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The phylogenetic position of *Isalorhynchus genovefae*, a Late Triassic rhynchosaur from Madagascar

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Abstract — New specimens of the rhynchosaur *Isalorhynchus genovefae* Buffetaut, 1983, have been found in the Makay Formation (Late Triassic of the Morondava Basin), Malio River area, southwest Madagascar. The material includes several maxillae as well as the first known rhynchosaur dentaries from the region. The maxilla bears a single longitudinal groove, with fewer than three longitudinal tooth rows both medial and lateral to it. The dentary possesses a single blade, with an additional row of teeth on its lingual surface. A phylogenetic study, based on the morphological features possible to measure for *Isalorhynchus*, as well as on previous cladistic analysis of Rhynchosauria, showed that the Malagasian rhynchosaur is nested within the genus *Hyperodapedon*, and a new combination – *H. genovefae* – is proposed. The phylogenetic study also depicts clear trends in the tooth evolution of Late Triassic rhynchosaurs, with the reduction of the medial structures in relation to the lateral ones, in both maxilla and dentary. © 2000 Éditions scientifiques et médicales Elsevier SAS

Madagascar / Rhynchosaurs / Triassic / *Hyperodapedon* / *Isalorhynchus genovefae*

Résumé — La position phylogénétique d'*Isalorhynchus genovefae*, rhynchosaure du Trias supérieur de Madagascar. De nouveaux spécimens du rhynchosaure *Isalorhynchus genovefae* Buffetaut, 1983, ont été découverts dans la formation Makay (Trias supérieur du bassin de Morondava), près de la rivière Malio, dans le sud-ouest de Madagascar. Le matériel comprend plusieurs maxillaires ainsi que les premiers dentaires de rhynchosaures découverts dans la région. Le maxillaire possède un seul sillon longitudinal, avec une ou deux rangées longitudinales de dents de chaque côté. Le dentaire possède une rangée de dents formant une lame sur la face occlusale de l'os, avec une rangée supplémentaire de dents sur sa face linguale. Une étude phylogénétique, basée sur les caractères morphologiques qu'il est possible de

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déterminer chez *Isalorhynchus*, couplée avec une analyse cladistique antérieure de l'ensemble des Rhynchosauria, indique que le rhynchosaure malgache se situe au sein même du genre *Hyperodapedon*, et une nouvelle combinaison – *H. genovefae* – est donc proposée. L'étude phylogénétique met également en évidence des tendances claires dans l'évolution de la denture des rhynchosaures du Trias supérieur, avec la réduction des structures médiales par rapport à celles latérales, à la fois sur le maxillaire et le dentaire. © 2000 Éditions scientifiques et médicales Elsevier SAS

Madagascar / Rhynchosaures / Trias / *Hyperodapedon* / *Isalorhynchus genovefae*

INTRODUCTION

Since the beginning of the twentieth century [52], research on Permo-Triassic tetrapods in Madagascar has been focused on the deposits of the Sakamena Group (Morondava Basin) in the southern part of the island. Late Permian rocks of the Lower Sakamena around Mount Eliva and Benenitra (*figure 1*) have yielded a very rich diapsid fauna, including the aquatic younginiformes *Hovasaurus*, *Thadeosaurus*, and *Acerosodontosaurus* [19, 26, 27], the probable early sauropterygian *Claudiosaurus* [19], and the gliding reptile *Coelurosauravus* [18]. These strata have also yielded a single synapsid taxon, the dicynodont *Oudenodon sakamenensis*, collected from an unknown locality between Benenitra and Ranohira [50]. Upper strata of the Sakamena Group, in the area of Ranohira (*figure 1*), yielded the owenettid procolophonoid *Barasaurus* [51, 53], as well as a probable rhinesuchid temnospondyl [52]. The age of these rocks is debatable, and they have been tentatively referred to as Late Permian to earliest Triassic [1, 6, 25, 52]. In the northern part of Madagascar, the ammonite beds of the Diego Basin have yielded a diverse fauna of Early Triassic age [6]. These deposits bear well known temnospondyls, including trematosaurids, rhytidosteids, lydekkerinids, and capitosaurids [35], a probable younginiform [46], as well as the early salientian *Triadobatrachus* [56].

Mid-Late Triassic deposits in Madagascar, by contrast, have produced comparatively few tetrapods. Fragmentary remains attributable to phytosaurs and to a metoposaurid temnospondyl were described from what are presumed to be Late Triassic rocks [28, 34, 65], in particular from deposits near Folakara, in the northwestern part of the island (*figure 1*). In addition, the southern part of the Morondava Basin yielded the rhynchosaur *Isalorhynchus genovefae* [16], which is the subject of the present work.

Isalorhynchus is based on very fragmentary remains found in the former collection of the laboratoire de paléontologie de l'université Paris-VI, but their exact provenance is unknown. Buffetaut [16] relied on indications found on the labels of

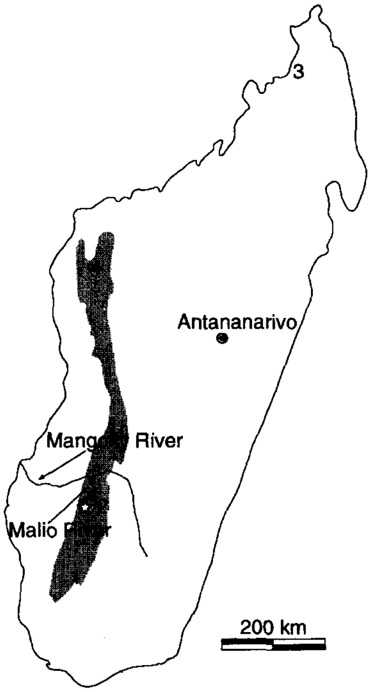

Figure 1. Map of Madagascar depicting the outcrop area (shading) of the Karroo deposits (Upper Carboniferous to Upper Triassic) of the Morondava Basin; modified from Razafimbelo [57]. The white star indicates the approximate location of the two prospected fossil sites. Numbers indicate other main Permo-Triassic tetrapod bearing areas in the island: **1**. Mount Eliva and Benenitra. **2**. Ranohira. **3**. Diego Basin. **4**. Folakara.

Figure 1. Carte de Madagascar montrant l'extension (en gris) des affleurements du Karroo (du Carbonifère supérieur au Trias supérieur) dans le bassin du Morondava ; modifié d'après Razafimbelo [57]. L'étoile blanche montre l'emplacement approximatif des deux sites fossilifères prospectés. Les chiffres indiquent les autres sites ayant livrés des tétrapodes sur l'île. **1**. Mont Eliva et Benenitra. **2**. Ranohira. **3**. Bassin de Diego. **4**. Folakara.

the material, which assigned the base of the Isalo II beds, Malio River (southwest Madagascar) as the source area of the specimens.

Recently, a much better picture of the Gondwanan stratigraphy in the Morondava Basin was provided by Razafimbelo [57]. The former Isalo II beds were renamed as the Makay Formation, which comprises the rocks outcropping in the Malio River area. Moreover, palynological studies in the Makay Formation confirmed the Late Triassic (Carnian) age of this stratigraphical unit, which shares a very similar palynoflora with Mediterranean and Western Australian strata of that age [57].

In spring 1996, fieldwork carried out by G.C. and L.B., together with Eugène Razafimbelo and Jean-Gilbert Rakotondratsimba from the University of Antananarivo, explored the Upper Triassic deposits of the Malio River area (Ihosy District, west of the Isalo National Park). Two fossil-bearing sites were found in the variegated marls of the Makay Formation near the village of Bereketa (*figure 1*). The first one, situated 2 km south of Bereketa on the west bank of the Malio River, yielded many rhynchosaur remains and a jaw fragment of a procolophonid. The remains were found scattered on the ground, but the exact fossiliferous layer could not be located. The second site, 5 km to the north of Bereketa, still on the west bank of the Malio river, only yielded unidentified reptile bones.

The fact that most of the bone remains recovered from the Makay Formation belong to rhynchosaurs is not unexpected, since these reptiles were the dominant first-level consumers in most terrestrial Carnian palaeocommunities, and very common in rocks of this age all around the world [7, 12, 13]. The newly collected rhynchosaur specimens comprise cranial fragments, including several maxillae and the first known rhynchosaur dentaries from the area, as well as postcranial remains. In the light of these new findings, this study provides descriptive notes on the anatomy of the Malagasian rhynchosaur, and deals with its phylogenetic position and taxonomic affinities. This is a question that, due to the scarcity of the material available until now, has not been satisfactorily answered in various previous accounts about rhynchosaur taxonomy [10, 29, 66].

More recently, a much richer tetrapod assemblage was reported in the southern part of the Morondava Basin [31, 32]. This fauna includes rhynchosaurs as well as procolophonids, prosauropod dinosaurs, sphenodontians, kannemeyeriid dicynodonts, traversodontid cynodonts, and 'eosuchians', and was tentatively dated as late Middle to early Late Triassic [32]. Based on the geographical coordinates provided by Flynn et al. [32], it seems that the new fossil localities are about 30–40 km west of the Malio River. Unfortunately, there is no direct evidence that the rocks outcropping in that area are from the same strata that yield the rhynchosaur specimens presented here.

DESCRIPTIVE ACCOUNTS

In total, the rhynchosaur material described by Buffetaut [16] and the newly collected remains represent about 40 identifiable specimens, including parts of three premaxillae, 14 maxillae, one basioccipital, four dentaries, several vertebrae, and some appendicular elements, including humera and an isolated astragalus. A femur referred to *Isalorhynchus* by Buffetaut [16] is of dubious affinity and may not belong to a rhynchosaur.

Whatley [67], based on a preliminary study of more complete specimens, suggested the presence of two rhynchosaur taxons in the Triassic deposits of the Morondava Basin. Yet, no indication of such diversity was found in the present study, and all the specimens are treated as belonging to a single taxon. This taxon is supposed to be *I. genovefae*, due to the presence of unique features (medial tooth-bearing area composed of fewer than three tooth rows and lateral tooth bearing area with a lateral edentulous platform) in the holotype and other maxillae. The assignment of other skeletal elements to that taxon is also suggested here, but this is not supported by the presence of autapomorphies.

This contribution focuses on skeletal elements of the Malio River rhynchosaur that are taxonomically important, according to the current orthodoxy in rhynchosaur classification: the maxilla, the dentary and the tarsus. The specimens described by

Buffetaut [16] are now housed at the Musée des Dinosaures, Esperaza, France (MDE), and the specimens collected in the 1996 expedition belong to the Antananarivo University, Antananarivo, Madagascar, being referred to here by their field numbers, preceded by the acronym MAL-1996.

Maxillae

Buffetaut [16] defined an almost complete maxilla (MDE-R18) as the holotype of *Isalorhynchus genovefae*, and also assigned the lateral portion of another one (MDE-R19) to that taxon. In 1996, a total of 12 additional maxillae and maxillary fragments were collected, allowing a much more accurate understanding of the morphology of this bone in *Isalorhynchus* (*figure 2, plate IA-E, table I*).

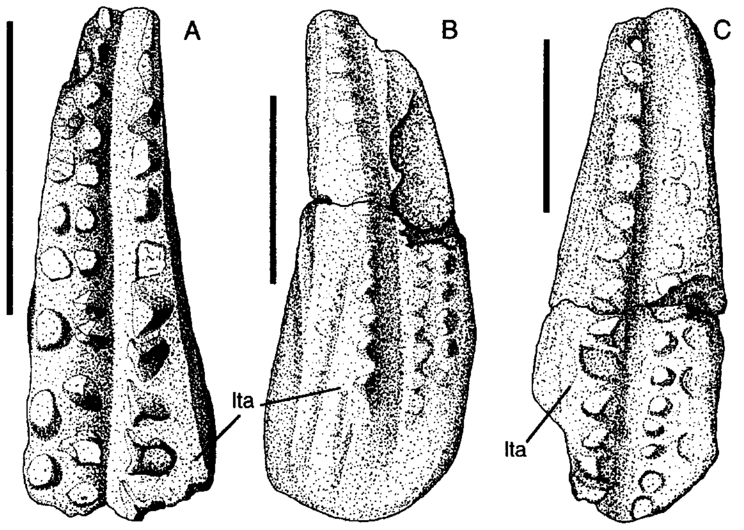

Figure 2. Maxillae of *Isalorhynchus genovefae* in ventral view.
A. MDE-R18 (holotype), left maxilla.
B. MAL-1996 1, right maxilla.
C. MAL-1996 2, right maxilla.
lta. Lateral toothless area.
Scale bar equals 20 mm.

Figure 2. Maxillaires d'*Isalorhynchus genovefae* en vue ventrale.
A. MDE-R18 (holotype), maxillaire gauche.
B. MAL-1996 1, maxillaire droit.
C. MAL-1996 2, maxillaire droit.
lta. Surface latérale édentée.
La barre d'échelle représente 20 mm.

Table I. Measurements of the twelve best-preserved maxillae of *Isalorhynchus genovefae*. **TW**: maximum width on the maxilla (mm); **LW**: Width of the lateral area of the maxilla (mm); **LT**: Number of longitudinal tooth rows in the lateral area of the maxilla; **MW**: Width of the medial area of the maxilla (mm); **MT**: Number of longitudinal tooth rows in the medial area of the maxilla. Bones with only the anteriormost portion preserved indicated by asterisk, uncertain measurements given as "?".

Tableau I. Mesures des douze maxillaires les mieux préservés d'*Isalorhynchus genovefae*. **TW** : largeur maximale du maxillaire en mm ; **LW** : largeur de la surface latérale du maxillaire en mm ; **LT** : nombre de rangées longitudinales de dents sur la surface latérale du maxillaire ; **MW** : largeur de la surface médiale du maxillaire en mm ; **MT** : nombre de rangées longitudinales de dents sur la surface médiale du maxillaire. Les os dont seule la partie la plus antérieure est préservée sont indiqués par un astérisque, les mesures estimées sont signalés par un « ? ».

Specimen	TW	LW	LT	MW	MT
MDE-R18	14	8	1	6	2
MDE-R19	?	8	2	?	?
MAL-1996 1	24	14	1	10	2
MAL-1996 2	22,5	14	1	8,5	2
MAL-1996 3	21	13	1	8	2
MAL-1996 4	19	10	1	9	?
MAL-1996 5	17,5	? 11	2	? 6,5	?
MAL-1996 6	16	9	2	7	2
MAL-1996 7*	13	7	1	6	1
MAL-1996 9*	17	9	1	8	1
MAL-1996 10	14	8	1	6	2
MAL-1996 14	18	?7	?2	?11	?2

Based on these specimens, it is possible to confirm that the holotype of *Isalorhynchus* (MDE-R18) belongs to a subadult individual, as already suggested by Buffetaut [16]. Two of the maxillae collected in 1996 (MAL-1996 1 and MAL-1996 2) are approximately 70 % wider than the holotype, and show signs of more advanced tooth wear. These specimens are, in fact, not as big as some described rhynchosaur maxillae [21, 62], but can be referred to an average adult sized rhynchosaur when compared to maxillae from the Late Triassic of Santa Maria and Ischigualasto Formations of South America (M.L., personal observation).

In *Isalorhynchus*, as in all other Mid-Late Triassic rhynchosaurs, the maxilla consists of a blunt body, the ventral surface of which bears teeth, and a thin anterolateral ascending process. The ascending process is not entirely preserved in any of the maxillae collected in the Malio River, but its presence can be attested by its basal portion, preserved in the dorsolateral part of the anterior side of some of these bones. The heavily-built ventral portion of the maxilla is triangular in ventral view, tapering anteriorly. The tooth-bearing area is convex ventrally, with the medial margin convex and the lateral concave. The ventral surface is divided into lateral and medial areas by a longitudinal groove. The groove extends along the entire length of the bone, and received the dentary blade during occlusion. In all but one of the studied maxilla (*table I*), the lateral area is wider than the medial.

The maxillae of *Isalorhynchus* bear teeth both laterally and medially to the longitudinal groove. As in other Mid-Late Triassic rhynchosaurs, there are two different types of teeth: a pyramidal type and a conical type [9]. The lateral area of the maxilla bears several teeth, which are organised in one or two longitudinal rows (cf. [21], fig. 12a). In the specimens with two rows, the lateral one is reduced, composed of fewer than three teeth that are restricted to the posterior portion of the bone. The medial longitudinal row, on the other hand, is much more developed. It includes about 15 teeth in the larger specimens, and extends along the entire length of the maxilla. All teeth of the medial row are of the pyramidal type, and this also seems to be true for the ones of the reduced lateral row.

A row of pyramidal teeth laterally adjacent to the maxillary groove is a well known feature of Late Triassic rhynchosaurs, having been recognised in specimens from different geographic areas [3, 8, 21, 62]. The extreme lateral part of the maxilla of *Isalorhynchus* is, however, distinctive. It presents a narrow edentulous platform (*figure 2, plate IA–E*), while other Late Triassic rhynchosaurs show this part of the bone covered with conical teeth.

The medial maxillary area also bears one or two longitudinal rows of teeth. Specimens with one row are, however, incomplete, and *Isalorhynchus* probably possessed a count of two tooth rows in that maxillary area. This number is unusually small, when compared to other Mid-Late Triassic rhynchosaurs [4, 8, 10, 21, 45]. The medialmost row is composed of typical conical teeth, but the shape of the teeth of the lateralmost row is uncertain. In smaller specimens (including the holotype, MDE-R18) those teeth are pyramidal, though much smaller than the pyramidal teeth of the lateral area of the maxilla. In larger specimens, however, a clear pyramidal morphology is not found, possibly due to wear.

Dentary

All four known dentaries of *Isalorhynchus* are incomplete, and only MAL-1996 8 is well-preserved enough to be described (*plate IF*). As in all Late Triassic rhynchosaurs, the dorsal surface of this bone bears a well developed longitudinal cutting blade composed of a single row of small packed teeth [4, 8]. This blade is placed on the lateral border of the dentary, and is more developed posteriorly.

The lingual surface of the dentary presents a prominent longitudinal ridge as in other Late Triassic rhynchosaurs [9, 45]. This ridge bears a longitudinal row of teeth, five of which are preserved in MAL-1996 8. These lingual teeth are conical, larger than the teeth of the blade, and more spaced out. The whole dorsal portion of the dentary occluded with the maxillary groove, as indicated by the extensive signs of wear in the teeth of both the blade and lingual surface of the dentary.

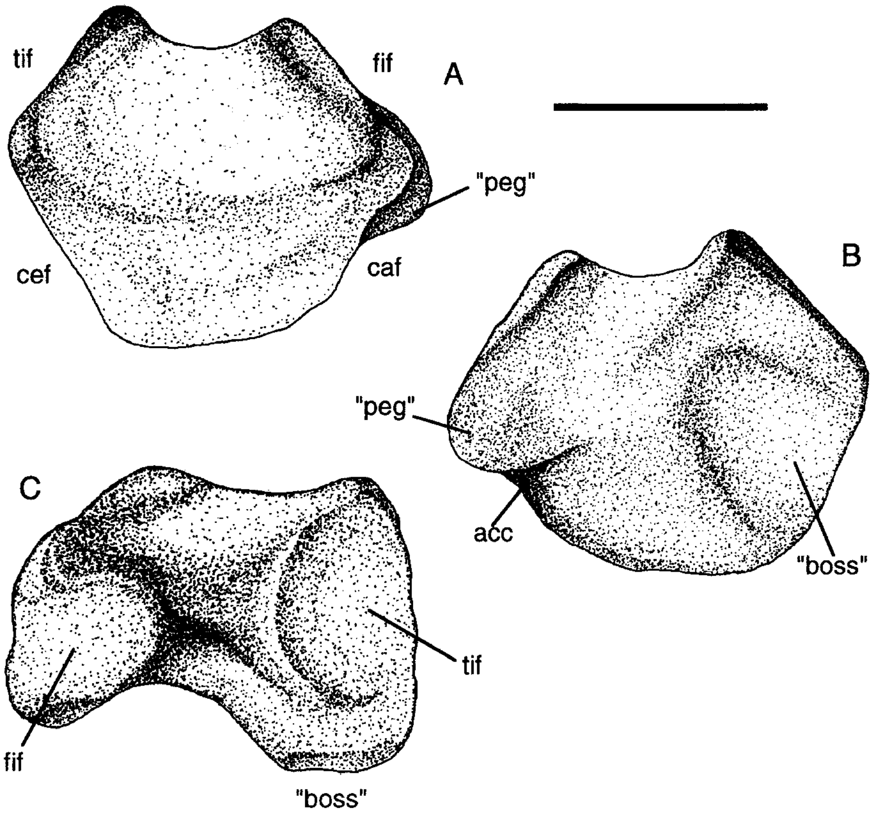

Figure 3. Left astragalus of *Isalorhynchus genovefae* MDE-R20.
A. Anterior view.
B. Posterior view.
C. Proximal view
acc. Astragalocalcaneal canal.
caf. Calcaneal articular facet.
cef. Centrale articular facet.
fif. Fibular articular facet.
tif. Tibial articular facet.
See Hughes [40] for discussion on the "peg" and "boss".
Scale bar equals 10 mm.

Figure 3. Astragale gauche d'*Isalorhynchus genovefae* MDE-R20.
A. En vue antérieure.
B. En vue postérieure.
C. En vue proximale.
acc. Canal astragalocalcanéen.
caf. Facette articulaire pour le calcanéum.
cef. Facette articulaire pour le central.
fif. Facette articulaire pour la fibula.
tif. Facette articulaire pour le tibia.
Voir Hughes [40] pour une discussion du *peg* et *boss*.
La barre d'échelle représente 10 mm.

Astragalus

An isolated left astragalus (MDE-R20) was comprehensively described by Buffetaut ([16]; p. 471 – intermédiaire), and is so far the best preserved tarsal element known for *Isalorhynchus (figure 3)*. It presents the typical morphology of a Mid-Late Triassic rhynchosaur astragalus [21, 40], with an anterior surface that is concave dorsally, a posterior boss, and clear articular facets for the tibia, fibula, calcaneum and centrale. The tarsus includes, therefore, three proximal elements, and the centrale must have been as big as the same element of other Late Triassic forms, since its articular facet is the largest on the astragalus. The tibial and fibular facets are smaller, and separated from each other by a marked thin ridge (*figure 3c*). The articular facet for the calcaneum faces latero-distally and is U-shaped. The posterior excavation in this articular facet, that borders the astragalar 'peg' distally (*figure 3b*), is homologous to the astragalocalcaneal canal of *Prolacerta* and *Proterosuchus* [30], but it is probably not perforated as in those basal archosauromorphs.

CLADISTIC STUDY

Buffetaut [16] accepted *Isalorhynchus* as somehow intermediate between Middle Triassic rhynchosaurs such as *Rhynchosaurus* and Late Triassic forms such as *Hyperodapedon*. More recent studies usually include *Isalorhynchus* within the highly derived Late Triassic Hyperodapedontinae sensu Benton, 1983 [10, 41], but some suggest possible links to Middle Triassic forms [29, 66].

The only clear consensus, present in all previous phylogenetic accounts about the taxon, is that *Isalorhynchus* is more derived than *Mesosuchus* and *Howesia*, the Early Triassic rhynchosaurs of the Karroo Supergroup of South Africa. Some morphological features of *Isalorhynchus* support this affinity, such as the absence of premaxillary teeth and the large size of the centrale (based on its articular facet on the astragalus). The key feature is, however, the jaw apparatus composed of maxillary grooves that occlude against dentary blades, structures only known in Mid-Late Triassic rhynchosaurs.

In order to define the phylogenetic position of *Isalorhynchus*, a series of both new and previously defined morphological transformation series are used, and the distribution of the characters among the better known Mid-Late Triassic rhynchosaurs is discussed. The transformation series were scored according to the adult morphology of these rhynchosaurs, in order to avoid the consideration of ontogenetic related morphological variations, which seem to be present at least in the jaw apparatus. Moreover, only transformation series which could be defined for *Isalorhynchus* were included in the analysis. Therefore, it is clear that this study is designed to define the position of *Isalorhynchus* within Rhynchosauria, and not to depict the whole evolution of this group during the Mid-Late Triassic.

Firstly, however, a homology hypothesis regarding the tooth arrangement of the Mid-Late Triassic rhynchosaurs must be defined, which will be applied in the transformation series discussed here. All rhynchosaurs with a single maxillary ventral groove also bear a single dentary blade that obviously slotted into that groove. The Brazilian rhynchosaur *Hyperodapedon huenei*, however, possesses a single dentary blade and two maxillary grooves [45]. In this form, the single dentary blade occludes with the lateral maxillary groove, which is also much larger than the medial. Therefore, it is suggested that the maxillary groove of the single-grooved rhynchosaurs is homologous to the lateral groove of the forms with two-grooved maxillae (which is termed the "main" or "cutting" groove). Along with this definition follow the homologies of all tooth-bearing areas lateral and medial to the maxillary grooves.

Transformation series used in the analysis

1. Maxillary area lateral to the main groove. 0 – crest-shaped, just wide enough to bear one or two longitudinal tooth rows; 1 – cushion-shaped, with a ventral surface enlarged enough to bear several longitudinal tooth rows (figure 4). In the Middle Triassic rhynchosaurs, including *Rhynchosaurus* and *Stenaulorhynchus*, the maxillary area lateral to the main groove is crest-shaped, a morphology also seen in "*Scaphonyx*" *sulcognathus* [2, 9, 10]. This part of the maxilla is much narrower than that medial to the main groove, and usually bears only one or two longitudinal rows of teeth. All other rhynchosaurs analysed herein present a much enlarged lateral area of the maxilla, which forms a cushion-shaped ventral surface. In the majority of the Late Triassic rhynchosaurs, this area bears at least three longitudinal tooth rows in juvenile and small specimens [8, 21, 39] and up to six in large adults [21, 45, 59]. *Isalorhynchus* also shows an enlarged cushion-shaped lateral maxillary area, which is almost as wide as the medial one, although fewer than three tooth rows are present (see transformation series 2).

2. Number of longitudinal tooth rows in the maxillary area lateral to the main groove. 0 – one or two; 1 – more than two (figure 4). As discussed above, *Rhynchosaurus* and *Stenaulorhynchus*, show only one or two longitudinal rows of teeth lying lateral to the main maxillary groove [9, 10]. "*Scaphonyx*" *sulcognathus* seems to present an increase in the number of those teeth, but most of the specimens do not possess more than two longitudinal tooth rows in the lateral maxillary area. The majority of Late Triassic rhynchosaurs, on the other hand, present at least three longitudinal tooth rows in the lateral area of the maxilla, implanted in the cushion-shaped tooth-bearing area [8, 21, 39, 62]. The medialmost of these rows is usually composed of pyramidal teeth, while the others are conical [3, 8, 21, 45, 62].

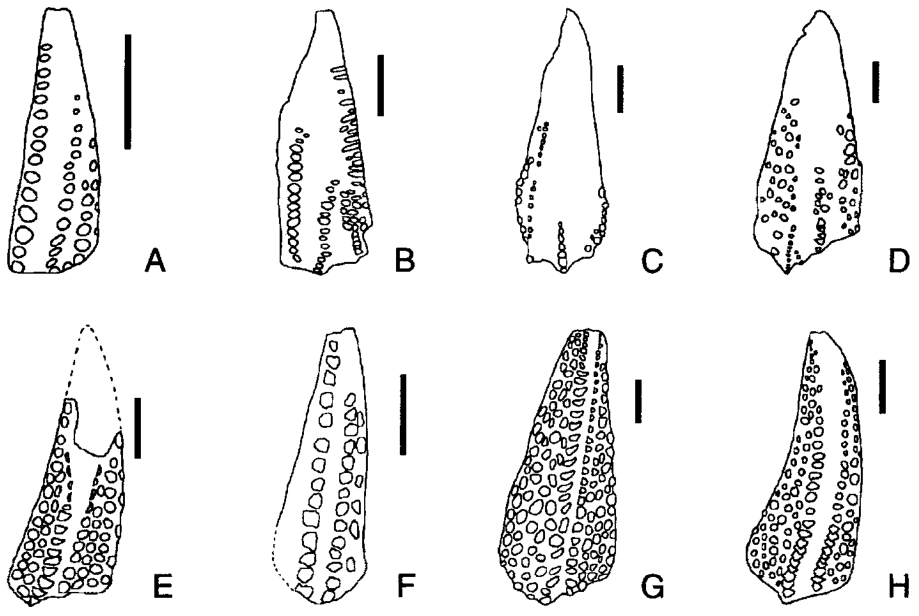

Figure 4. Schematic representation of maxillae of Mid-Late Triassic rhynchosaur, ventral view.
A. *Rhynchosaurus brodiei*, modified from Benton [10].
B. *Stenaulorhynchus stockleyi*, modified from Benton [9].
C. "*Scaphonyx*" *sulcognathus*, modified from Azevedo [2].
D. *Hyperodapedon huenei*, modified from Langer and Schultz [45].
E. *H. gordoni*, modified from Benton [8].
F. *Isalorhynchus genovefae*.
G. *H. huxleyi*, modified from Chatterjee [21].
H. *H. sanjuanensis*.
Scale bar approximately 15 mm.

Figure 4. Schéma de maxillaires de rhynchosaures du Trias moyen à supérieur en vue ventrale.
A. *Rhynchosaurus brodiei*, modifié d'après Benton [10].
B. *Stenaulorhynchus stockleyi*, modifié d'après Benton [9].
C. « *Scaphonyx* » *ulcognathus*, modifié d'après Azevedo [2].
D. *Hyperodapedon huenei*, modifié d'après Langer et Schultz [45].
E. *H. gordoni*, modifié d'après Benton [8].
F. *Isalorhynchus genovefae*.
G. *H. huxleyi*, modifié d'après Chatterjee [21].
H. *H. sanjuanensis*.
La barre d'échelle représente approximativement 15 mm.

Although *Isalorhynchus* possesses a wide cushion-shaped lateral maxillary area, none of the studied maxillary fragments (*table I*) bears more than two lateral rows of pyramidal teeth.

3. Number of longitudinal tooth rows in the maxillary area medial to the main groove. 0 – more than two; 1 – one or two (figure 4). Adult rhynchosaurs with two maxillary grooves, including *Rhynchosaurus*, *Stenaulorhynchus*, "*Scaphonyx*" *sulcognathus*, and *Hyperodapedon huenei* [4, 9, 10, 45], usually possess at least four longitudinal tooth rows in the medial maxillary area: one on the central crest, and more than two on the medial one. Among the rhynchosaurs with a single-grooved maxilla, including *Hyperodapedon gordoni*, *H. huxleyi* and *H. sanjuanensis*, the medial area tends to be narrower [8, 21, 62]. Nevertheless, adult forms of these rhynchosaurs present at least 2–3, but usually many more, longitudinal tooth rows in that area. In *Isalorhynchus* the larger specimens present a maximum of two longitudinal rows in the medial area of the maxilla, and this seems to be a unique feature of this taxon.

4. Medial maxillary groove [22]. 0 – present; 1 – absent (figure 4). Rhynchosaurus and *Stenaulorhynchus*, possess two grooves on the ventral surface of the maxilla [9, 10, 38], as do two Late Triassic forms, "*Scaphonyx*" *sulcognathus* and *Hyperodapedon huenei* [4, 45]. Most Late Triassic rhynchosaurs, however, have just one maxillary ventral groove, including *Hyperodapedon gordoni*, *H. huxleyi*, and *H. sanjuanensis* [8, 21, 39, 62]. This is also the case in *Isalorhynchus*, in which none of the known maxillae shows traces of a second medial groove.

5. Maxillary lingual teeth [20]. 0 – present; 1 – absent. Maxillary lingual teeth are well known in all Middle Triassic rhynchosaurs, including *Rhynchosaurus* and *Stenaulorhynchus* [9, 10]. Among Late Triassic forms, the character is not easy to determine. "*Scaphonyx*" *sulcognathus* and *Hyperodapedon huenei* clearly bear maxillary lingual teeth [4, 45]. *H. huxleyi* and *H. sanjuanensis*, on the other hand, present a medial border of the maxilla that finishes abruptly, and no lingual teeth are present [21, 39, 62]. The medial border of the maxilla of *H. gordoni*, on the contrary, does not finish abruptly, since the occlusal and lingual surfaces are not well defined, and some teeth are placed in a somehow dubious position ([8]; fig. 15). This condition, however, will be treated here as absence of 'true' maxillary lingual teeth. *Isalorhynchus genovefae* clearly lacks lingual teeth on the maxilla.

6. Relative width of the maxillary areas medial and lateral to the main groove [22]. 0 – medial area of the same width or wider or than the lateral; 1 – lateral area wider (figure 4). In *Rhynchosaurus* and *Stenaulorhynchus* the maxillary area lateral to the main groove is very narrow, being at least two times narrower than the medial area [9, 10, 38]. "*Scaphonyx*" *sulcognathus* is the only Late Triassic form that also presents this feature [4]. A variable condition is seen in Late Triassic rhynchosaurs with a broad and cushion-shaped lateral area of the maxilla. In these forms, the lateral tooth-bearing area can be slightly narrower (*H. huenei* [45]), about the same width (*Hyperodapedon gordoni* [8, 9]), or much wider (*Hyperodapedon huxleyi* and *H. sanjuanensis* [21, 39, 62]) than the medial one. The condition in *Isalorhynchus* is not particularly easy to determine, but out of eleven maxillary fragments (*table I*), ten present a wider lateral area.

7. Relative number of longitudinal tooth rows on the maxillary areas medial and lateral to the main groove. 0 – more medial rows; 1 – more lateral rows (figure 4).

All rhynchosaurs with two ventral grooves on the maxilla [4, 9, 10, 45] present more longitudinal tooth rows on the medial than on the lateral side of the lateral cutting groove. Among the single-grooved forms, *Hyperodapedon gordoni* also possesses more medial rows [8], while *H. huxleyi* and *H. sanjuanensis* present more lateral ones [21, 62]. Among the studied maxillae of *Isalorhynchus* (*table I*), the great majority possesses more medial rows, and none more lateral rows.

8. Number of dentary cutting blades [20]. *0 – two; 1 – one.* Double-bladed dentaries are known in Middle and Late Triassic rhynchosaurs, including *Stenaulorhynchus*, *Rhynchosaurus* and "*Scaphonyx*" *sulcognathus* [4, 9, 10, 38]. Rhynchosaurs with single-bladed dentaries, are restricted to the Late Triassic, and include *Hyperodapedon gordoni*, *H. huxleyi*, *H. huenei*, and *H. sanjuanensis* [8, 9, 21, 39, 45, 62]. *Isalorhynchus* clearly presents only one dentary blade.

9. Teeth on the lingual surface of the dentary [20]. *0 – present; 1 – absent.* The total absence of teeth on the lingual surface of the dentary is a feature only present in *H. sanjuanensis*, among the taxons studied here [39, 62]. All other Mid-Late Triassic rhynchosaurs possess some kind of teeth on the lingual surface of the dentary, even though the number and morphology of such teeth varies considerably [9, 10, 21]. This is also the case of *Isalorhynchus*.

This transformation series, which represents an autapomophy of *Hyperodapedon sanjuanensis*, is clearly uninformative in the context of this cladistic analysis. It was, however long used as an important feature to distinguish amongst the Late Triassic rhynchosaurs, and is presented here for the better understanding of its phylogenetic meaning.

10. Primary lingual teeth on the dentary [45]. *0 – present; 1 – absent.* Among the Mid-Late Triassic rhynchosaurs, two different kinds of teeth enter the lingual surface of the dentary. Primary lingual teeth [45] are known in *Stenaulorhynchus*, *Rhynchosaurus*, and "*Scaphonyx*" *sulcognathus* [4, 9, 10, 38], and lie medially to the medial dentary blade. Rhynchosaurs with a single dentary blade (*Hyperodapedon huenei*, *H. gordoni*, *H. huxleyi*, and *H. sanjuanensis*), on the other hand, only present one lingual tooth row that lies on an antero-posteriorly elongated ridge [9, 45]. These teeth are here accepted as homologous to those lying on the medial dentary blade of the two-bladed rhynchosaurs, and the lingual teeth of these forms (primary lingual teeth) are believed to be absent in the single-bladed members of the group. This is the case in *Isalorhynchus*.

11. Relative size of astragalar articular facets for the tibia and centrale. 0 – Tibial facet larger; 1 – Centrale facet larger (figure 5). The astragalus of the Middle Triassic rhynchosaurs, including *Rhynchosaurus* and *Stenaulorhynchus*, bears a tibial articulation facet that is far longer than the facet for the centrale [10, 39, 40]. All known Late Triassic forms, however, show a centrale/astragalus articular facet that is longer than the tibia/astragalus facet. This feature is present in "*Scaphonyx*" *sulcog-*

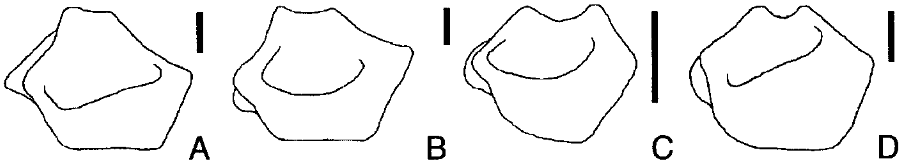

Figure 5. Astragala of Mid-Late Triassic rhynchosaurs, anterior view.
A. Right astragalus of *Stenaulorhynchus stockleyi*.
B. Right astragalus of "*Scaphonyx*" *sulcognathus*.
C. Left astragalus (reversed) of *Isalorhynchus genovefae*.
D. Left astragalus (reversed) of *Hyperodapedon sanjuanensis*, modified from Hughes [40].
Scale bar approximately 10 mm.

Figure 5. Astragales de rhynchosaures du Trias moyen à supérieur en vue antérieure.
A. Astragale droit de *Stenaulorhynchus stockleyi*.
B. Astragale droit de « *Scaphonyx* » *sulcognathus*.
C. Astragale gauche (inversé) d'*Isalorhynchus genovefae*.
D. Astragale gauche (inversé) d'*Hyperodapedon sanjuanensis*, modifiée d'après Hughes [40].
La barre d'échelle représente approximativement 10 mm.

nathus, *Hyperodapedon gordoni*, *H. huxleyi* and *H. sanjuanensis*, and is also clearly seen in *Isalorhynchus*.

Parsimony analysis and results

To assess the phylogenetic relationship among *Isalorhynchus* and the other Mid-Late Triassic rhynchosaurs, a parsimony analysis was carried out with the eleven transformation series described above scored for eight taxons – *Rhynchosaurus* ([10]; based on *R. articeps* and *R. brodiei*), *Stenaulorhynchus* [9, 38], "*Scaphonyx*" *sulcognathus* [2, 4], *Hyperodapedon huenei* [45], *H. gordoni* [8, 9], *H. huxleyi* [21], *H. sanjuanensis* [39, 62], and *Isalorhynchus genovefae* (*table II*). Another Late Triassic species of *Hyperodapedon*, *H. mariensis* [45], was not included in the analysis since it is identical to *H. huxleyi* in the transformation series here considered.

The analysis was performed using PAUP version 3.1.1 [63] on a Macintosh PowerBook G3 computer. The tree was not rooted, and the branch-and-bound option was used to search for the most parsimonious tree (MPT). A single MPT with 12 steps (C.I., excluding uninformative transformation series: 0.900; R.I.: 0.947) was found (*figure 6*).

DISCUSSION

Phylogenetic position and classification of *Isalorhynchus*

The parsimony analysis presented here was based only on transformation series that could be defined for *Isalorhynchus*. This analysis, however, is not enough to

Table II. Transformation matrix used in the parsimony analysis. Unknown characters are given as "?". See main text for the definition of the transformation series.

Tableau II. Matrice de caractères utilisée pour l'analyse de parcimonie. Les caractères non déterminables sont signalés par un « ? ». Voir le texte principal pour la définition des séries de transformations.

	Characters										
Taxons					5					10	
Rhynchosaurus	0	0	0	0	0	0	0	0	0	0	0
Stenaulorhynchus	0	0	0	0	0	0	0	0	0	0	0
Isalorhynchus genovefae	1	0	1	1	1	1	0	1	0	1	1
"Scaphonyx" sulcognathus	0	0	0	0	0	0	0	0	0	0	1
Hyperodapedon huenei	1	1	0	0	0	0	0	1	0	1	?
Hyperodapedon gordoni	1	1	0	1	1	0	0	1	0	1	1
Hyperodapedon huxleyi	1	1	0	1	1	1	1	1	0	1	1
Hyperodapedon sanjuanensis	1	1	0	1	1	1	1	1	1	1	1

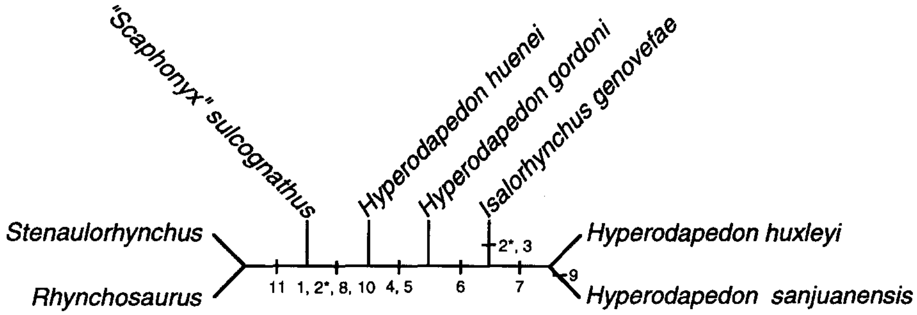

Figure 6. Most Parsimonious Tree resulting from the unrooted cladistic analysis of the data set of *table II* (12 steps, C.I., excluding uninformative transformation series: 0.900, R.I.: 0.947). Homoplasies indicated by an asterisk.

Figure 6. Arbre non enraciné le plus parcimonieux résultant de l'analyse cladistique de la matrice de données du *tableau II* (12 pas, indice de cohérence excluant les séries de transformations non informatives : 0,900, indice de retention : 0,947). Les homoplasies sont indiquées par un astérisque.

determine the phylogenetic position of this taxon, and a complete score of taxons and transformation series must be taken into account. Such comprehensive studies have been carried out recently by Dilkes [29], on the phylogenetic interrelationships among Middle and Late Triassic rhynchosaurs, and Langer and Schultz [45] on the interrelationships amongst Late Triassic members of the group. The latter will be used here as a framework to define the phylogenetic position of *Isalorhynchus*.

The only incongruity between the topology presented here (*figure 6*) and the one of Langer and Schultz [45] is the relative position of *Hyperodapedon huxleyi*. This taxon is placed here as the sister taxon of *H. sanjuanensis*, but it was accepted as the sister taxon of *H. gordoni* by those authors. This difference is not unexpected, since the features that unambiguously link *H. huxleyi* to *H. gordoni* in Langer and Schultz's [45] study are represented in the postcranial skeleton. These postcranial characteristics are unknown for *Isalorhynchus*, and were not included in the present cladistic analysis.

There are five different and equally parsimonious ways to fit *Isalorhynchus* into the topology presented by Langer and Schultz [45], taking into account the 11 transformation series analysed here (*figure 7*). *Isalorhynchus* can be placed either as the sister taxon of each of *Hyperodapedon gordoni*, *H. huxleyi* or *H. sanjuanensis*, the sister taxon of a clade including these three forms, or even as the sister taxon of the clade composed of *H. gordoni* and *H. huxleyi*. All those five possible arrangements imply two extra homoplasies, leading to an increase of two steps compared to the most parsimonious topology here presented (*figure 6*). A reversal to the plesiomorphic character of the transformation series 6 (medial tooth-bearing area of the maxilla of the same width or wider than the lateral) must be postulated for *H. gordoni*, while a convergent acquisition of the apomorphic character of transformation series 7 (more lateral than medial longitudinal tooth rows on the maxilla) took place in *H. huxleyi* and *H. sanjuanensis* (*figure 7*).

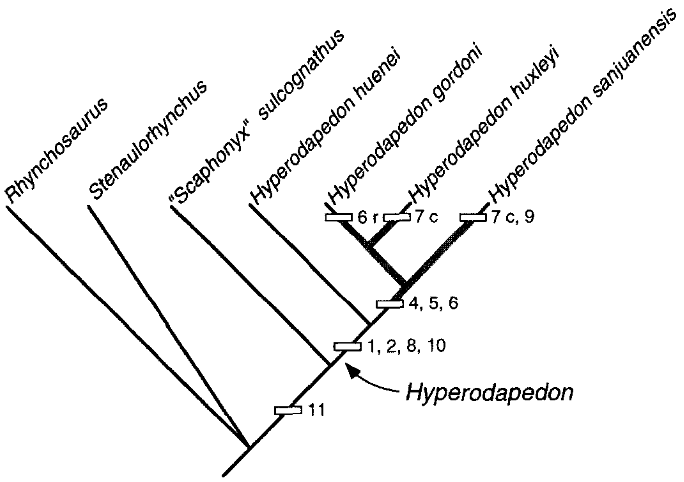

Figure 7. Cladogram presented by Langer and Schultz [45] depicting the phylogenetic interrelationships among Mid-Late Triassic rhynchosaurs. Thicker grey lines indicate the possible phylogenetic position of *Isalorhynchus genovefae* , based on the transformation series as defined in this study. The transformation series are plotted with their respective numbers, "r" indicates reversals and "c" convergences. The stem-based *Hyperodapedon* [45] is indicated by an arrow. This composition of data accepts the characters present in *Stenaulorhynchus* and *Rhynchosaurus* (*table II*) as plesiomorphic, with transformation series optimised by Deltran.

Figure 7. Cladogramme publié par Langer et Schultz [45] montrant les relations phylogénétiques au sein des rhynchosaures du Trias moyen à supérieur. Les lignes grises épaissies indiquent les différentes positions possibles pour *Isalorhynchus genovefae*, basées sur les séries de transformations définies dans cette étude. « r » indique une réversion et « c » une convergence. Le groupe souche *Hyperodapedon* [45] est indiqué par une flèche. L'arrangement des données accepte les caractères présents chez *Stenaulorhynchus* et *Rhynchosaurus* (*tableau II*) comme étant plésiomorphiques, avec des séries de transformations optimisées par Deltran.

Regardless of its exact phylogenetic position, *Isalorhynchus* is more derived than *H. huenei*, and is thus nested within the genus *Hyperodapedon*, a stem-based taxon as defined by Langer and Schultz [45]. This situation characterizes *Isalorhynchus* as a junior subjective synonym of *Hyperodapedon* and demands the proposal of a new nominal combination – *Hyperodapedon genovefae* – to designate the Malio River rhynchosaur.

RHYNCHOSAURIA Osborn, 1903

HYPERODAPEDONTIDAE Lydekker, 1885

Hyperodapedon Huxley, 1859

Type species: *Hyperodapedon gordoni* Huxley, 1859

Junior generic subjective synonyms:

Stenometopon Boulenger ([15] p. 178)
Macrocephalosaurus Tupi-Caldas ([64] p. 339) *non* Gilmore [33]
Paradapedon Huene ([38] p. 111)
Supradapedon Chatterjee ([22] p. 58)
Isalorhynchus Buffetaut ([16] p. 467)

Described rhynchosaurs attributable to *Hyperodapedon*:

Hyperodapedon gordoni ([43] pp. 138–146) – partim
Hyperodapedon huxleyi sp. nov. ([47] pp. 177–178)
Hyperodapedon Huxley ([48] 3–20, pls. I–II, III.1–5)
Hyperodapedon gordoni ([44], pp. 675–692, figs 1, 4, 7, 8, pl. XXVI)
Hyperodapedon Huxley ([49] pp. 297–299, figs. 67–69)
Hyperodapedon gordoni ([17] pp. 486–482, 34, figs. 1–2)
Hyperodapedon gordoni Huxley ([15] pp. 175–178, fig. 1, pl. 11)
Stenometopon taylori gen. et sp. nov. ([15] pp. 178–182, figs. 2–3, pls. 12–13)
Scaphonyx australis Huene ([37] pp. 5–15, figs. 5–7, pl. I.1–3) – *Scaphonyx australis* Huene, 1926, is *nomen dubium*
Macrocephalosaurus mariensis gen. et sp. nov. ([64] pp. 334–339, figs. 244–246)
Cephalonia lotziana Huene ([39] pp. 259–294, figs. 52–56, pls. 31–33) – some specimens are of uncertain affinity, *Cephalonia lotziana* Huene, 1926, is *nomen dubium*
Scaphonyx fischeri Woodward ([39] pp. 294–312, figs. 57–64, pls. 34–38) – some specimens are of uncertain affinity, *Scaphonyx fischeri* Woodward, 1907, is *nomen dubium*
Scaphonyx stockleyi sp. nov. ([14] pp. 1–3, fig. 1)
Rhynchosauridae – "Nova Scotia rhynchosaur" – ([5] p. 107)
Scaphonyx Woodward, 1907 ([62] pp. 343–350, pls. 2–4)
Paradapedon huxleyi (Lydekker) ([21] pp. 213–250, figs. 2–28)
Rhynchosauridae gen. et sp. nov. ([23] pp. 290–292, fig. 1)
Hyperodapedon gordoni Huxley, 1859 ([8] pp. 613–686, figs. 1–40)
Hyperodapedon ([9] pp. 743–752; figs. 16, pls. 66–67)
Scaphonyx sanjuanensis ([3] pp. 70–73, fig. 3)
Scaphonyx fischeri Woodward, 1907([11] pp. 339–345, figs. 1–9, 12)

Hyperodapedon sp. ([60], p. 47)
Hyperodapedon sp. ([55] pp. 7–9, figs. 3–5)
Hyperodapedon Huxley, 1859 ([24] p. 534)
Hyperodapedon huenei sp. nov. [45]

Revised diagnosis: Rhynchosaur with skull broader than long; ventral process of the squamosal plate-like; no parietal foramen; beak-shaped edentulous premaxillae; frontal ornamented with lateral grooves showing approximately the same depth in all its extension; no frontal-postorbital contact; no discrete supratemporal; occipital condyle in the plane defined by the quadrate and squamosal; short basipterygoid process; basioccipital longer than the basisphenoid; parietal longer than the frontal; well-developed *anguli oris* crest; posterior parietal process directed laterally; orbits directed upwards; maxilla not bordering the inferior orbital foramen; depth of the mandible more than a quarter of its length; dentary longer than half the length of the mandible; one dentary blade; pterygoid toothless; area lateral to the main groove of maxilla cushion-shaped, with a ventral surface enlarged enough to bear several longitudinal tooth rows; no primary lingual teeth on the dentary; no posterior process of the coracoid; centrale larger that half of the astragalus; articular facet of tibia and astragalus smaller than of centrale and astragalus; first metatarsal wider than long; fourth distal tarsal subequal in size of the other distal tarsale.

Apomorphies: ventral process of the squamosal plate-like; frontal ornamented with lateral grooves showing approximately the same depth in all its extent; one dentary blade; area lateral to the main groove of maxilla cushion-shaped; no primary lingual teeth on the dentary.

Variable features: second jugal crest dorsal to the *anguli oris* present or not; one or two ventral grooves on maxilla; number of longitudinal rows in area lateral to the main groove of maxilla varying from one to more than five; variable relative width of medial and lateral tooth-bearing areas of maxilla; variable relative number of longitudinal tooth rows on the medial and lateral tooth-bearing areas of maxilla; maxillary lingual teeth present or not; secondary lingual teeth on the dentary present or not; anterior iliac blade shorter than, or the same length, as the posterior blade; humerus shorter than, or the same length, as the femur; coracoid foramen between the scapula and the coracoid, or excluded from the scapula.

Comments: a revision of the diagnosis of *Hyperodapedon* is necessary to account for the new anatomical information provided by *H. genovefae*. In particular, a classic morphological definition of the genus, provided by Lydekker [49], is no longer valid in light of these findings. That author suggested that the presence of more than two longitudinal tooth rows in the lateral area of the maxilla would be diagnostic for *Hyperodapedon*, a definition alluded to by Langer and Schultz [45] in proposing a new diagnosis, as well as a phylogenetic definition, for the genus. In fact, Lydekker's [49] diagnostic character (transformation series 2) is apomorphic for *Hyperodapedon*, but it is not present in all species of the genus, having been reversed in *H. genovefae* (*figure 6*). Therefore, although the stem-based definition of *Hyperodapedon* provided by Langer and Schultz [45] is still valid, it unfortunately includes a taxon (*H. genovefae*) that does not present a classic diagnostic feature of the genus.

Distribution: Late Triassic (Carnian) of South America (southern Brazil [45, 60] and northern Argentina [24]), Africa (Tanzania [14], Zimbabwe [55] and Madagascar), Europe (northern Scotland [8]), North America (Nova Scotia [5]), and India [21].

Hyperodapedon genovefae (Buffetaut, 1983)

Synonymy:

Isalorhynchus genovefae gen. et sp. nov. ([16] pp. 467)
Isalorhynchus ([10] p. 298)
Isalorhynchus genovefae ([41] p. 933)
Isalorhynchus ([66] pp. 141–148)
Isalorhynchus ([29] p. 521)

Holotype: MDE-R18 – left maxilla [16].

Locality and Horizon: Malio River area, south-western Madagascar. Stratum related to the Makay Formation, Late Triassic (Carnian) of the Morondava Basin [57].

Diagnosis: *Hyperodapedon* with lateral maxillary area cushion-shaped, wider than the medial, and bearing fewer than three longitudinal tooth rows; single maxillary groove; more teeth in the medial than in the lateral maxillary area; fewer than three longitudinal tooth rows in the medial maxilla area (autapomorphy); edentulous platform in the lateral part of the maxilla (unique feature); no maxillary lingual teeth; one row of dentary lingual teeth.

Comments: The age of the tetrapod-bearing strata of the Morondava Basin is controversial. Based mainly on the taxonomic affinities of "*Isalorhynchus*", estimations of Middle [16] and Late [41] Triassic age were given, and the present study supports the second alternative. The genus *Hyperodapedon* is traditionally found in Mid-Late Carnian (Ischigualastian [13, 58]) strata around the world, and no earlier record is known. Therefore, *H. genovefae* indicates a Late Triassic age for its type-stratum in the Malio River area.

The new Triassic tetrapod assemblage of the Morondava Basin described by Flynn et al. [31, 32] was dated as Ladinian or Early Carnian. According to these authors [32], the presence of "*Isalorhynchus*" in that fauna supports its pre-Ischigualastian age, because the phylogenetic position of that taxon was considered to be outside the clade encompassing Ischigualastian rhynchosaurs. Alternatively, if *Isalorhynchus* is a synonym of *Hyperodapedon*, as claimed here, the rhynchosaur fauna would suggest an Ischigualastian rather than a pre-Ischigualastian age for that new assemblage.

Palaeogeographic reconstructions suggest that Madagascar was close to East Africa and Peninsular India during Late Triassic times [61]. The *Hyperodapedon* forms found in Late Triassic strata of these areas, however, are more similar to the European and South American species [8, 39, 62] than to *H. genovefae*. *H. huxleyi*, from the Maleri and Tiki Formations of Central India [21], and the *Hyperodapedon* from probable Upper Triassic beds in Tanzania [14] do not present the unusual derived features of *H. genovefae* (transformation series 2 and 3), but show, on the contrary, a conservative dental arrangement that is closer to the classical morphology of the genus. Such a situation suggests the existence of geographic barriers isolating the Malagasian rhynchosaur fauna from neighbouring continental areas in Late Triassic times. This supports the conclusion of Flynn et al. [31], who suggested that the whole terrestrial biota of the island showed endemic characteristics since the Early Mesozoic.

Tooth evolution in the Mid-Late Triassic rhynchosaurs

Most of the information included in the parsimony analysis performed here (all but transformation series 11) are related to the tooth arrangement of rhynchosaurs. It is tempting, therefore, to present some discussion on the dental evolution of this reptile group during the Mid-Late Triassic based on the resulting tree topology (*figure 6*). For this purpose, Middle Triassic rhynchosaurs (*Stenaulorhynchus* and *Rhynchosaurus*) and "*Scaphonyx*" *sulcognathus* were used to "root" the MPT (*figure 8*), though they share the more plesiomorphic tooth arrangement among the rhynchosaurs considered in this study [10, 29, 45].

The primitive tooth arrangement of *Stenaulorhynchus*, *Rhynchosaurus* and "*Scaphonyx*" *sulcognathus* [2, 9, 10] comprises two well-developed maxillary grooves, which divide the ventral surface of the bone into three tooth-bearing areas. The lateral and central areas usually do not bear more than two longitudinal rows of teeth (the central one only). The medial area, on the other hand, bears several transverse rows of lingual and occlusal teeth that enter the maxilla from its posterolateral margin. The dentaries of these rhynchosaurs have two blades that fit into the two maxillary grooves. The lateral blade bears a single longitudinal tooth row, and the medial blade bears several rows on its occlusal and lingual surface.

The next step in rhynchosaur dental evolution (*figure 8*) is represented by *Hyperodapedon huenei*. This form bears a unique combination of an apomorphic loss of the medial dentary blade with the retention of two maxillary grooves, though the medial groove is strongly reduced. Moreover, this taxon already presents other apomorphic dental features, such as the loss of primary lingual teeth on the dentary (see discussion in Langer and Schultz [45]) and the increase in width and number of tooth rows on the maxilla lateral to the main groove. *H. huenei* also presents the two types of maxillary teeth – pyramidal and conical – which have not been demonstrated in

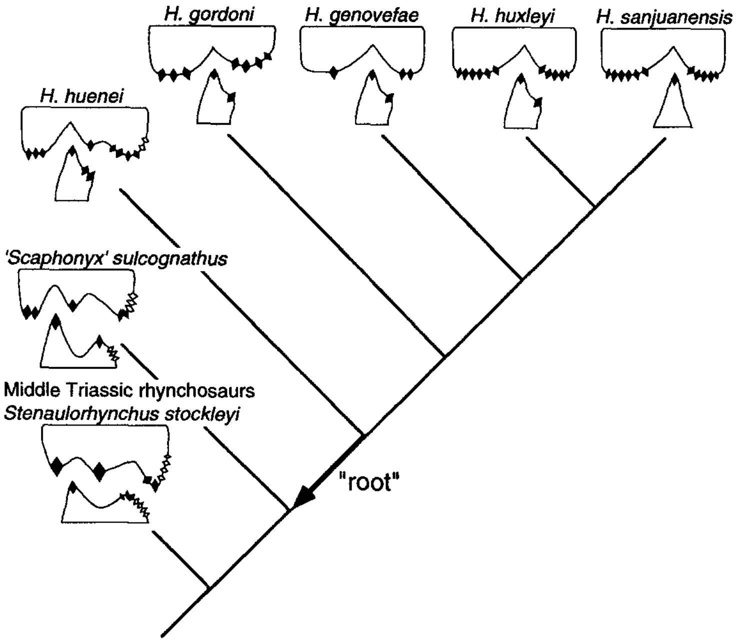

Figure 8. Phylogenetic hypothesis of *figure 6* rooted in *Stenaulorhynchus* and "*Scaphonyx*" *sulcognathus*, and depicting the tooth evolution of the Mid-Late Triassic rhynchosaurs. For each taxon a transverse section through the maxilla and dentary is given. Primary lingual teeth [45] in white, other teeth in black.

Figure 8. Hypothèse phylogénétique de la *figure 6* enracinée, avec *Stenaulorhynchus* et « *Scaphonyx* » *sulcognathus*, montrant l'évolution de la denture des rhynchosaures du Trias moyen à supérieur. Pour chaque taxon, une coupe transverse du maxillaire et du dentaire est donnée. Les dents linguales primaires [45] sont en blanc, les autres dents sont en noir.

more primitive rhynchosaurs. The pyramidal teeth are seen in only two longitudinal rows, i.e. laterally and medially adjacent to the main maxillary groove, while the conical teeth enter the maxilla in transverse rows (cf. [21] fig. 12). This tooth arrangement suggests that the pyramidal teeth of *Hyperodapedon* are homologous to the teeth on the lateral and central maxillary ridges of the rhynchosaurs with two maxillary grooves.

In all other species of *Hyperodapedon* (*figure 8*) the medial maxillary groove and the typical lingual maxillary teeth are lost. The pyramidal teeth, however, are still present, and arranged in longitudinal rows both medially and laterally ([3] fig. 1, [39], pl. 31.1b), but more often only laterally ([62] pl. 3e, [21] fig. 14, [8] fig. 15), to the maxillary groove. Older individuals tends to loose these teeth ([21] fig. 13), which are more clearly seen in younger specimens ([39] pl. 31, fig. 1b, [21] fig. 14).

The rhynchosaurs that show the most derived dental features are *Hyperodapedon genovefae*, *H. huxleyi* and *H. sanjuanensis* (*figure 8*). These taxons share a reduction of the medial maxillary tooth-bearing area, which becomes narrower than the lateral area. Afterwards, the number of tooth rows on the lateral area of the maxilla also increases, and outnumbers the ones on the medial area. This feature defines *H. huxleyi* and *H. sanjuanensis* as more derived than *H. genovefae.*

Some autapomorphic features were also defined in the analysis (*figures 6, 8*). *Hyperodapedon sanjuanensis* shows a complete loss of teeth on the lingual surface of the dentary, and *H. genovefae* presents a unique extra reduction of the number of tooth rows in the medial area of the maxilla. Moreover, *H. genovefae* retains the primitive count of fewer than three longitudinal tooth rows on the lateral area of the maxilla, which is interpreted as an autapomorphic reversal.

As already discussed (transformation series 2), the development of conical teeth in the lateral maxillary area of *Hyperodapedon genovefae* is strongly reduced, with these teeth totally failing to appear. Similarly, the extreme reduction in the number of tooth rows on the medial area of that bone (transformation series 3) affects mostly the conical teeth, and the single lateral row of pyramidal remains present in most specimens. This simultaneous reduction, in the same taxon, of both medial and lateral maxillary conical teeth suggests that their development should be regulated by the same mechanism.

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Plate I

Isalorhynchus genovefae

A. Left maxilla MDE-R18 (Holotype), ventral view.
B. Left maxilla MAL-1996 3, ventral view.
C. Left maxilla MAL-1996 10, ventral view.
D. Right maxilla MAL-1996 2, ventral view.
E. Right maxilla MAL-1996 1, ventral view.
F. Right dentary MAL-1996 8; **1:** lateral view, **2:** medial view.
Bar scale = 10 mm.

Planche I

Isalorhynchus genovefae

A. Maxillaire gauche MDE-R18 (Holotype), vue ventrale.
B. Maxillaire gauche MAL-1996 3, vue ventrale.
C. Maxillaire gauche MAL-1996 10, vue ventrale.
D. Maxillaire droit MAL-1996 2, vue ventrale.
E. Maxillaire droit MAL-1996 1, vue ventrale.
F. Dentaire droit MAL-1996 8; **1 :** vue latérale, **2 :** vue médiale.
Barre d'échelle = 10 mm.

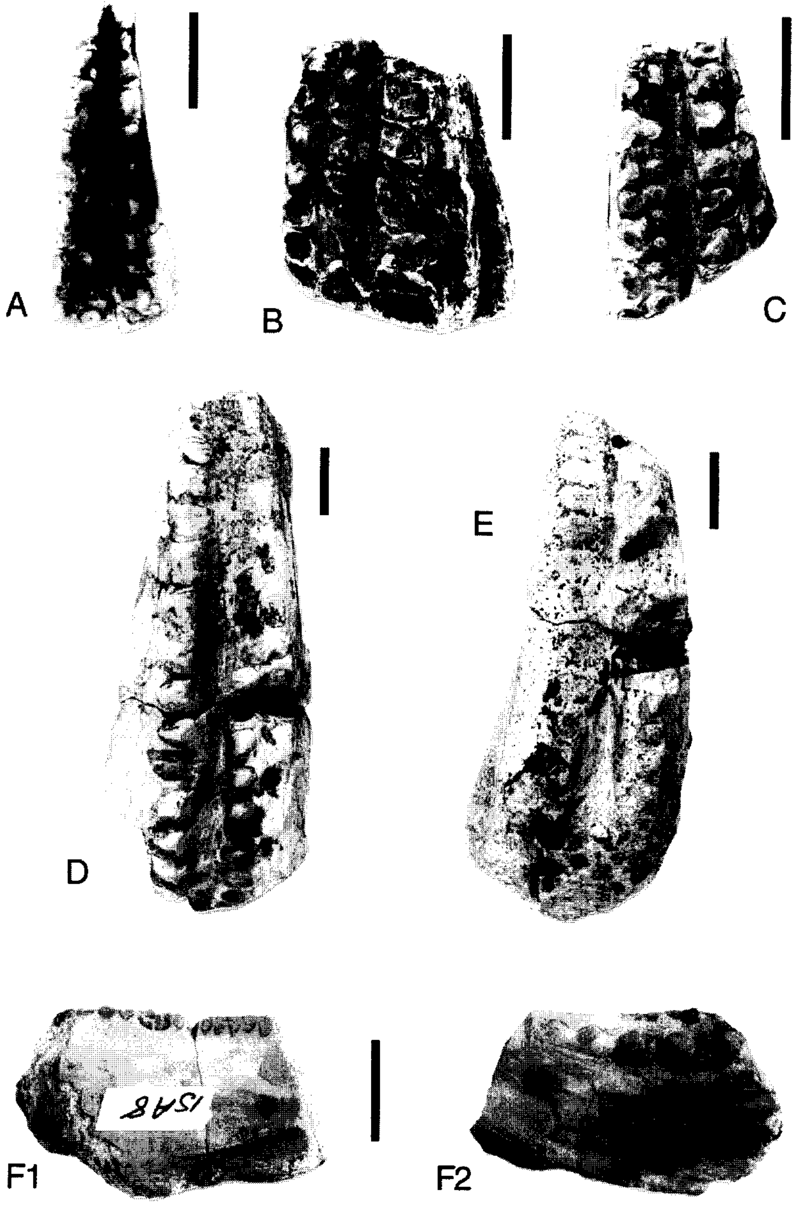

Plate I