interval not well represented by continental vertebrate assemblages elsewhere in the world. It contains two new prosauropod dinosaurs, representing some of the earliest dinosaur occurrences known globally. This assemblage provides information about the poorly understood transition to the dinosaur-dominated faunas of the latest Triassic.

A historical perspective of Madagascar's unique modern fauna and flora has long been obscured by the island's meager Mesozoic-Cenozoic fossil record (*1*). An outline of precisely how the Malagasy biota formed over time is only beginning to emerge from phylogenetic analyses of living groups and paleontological discoveries from the Cretaceous (*1*). Research (*2*) in older strata provides complementary evidence about this diversification and insights into the origin of dinosaurs (*3*).

Much of Madagascar's sedimentary sequence occurs within two large western basins (*4*). Fossils described below are from the southern of these (Morondava Basin) and are derived from the geographically widespread Isalo "Group" (*2*, *5*), a lithostratigraphic unit from which only three adequately represented tetrapod taxa have been described (*2*, *6*, *7*).

We recovered diverse terrestrial vertebrate remains near the base of the Isalo II in the region east of Sakaraha (about 22° to 23°S, 44° to 44.5°E). Silicified wood and fragments of the rhynchosaur *Isalorhynchus* (*7*) were the only fossils known previously from the region. The geochronology of this portion of the Isalo "Group" has long been poorly understood, reflecting limited biostratigraphic control and lack of interfingering marine units. The Isalo II is traditionally considered to be Early to Middle Jurassic in age (*5*, *8*), but Buffetaut (*7*) argued that it is considerably older (Middle Triassic). Our findings confirm Buffetaut's estimate of a Triassic (but not necessarily Middle Triassic) age for the base of the Isalo II in this region.

Our basal Isalo II sites have yielded abundant remains of a variety of diapsid reptiles, including two prosauropod dinosaurs, two rhynchosaurs [*Isalorhynchus*, originally described as a rhynchosaurine (*7*), all others of which are Ladinian or older, plus a second new taxon (*9*)], and a sphenodontian. Several synapsids also occur, including a kannemeyeriid dicynodont and at least four eucynodont species. These phylogenetically important occurrences greatly improve the basis for biostratigraphic correlation of the basal Isalo II beds (see below).

Of the two new prosauropods, one most resembles *Azendohsaurus* from the Carnian Argana Formation of Morocco (*10*). The Malagasy taxon is known from several maxillae and dentaries (Fig. 1A); it is referred to the Prosauropoda on the basis of the following synapomorphies (*10*): (i) a downward curvature of the anterior dentary, (ii) a robust dorsal process of maxilla, with its base located in the anterior third of the bone, and (iii) a series of small nutrient foramina on the medial face of the maxilla. Furthermore, it shares the following derived characters with *Azendohsaurus* (*10*): (i) prominent longitudinal keel on the medial face of the maxillary, (ii) fossa on the medial face of the maxilla posterior to the dorsal fossa, (iii) a neck between the crown and root of teeth consistently present, and (iv) anteroposterior expansion of crowns always beginning at their bases. There are differences between the jaws and teeth of the Isalo II and Moroccan material: (i) a maxillary tooth count of 11 to 13, as opposed to 15 or 16 in *Azendohsaurus*, (ii) the presence of prominent wear facets on the maxillary teeth (absent in *Azendohsaurus*), and (iii) the presence of an attenuate, caudoventrally projecting posterior process on the maxilla (absent in *Azendohsaurus*). We defer assigning the Malagasy form to *Azendohsaurus* or a new taxon, awaiting the anticipated recovery of more complete material.

The second basal Isalo II dinosaur (Fig. 1B) is also a prosauropod. Its tooth morphology (elongate crowns and tightly packed teeth lacking expanded crowns) is distinct from that of the other Isalo II prosauropod and *Azendohsaurus*. This kind of dentition typifies most other prosauropods, including anchisaurids such as *Sellosaurus* (*11*) and *Thecodontosaurus* (*12*).

The basal Isalo II dinosaurs are most remarkable for their great antiquity. The horizon's age is now better constrained biostratigraphically, permitting temporal correlation to other terrestrial faunas worldwide. Rhynchosaurs and dicynodonts are not known elsewhere after the Carnian [early Late Triassic (*13*)], whereas prosauropods and sphenodontians are not known elsewhere before the Carnian (*13*), suggesting an undifferentiated Carnian age at a minimum (Fig. 2) and an approximate temporal correlation to the Ischigualasto Formation of Argentina [generally considered to be middle or late Carnian in age, on the basis of faunal evidence (*3*, *13*)], which hosts the most complete early dinosaurs known.

Given that the basal Isalo II fauna is at least as old as Carnian, previously undocumented taxon co-occurrences provide evidence that it is either older than other dinosaur-bearing faunas worldwide or represents a unique Carnian fauna preserving the latest occurrences of several other taxa. The pres-

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ence of at least three traversodontid (*14*) eucynodonts in the Isalo II fauna matches pre-Carnian diversity levels for this group but exceeds that of middle Carnian and later faunas. In particular, fragmentary dental remains closely resembling Middle Triassic forms from Tanzania (*15*) were recovered, as were cranial material of a new taxon (*2*) (Fig. 3) and one similar to the Middle Triassic (Ladinian) South American *Massetognathus* (*16*). The basal Isalo II thus records the only known co-occurrence of a taxon near *Massetognathus* (and other eucynodonts) plus dinosaurs, suggesting either that these beds hold (i) the youngest known record of various eucynodonts (and a rhynchosaur basal to Carnian forms; see below) or (ii) dinosaurs predating the Ischigualasto Formation in Argentina, generally considered the earliest dinosaur-bearing formation because of associated radioisotopic dates (*3*).

Additional evidence favors the latter alternative, that the basal Isalo II beds mark the earliest occurrence of dinosaurs, as the likelier explanation of these taxic co-occurrences. Several plesiomorphic features in *Isalorhynchus* support its exclusion from a clade encompassing all Carnian rhynchosaurs [that is, that it represents either a form basal to, or the nearest outgroup of, hyperodapedontines—depending on that name's definition—possibly predating the Carnian radiation of the rest of that clade (*7*, *9*)]. One of the new basal Isalo II traversodontids (Fig. 3) is the plesiomorphic outgroup to *Scalenodontoides* + *Exaeretodon* (*2*), the earliest occurrence of the latter taxon being Ladinian (*17*–*20*). A pre-Carnian age may also be indicated by the absence of aetosaurs, which first appear (typically abundantly) in the Carnian (*13*, *21*). Collectively, this evidence (Fig. 2) suggests that either a Middle Triassic or early Carnian (rather than middle or late Carnian) age for the fauna is likely, and the basal Isalo II beds may represent a stratigraphic interval not well sampled previously by a continental tetrapod assemblage.

Thus, the basal Isalo II fauna is Carnian or older in age, making its prosauropods among the oldest dinosaurs known. Moreover, they represent the oldest (and only Triassic) dinosaurs known from Madagascar. A more precise temporal placement of the basal Isalo II fauna relative to other early dinosaur faunas worldwide awaits more complete biostratigraphic analysis of the other elements of this rich assemblage.

As mentioned, the basal Isalo II beds are yielding an assemblage of biostratigraphically informative eucynodonts, including a skull and mandibles (UA-10601; Fig. 3) representing a new taxon closely allied to *Exaeretodon*, *Scalenodontoides*, and *Gomphodontosuchus* (*2*, *17*–*18*, *22*–*25*). Membership of these and other taxa in a basal clade of eucynodonts—usually termed Traversodontidae (*14*)—is currently disputed [for example, (*18*) versus (*19*)]. UA-10601 possesses several derived cranial and dental features typical of traversodontids (*18*, *20*), but it clearly differs from other members of the clade in a unique combination of primitive and derived characters (*2*) (Fig. 3).

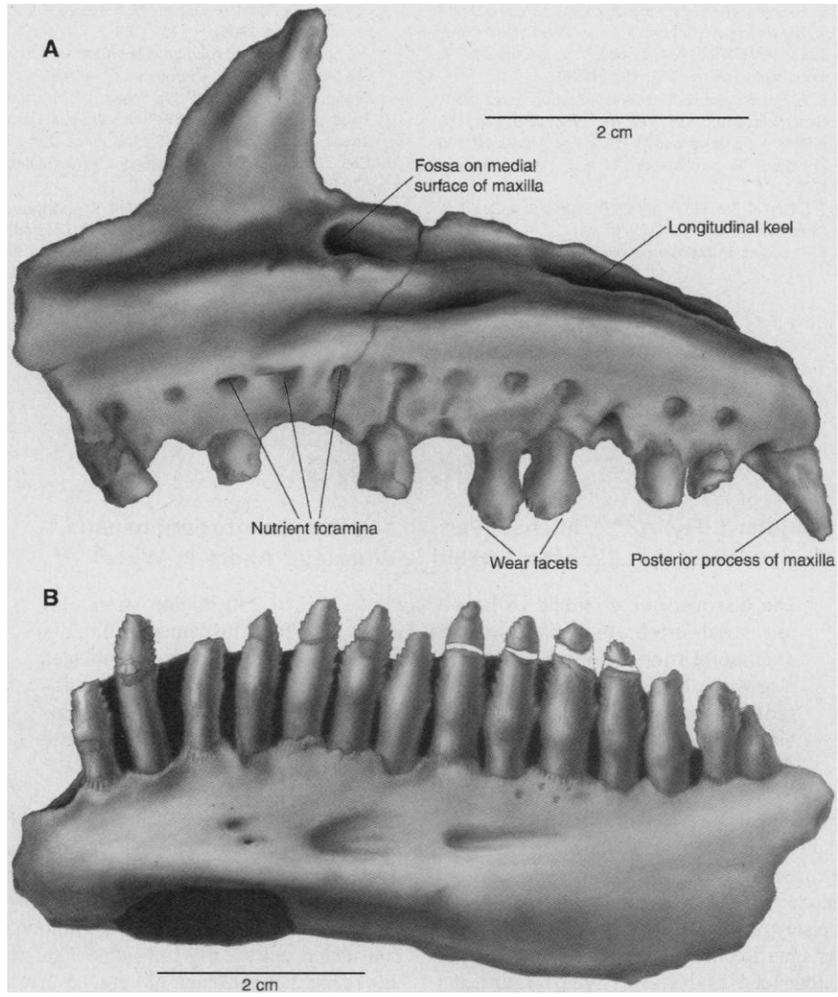

Fig. 1. Medial view of prosauropod right maxilla (UA-10603) from the basal Isalo II beds, closely allied to *Azendohsaurus* (*10*) from the Argana Formation (Carnian) of Morocco (**A**). Second basal Isalo II prosauropod, displaying a more "typical" prosauropod dentition, currently known from partial left dentary (UA-10604); lateral (buccal) view is shown (**B**).

A restricted phylogenetic analysis (*26*) of a subset of early eucynodonts indicates that UA-10601 is the nearest outgroup to *Scalenodontoides* + *Exaeretodon*. The earliest occurrence of *Exaeretodon* is the Ladinian (late Middle Triassic) portion of the Santa Maria Formation of Brazil (*17*–*20*), consistent with a pre–Late Triassic age for the basal Isalo II fauna.

The presence of unique taxa such as *Isalorhynchus* and the new eucynodonts, as well as the biostratigraphic paradox discussed above, indicates that the basal Isalo II assemblage will prove instrumental in clarifying the important biotic transition (*13*) from the eucynodont-, rhynchosaur-, and pseudosuchian-dominated faunas of the Middle Triassic to the dinosaur-dominated faunas of the latest Triassic.

Complementing the Triassic material discussed above, we discovered Jurassic terrestrial faunas in the Mahajanga Basin [Isalo III, "facies continental" (*4*, *5*), including the oldest tribosphenic mammal (*2*) and the earliest theropod from Madagascar] and in the northern Morondava Basin [Hourcq's (*27*) "série d'Andafia"]. Together, these Triassic-Jurassic faunas attest to the enormous paleontological promise of Madagascar's Isalo "Group".

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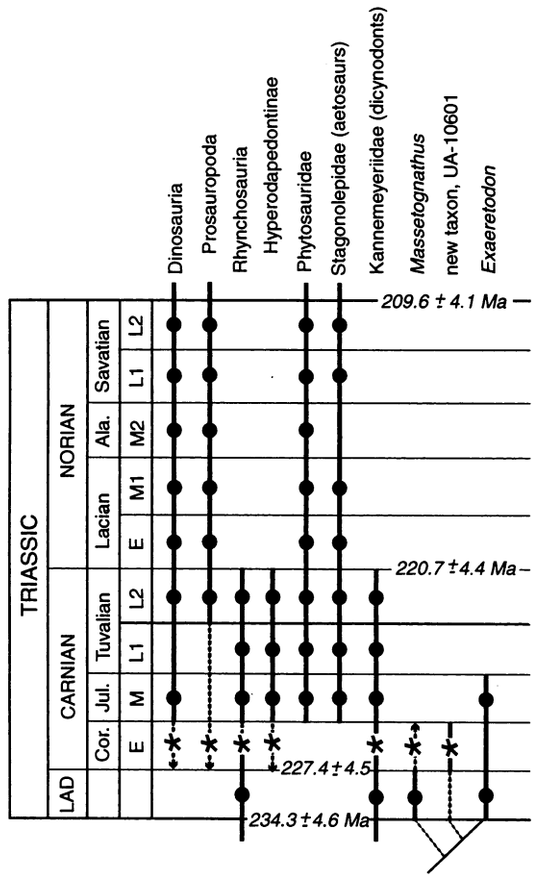

Fig. 2. Temporal information for biostratigraphically informative Middle and Late Triassic nonmarine vertebrate taxa; modified from (*13*) with dates from (*28*). Prosauropoda and Hyperodapedontinae (the Isalo taxon is basal to all Carnian hyperodapedontines) are subgroups within Dinosauria and Rhynchosauria, respectively. Black dots indicate that material of the indicated taxon is known for a temporal interval; asterisks indicate occurrences in the basal Isalo II beds. Dotted lines joining the three taxa (bottom right) indicate phylogenetic relationships of these synapsids (see text). On the basis of this biostratigraphy, the Isalo II beds are tentatively considered early Carnian (Cor., Cordevolian) in age, although they could be older (see text). The middle Carnian (Jul., Julian) age for Ischigualasto taxa is based on (*3*). Ma, million years ago; Ala., Alaunian

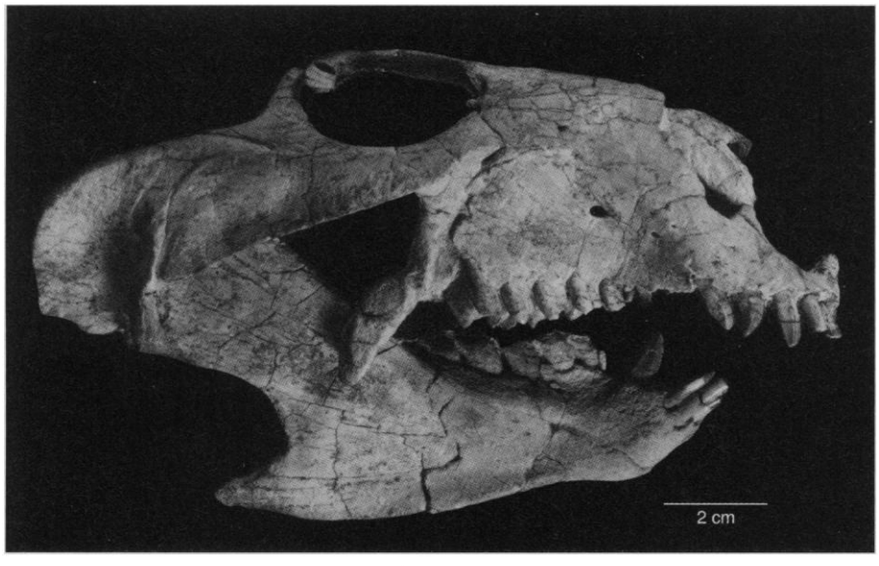

Fig. 3. Traversodontid skull and mandible (UA-10601, University of Antananarivo, Madagascar; length = 15.8 cm) from the basal Isalo II beds, lateral view. Noteworthy features are as follows: there is a small suborbital process of the jugal, the posterior part of the zygomatic arch is shallow dorso-ventrally, the postorbital bar is slender, the thin splint of jugal extends far posteriorly above squamosal, the anterior tip of squamosal forms a sharp point near the level of the ventral orbital rim, and the ventral border of mandible is concave in the region ventral to the diastema. The dental formula is I3/38, C1/1, PC8/6-7.

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References and Notes

[1] **Predatory Dinosaur Remains from Madagascar: Implications for the Cretaceous Biogeography of Gondwana**

Scott D. Sampson; Lawrence M. Witmer; Catherine A. Forster; David W. Krause; Patrick M. O'Connor; Peter Dodson; Florent Ravoavy

Science, New Series, Vol. 280, No. 5366. (May 15, 1998), pp. 1048-1051.

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[3] **The Ischigualasto Tetrapod Assemblage (Late Triassic, Argentina) and ⁴⁰ Ar/ ³⁹ Ar Dating of Dinosaur Origins**

Raymond R. Rogers; Carl C. Swisher III; Paul C. Sereno; Alfredo M. Monetta; Catherine A. Forster; Ricardo N. Martinez

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