THE FIRST DICYNODONT FROM THE LATE PERMIAN OF MALAGASY

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ABSTRACT. Until now, no therapsid was known with any certainty from Malagasy. The present specimen, discovered in 1948, but never described, is the first record of a complete dicynodont skull from this country. A description of the skull is given and it is referred to a new species of the genus Oudenodon. The rarity of dicynodonts in Malagasy may be because of environmental differences from the adjoining landmass of Africa.

RESUMÉ. La présence de théropodes à Madagascar n’avait jamais été montrée avec certitude. Le présent spécimen, collecté en 1948 mais jamais décrit, est la première découverte d’un crâne presque complet de dicynodonte dans cette région. Une description du crâne en est donnée et il est attribué à une nouvelle espèce du genre Oudenodon. La rareté des dicynodontes à Madagascar peut être due aux conditions de milieu, différentes de celles régnant sur la masse continentale africaine contiguë.

The Permo-Triassic of Malagasy, sometimes called the ‘Malagasy Karoo’ is known for the richness of its fossils which have been found in reptile-bearing nodules from the Lower Sakama Formation (Late Permian), (Piveteau 1926, 1957; Carroll 1981; Currie 1981). Reptiles, such as Hovasaurus, Thadeosaurus, Tangasaurus, and Claudiosaurus, are well represented and constitute a typical Malagasy fauna, unknown elsewhere. Until now, except for a fragmentary and unpublished specimen noted by Piveteau (1957), from below the Cistecephalus zone and provisionally referred to as a therapsid, the therapsids did not seem to be represented in this fauna. The abundance of diapsids and the rarity of therapsids characterize the Malagasy Karoo in comparison with the South African Karoo, where therapsids are abundant. However, the study of a new specimen, housed in the collections of the Université Paris 6, confirms the presence of therapsids in the Late Permian of Malagasy.

THE MATERIAL

Locality and material
The specimen was collected in 1948 by François Tordo, a French geologist then working for the Malagasy Petroleum Company. It consists of a partially crushed skull, coming from a locality whose exact position is unknown, between Ranohira and Benenitra (south Malagasy). The skull was in a calcareous nodule from the upper part of the psammitic sandstone constituting the latest part of the Lower Sakama Formation (Late Permian) (Text-fig. 1). The matrix has been removed by acid processing. The skull is nearly complete, but dorsoventrally crushed with a broken skull roof (Text-fig. 2). The bone surface is weathered and sutures are indistinct. The anterior part of the snout is slightly distorted by shearing, and the posterolateral part of the right temporal fenestra is preserved only as a film of bone. The total length of the specimen is 160 mm, and the maximal width is 95 mm. The lower jaw is mostly complete and preserved in situ. The lateral bones of the right ramus and of the posterior part of the left ramus are missing. In the palate, the pterygoids and right basioccipital tuber are visible. The anteriormost part of the palate is not visible. The atlas, axis and three succeeding vertebrae are also preserved.

Description
In dorsal view, the pre-orbital region is short in comparison with the post-orbital, even allowing for distortion (Text-fig. 3a). The postorbitals are large and rise to form a low sagittal crest ending at the level of the pineal foramen. Anteriorly, they are separated by a small shield-shaped preparietal. They constitute the anterior and

medial border of the temporal fenestrae, and all of the posterior edge of the orbital opening. The squamosals are very large, forming the posterior and lateral borders of the temporal fenestrae. Because the skull roof is damaged, the postfrontals are not visible, but their impression persists as a depression. They were elongated, with a triangular shape, and seem to have contacted only the postorbitals. The left prefrontal persists as an elongated bone bordering the antero-superior edge of the orbital opening. The frontals seem to be large, but their anterior limits cannot be determined. Likewise, the narinal area cannot be observed because of the anterior distortion and loss of the snout. The measurements of the temporal fenestrae are as follows: left: length, 58 mm; width, 30 mm; right: length, 59 mm; width, 31 mm.

In lateral view, the general outline of the skull is modified by the dorsoventral crushing (Text-fig. 3c). The specimen is totally edentulous. The maxilla is large and extends vertically. The jugal is antero-posteriorly elongated, forming the inferior and posterior edges of the orbital opening. The mandible is strong, with a thick and high anterior part composed of the dentary. Posteriorly, the mandible is thinner. The articular is divided into lateral and median articulatory condyles.

The ventral view is more difficult to observe (Text-fig. 3b). The palate is largely damaged, and the postero-lateral part of the skull is destroyed. The mandibular symphysis is strong and anteriorly extended. Conversely, the posterior part of each ramus is narrow.

Identification

The short snout, elongate temporal fenestra, large laterally-expanded squamosal, and distinctive articular confirm that this specimen is a dicyonodont. Among the dicyonodonts, this specimen can be compared with the four main Permian genera: Dicynodon, Oudenodon, Dictodon and the rare Kingoria (Cluver and Hotton 1981). Because of the lack of a caniniform tusk, it cannot belong to Dicynodon. The absence of the distinctive square caniniform process indicates that the specimen does not belong to the genus Dictodon. To distinguish between Oudenodon and Kingoria, it is necessary to know the state of certain characters of the lower jaw, in particular whether a dorsal dentary sulcus is present or not. The present specimen does not have the anterior dorsal surface of the jaw ramus completely exposed, but the dorsal edge of the dentary which is visible is sharp-edged.
as would be expected of the medial wall of a dorsal dentary sulcus, as present in *Oudenodon*. Another feature which indicates an assignment to *Oudenodon* is the suggestion of a large palatal exposure of the palatine bone. This would be small in *Diictodon* and *Kingoria*.

King (1988) lists three species of *Oudenodon*. The genotype is *Oudenodon bainii* Owen, 1860, known from South Africa. *O. grandis* (Haughton 1917) is also from South Africa, while *O. huangwensis* (Boonstra 1938) is known from Zambia (Keyser 1975).

The present specimen presents two features which distinguish it from the known species of *Oudenodon*. First, the lateral dentary shelf is drawn up into a pronounced boss anteriorly which is continued postero-ventrally as a sharp ridge (Text-fig. 3c). Secondly, the posterior edge of the mandibular fenestra is drawn up into a blunt ridge oriented antero-ventrally, forming an anterior shelf to the reflected lamina of the angular (Text-fig. 3c). On account of these features the present specimen is assigned to a new species of *Oudenodon*.

**SYSTEMATIC PALAEONTOLOGY**

Suborder ANOMODONTIA Owen, 1859  
Infraorder DICYNODONTIA Owen, 1859  
Superfamily PRISTERODONTOIDEA Cluver and King, 1983  
Family DICYNODONTIDAE Cluver and King, 1983  
Subfamily CRYPTODONTINAE Owen, 1859  
Genus Oudenodon Owen, 1860

*Diagnosis.* Given by King (1988).
TEXT-FIG. 3. Oudenodon sakamenensis, Late Permian, south Malagasy. Type specimen PVHR 288. a, Dorsal view; b, ventral view; c, right lateral view.
Oudenodon sakamenensis sp. nov.

Text-figures 2 and 3

Etymology. From Sakama, the name of the Formation and of the river which crosses this area.

Holotype. Nearly complete skull, PVHR 288, preserved at the Laboratoire de Paléontologie des Vertébrés de l'Université Paris 6.

Type locality. Between Ranohira and Benenitra, South-western Malagasy.

Horizon. Top of the Lower Sakama Formation, Late Permian.

Diagnosis. Medium to small member of the genus, skull longer than broad. Lower jaw with lateral dentary shelf drawn up into a boss anteriorly and extending postero-ventrally as sharp-edged ridge; reflected lamina of angular bearing a pronounced blunt shelf anteriorly.

PALEOBIOBIOGEOGRAPHICAL SIGNIFICANCE

Dicynodonts are known from South Africa, eastern Africa, Morocco, India, China, Antarctica, Europe, USSR, and North and South America, but until now had not been reported from Malagasy. Oudenodon is known from South Africa, Zambia and, now, Malagasy. In South African localities, dicynodonts are very abundant fossils, and Oudenodon is a common genus from Cistecephalus Zone localities, and even more so in the succeeding Daptocephalus Zone (King 1986). It is therefore puzzling that these abundant therapsids should be found so rarely in the otherwise reptile-rich fauna of Malagasy.

Two alternative explanations present themselves. First, that Malagasy was separated from South and East Africa by some kind of barrier (sea, mountain) during the Late Permian, preventing easy migration of dicynodonts to Malagasy. In this case, an impoverished dicynodont fauna, composed of species very distinct from the mainland forms, would be expected. This explanation can be dismissed for two reasons. First, it is known that Malagasy was part of the same landmass as Africa during the Late Permian. There was no ocean barrier to migration, and no evidence of other kinds of barrier. Secondly, although the present Malagasy dicynodont is specifically distinct from mainland African forms, it is not particularly different, and no more different than is the Zambian Oudenodon from the South African.

The second explanation to account for the rarity of therapsids in Malagasy is that the conditions of fossilisation there were very different from those in South Africa. This has been suggested by Piveteau (1926), Currie (1981) and Carroll (1981). This would imply that the habitats in which dicynodonts and other therapsids were abundant in South Africa were not those habitats which have been sampled in the Malagasy sediments. There are some indications that some of the Malagasy diapsids coming from the same locality (Hovasaurus, Claudiosaurus) were aquatic or semi-aquatic (Currie 1981; Carroll 1981; de Buffrénil and Mazin 1989), and it may, therefore, be that dicynodonts were occupying more terrestrial environments which are not sampled in these Malagasy localities. By contrast, South African localities, where no similar small diapsid assemblages are known, may represent the more terrestrial (or less aquatic) habitats. Further sedimentological and palaeontological sampling of contemporaneous localities in Malagasy, and functional anatomical study of the fossils they contain, is needed before this conclusion can be substantiated.

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ABBREVIATIONS USED IN TEXT-FIGURES

ang: angular; art: articular; b.o.t: basioccipital tuber; d: dentary; f: frontal; FT: temporal fenestra; j: jugal; l: lachrymal; l.d.s.: lateral dentary shelf; m: maxilla; ORB: orbital opening; p: palatal; p.f: pineal foramen; p.o: postorbital; p.p: postparietal; pfr: prefrontal; p.t: pterygoid; q: quadrate; q.j: quadratojugal; r: ridge; spl: splenial; s.q: squamosal.