

# A new therioherpetid cynodont from the Santa Maria Formation (middle Late Triassic), southern Brazil

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Abdala F. & Ribeiro A. M. 2000. — A new therioherpetid cynodont from the Santa Maria Formation (middle Late Triassic), southern Brazil. *Geodiversitas* 22 (4) : 589-596.

## ABSTRACT

A new cynodont with sectorial postcanines, from the Santa Maria Formation of southern Brazil, is described. *Charruodon tetracuspидatus* n. gen. n. sp., represented by a fragmentary lower jaw, shows a postcanine morphology close to that of *Therioherpeton cargini*, thereby justifying a tentative inclusion of the new species within the family Therioherpetidae. Comparisons among cynodonts with sectorial teeth are suggestive of a sequence of morphological changes in the sectorial postcanines of advanced cynodonts.

## KEY WORDS

Cynodontia,  
Therioherpetidae,  
middle Late Triassic,  
Brazil,  
sectorial tooth.

## RÉSUMÉ

*Un nouveau cynodonte thérioherpétidé de la Formation Santa Maria (Trias supérieur) du Sud du Brésil.*

Un nouveau cynodonte aux dents postcanines sectoriales, provenant de la Formation Santa Maria au Sud du Brésil, est décrit. La morphologie des dents postcanines de *Charruodon tetracuspидatus* n. gen. n. sp., représentée par un fragment de mandibule, est proche de celle observée chez *Therioherpeton cargini*, ce qui par conséquent l'inclut dans la famille des Therioherpetidae. Des comparaisons avec d'autres cynodontes ayant une dentition sectoriale viennent suggérer une série de modifications morphologiques qui affectent les postcanines sectoriales chez les cynodontes évolués.

## MOTS CLÉS

Cynodontia,  
Therioherpetidae,  
Trias supérieur,  
Brésil,  
dent sectoriale.

## INTRODUCTION

The Santa Maria Formation in southern Brazil is well-known for its abundant Triassic continental fauna (Barberena *et al.* 1985; Schultz 1995). Ranging from ?Ladinian to Norian, this formation preserves a heterogeneous sample of the vertebrates of the epoch (see Barberena *et al.* 1985 for a list of taxa).

Important components of the Santa Maria fauna are non-mammalian cynodonts, a paraphyletic assemblage that includes the closest relatives of the early mammals (i.e. Mammaliaformes *in* Rowe 1988). The transition to mammals is one of the best documented evolutionary events in the fossil record, allowing detailed examination of the successive changes leading to the origin of a major group (Kemp 1982; Hopson & Barghusen 1986; Sidor & Hopson 1998).

Non-mammalian cynodonts are represented in Brazil by the numerically dominant traversodontids, characterized by transversely broad postcanines (Barberena 1974), and by the medium-to-large-sized chiniquodontids, distinguished by sectorial postcanine teeth (Romer 1969; Teixeira 1982; Abdala 1996). In addition, there are smaller forms such as *Thrinaxodon brasiliensis* Barberena, Bonaparte & Teixeira, 1987, which features cingular cusps along the base of the crown of postcanine teeth, and *Therioherpeton cargini* Bonaparte & Barberena, 1975, which has fully sectorial postcanines. The latter species, represented only by the holotype, comes from Santa Maria city and was proposed as a probable mammal ancestor by Bonaparte & Barberena (1975).

In the paleontological collection of the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica de Rio Grande do Sul, a fragment of the left lower jaw of a small cynodont was found bearing a sectorial tooth. The specimen comes from the same locality (Fig. 1) in which the traversodontid cynodont *Exaeretodon* Cabrera, 1943 and the basal archosaur *Proterochampsa nodosa* Barberena, 1982 were discovered.

Close inspection of the jaw fragment revealed the presence of a replacement tooth with a sectorial

crown morphology resembling that seen in *Therioherpeton*. The purpose of this paper is to provide a description of this new cynodont material and compare it with that of other sectorial-toothed cynodonts.

## ABBREVIATIONS

- MCP PV Paleontological collection of the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica de Rio Grande do Sul;  
 PVL Paleontologia de Vertebrados Lillo collection, Universidad Nacional de Tucumán;  
 The cusp terminology follows that used by Hopson & Crompton (1969: 23) to describe the molars of *Morganucodon* (= *Eozoetrodon*).

## SYSTEMATIC PALEONTOLOGY

Order THERAPSIDA Broom, 1905  
 Suborder CYNODONTIA Owen, 1861  
 Family THERIOHERPETIDAE  
 Bonaparte & Barberena, 1975

Genus *Charruodon* n. gen.

TYPE SPECIES BY ORIGINAL DESIGNATION. — *Charruodon tetracuspидatus* n. sp.

ETYMOLOGY. — In honor to the Charruas, a native South American tribe that lived in southern Brazil, and from the Greek *odon* which means tooth.

DIAGNOSIS. — As for the species, by monotypy.

*Charruodon tetracuspидatus* n. sp.  
 (Figs 2; 3; Tables 1; 2)

HOLOTYPE. — Fragment of the left dentary horizontal ramus, with alveoli for three incisors, roots of the canine and three postcanines, and a fifth tooth with a well-preserved crown (Figs 2; 3) (MCP-3934 PV).

ETYMOLOGY. — *tetracuspидatus*, in reference to the four-cusped crown morphology.

LOCALITY. — 29°42'07.44''S, 52°51'43.95''W, approximately 8 km West of the city of Candelaria in the State of Rio Grande do Sul, southern Brazil.

HORIZON. — Santa Maria Formation. The presence of *Exaeretodon* and *Proterochampsa* here is strongly suggestive of a Carnian age for this stratum of the formation (Rogers *et al.* 1993).

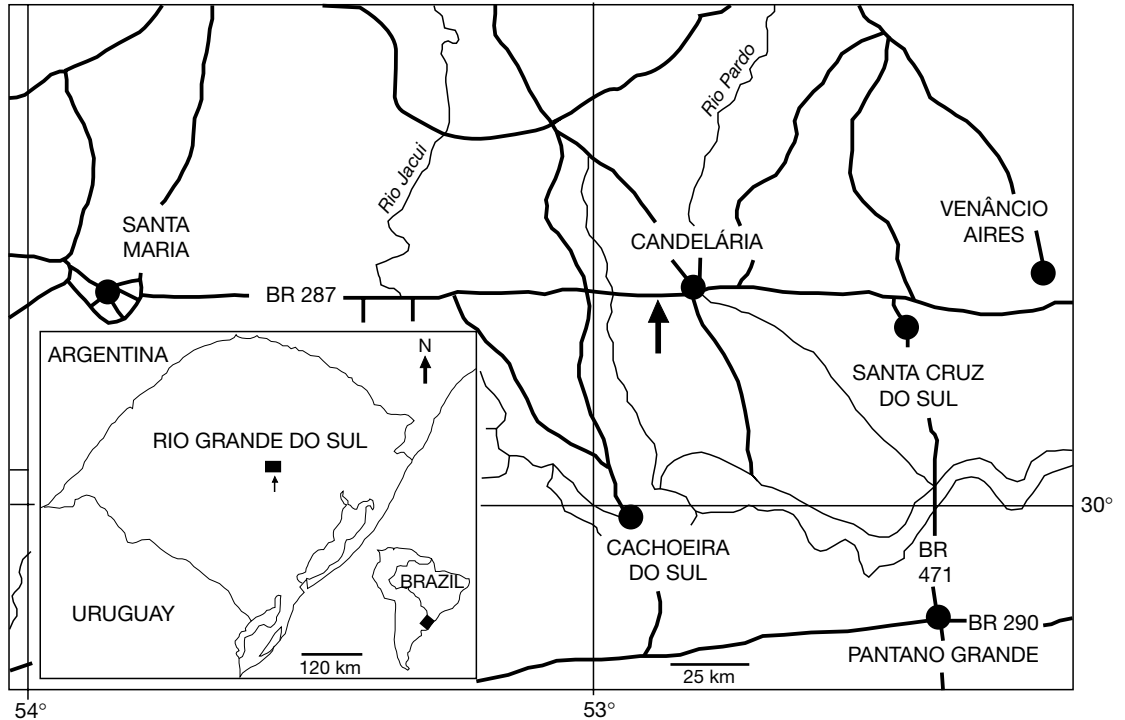


Fig. 1. — Map showing the location of the fossil outcrop.

**DIAGNOSIS.** — Lower jaw with a high horizontal ramus when compared with the postcanine size, approximately 0.31 with respect to the anteroposterior length of the crown of the fifth postcanine; four well-developed cusps on the crown of the postcanine; second cusp “a” is the largest, followed closely in size by the third (“c”); the three posterior cusps (“a”, “c” and “d”) are directed posteriorly; a sharp constriction distinguishes the crown from the root; roots undivided.

#### DESCRIPTION

The dentary fragment extends from an open and high symphysis to the level of the third postcanine (Fig. 2A, B). There are three alveoli for the incisors. The root of the canine is larger than those of the incisors and postcanines, but has undergone some transverse compression during fossilization. The mental foramen is located at the level of the second postcanine, and closer to the symphysis are some nutritive foramina (Fig. 2B). Three postcanines are represented only by their roots. All ap-

pear relatively small compared with the anterior height of the jaw. Originally, the region preserved extended as far posteriorly as the fifth alveolus, which contained a replacing tooth that preserved a complete crown. This tooth was isolated and prepared in order to examine its crown morphology (Fig. 3). Four aligned cusps are present and there is no indication of a cingulum. The main cusp “a” is slightly larger than the first posterior accessory cusp “c” from which it is separated by a notch. Both of these cusps are slightly recurved posteriorly. The second posterior accessory cusp “d” is the lowest. It is posteriorly directed and well-separated from cusp “c” by a notch. The anterior accessory cusp “b” is relatively small and closely united with the main cusp by a high crest. In occlusal view, the crown is bulbous, with convex labial and lingual sides, the latter being particularly rounded. The root is undivided and distinguished from the crown by a prominent constriction.

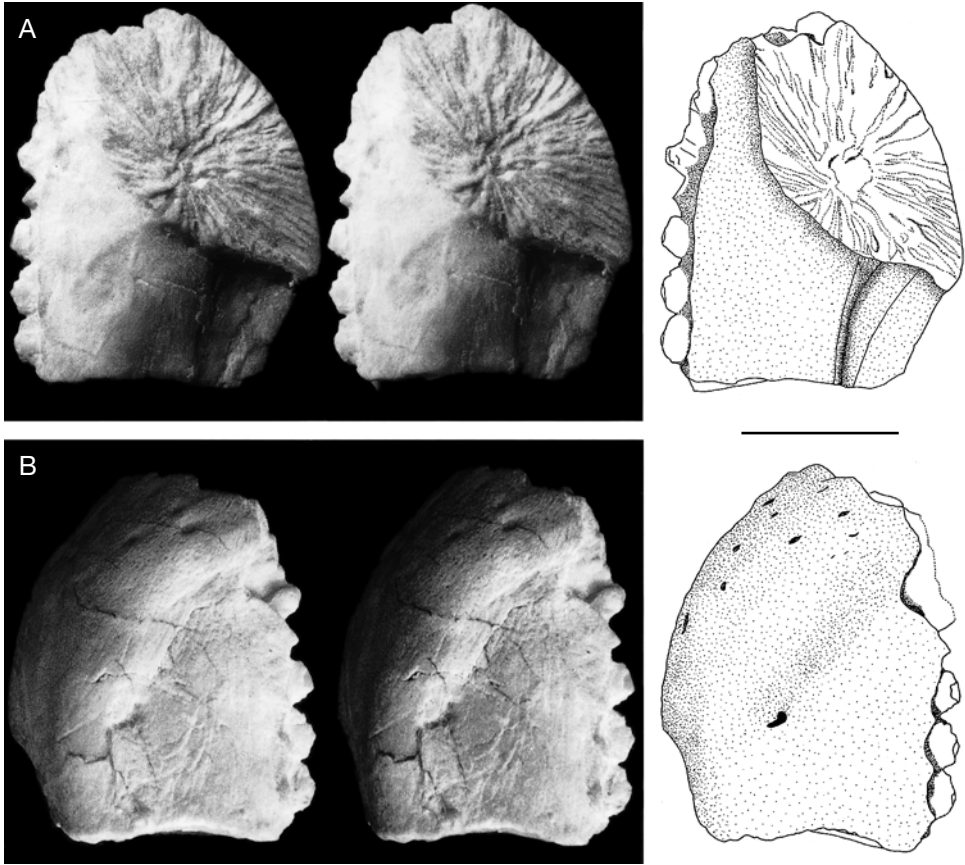


FIG. 2. — Stereopair and line drawing of the mandibular ramus of *Charruodon tetracuspidatus* n. sp. (MCP-3934 PV); **A**, labial view; **B**, lingual view. Scale bar: 10 mm.

TABLE 1. — *Charruodon tetracuspidatus* n. sp., holotype. Measurements of the specimen MCP-3934 PV (mm).

Total length of specimen	23.5
Height at the level of the first postcanine	15.2
Anteroposterior length of the root of the canine	5.0
Anteroposterior length of the root of postcanine 1	2.8
Anteroposterior length of the root of postcanine 2	3.0
Anteroposterior length of the root of postcanine 3	3.0

TABLE 2. — *Charruodon tetracuspidatus* n. sp., holotype. Measurements of the fifth postcanine (mm).

Crown length	4.8
Crown height	3.0
Crown width	1.8

## DISCUSSION AND CONCLUSION

Several new Late Triassic European cynodonts have been described over the past two decades mainly on the basis of isolated teeth (Hahn *et al.* 1984, 1988, 1994; Sigogneau-Russell & Hahn 1994; Godefroit 1997; Godefroit & Battail 1997). As outcome of these findings, different systematic proposals for cynodont taxonomy have emerged to incorporate the new evidence. Battail (1991) recognized Dromatheriidae, Chiniquodontidae and Therioherpetidae, among others, as valid cynodont families, all characterized by the presence of sectorial postcanines bearing a faint cingulum or lacking one entirely.

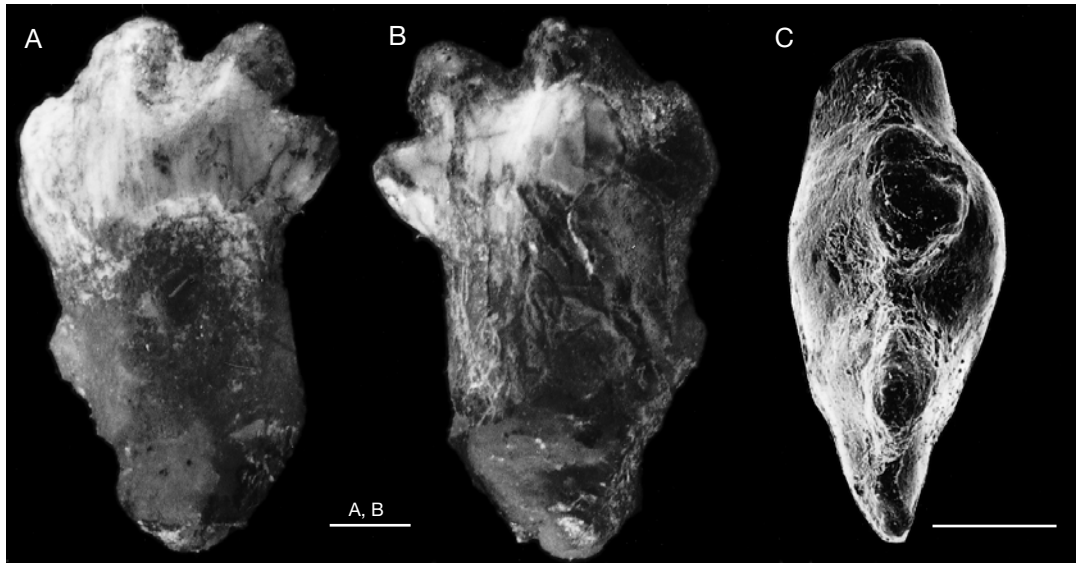


FIG. 3. — Fifth tooth of *Charruodon tetracuspιδatus* n. sp. (MCP-3934 PV); **A**, labial view; **B**, lingual view; **C**, crown view. Scale bars: 10 mm.

Chiniquodontids are Middle to Late Triassic cynodonts that are restricted to South America (*sensu* Abdala 1996, but see Battail 1991; Hopson & Barghusen 1986; Hopson 1991). The postcanines of chiniquodontids lack cingula and have undivided roots (Abdala 1996). The crowns of the posterior postcanines possess four cusps with the anterior accessory cusp being faintly defined (Fig. 4A). The anterior postcanines are less complex, with only a central cusp and a posterior accessory cusp. The main cusp is notably more developed than the others and curved sharply backwards in chiniquodontids (Abdala 1996), a clearly different morphology from that developed in *Charruodon tetracuspιδatus*.

Dromatheriids, from the Late Triassic of United States and Europe, are represented by scarce material comprising an incomplete lower jaw and isolated teeth (Lucas & Oakes 1988; Battail 1991). They were considered *Cynodontia incertae sedis* by Hopson & Kitching (1972), but they are better represented with the discovery of new European material (Godefroit & Battail 1997). The group, as currently defined, is noticeably heterogeneous, showing different kinds of crown

morphologies (see in Godefroit & Battail 1997). Some diagnostic features of dromatheriids, such as the low dentary ramus and symphysis and the narrower crowns (Battail 1991; Godefroit & Battail 1997) contrast with the new material described herein. Nevertheless, the crown morphology of *Charruodon tetracuspιδatus* is mostly coincident (e.g., in the development and curvature of its cusps) to that of *Meurthodon gallicus* Sigogneau-Russell & Hahn, 1994, from Saint-Nicolas-du-Port, France (Fig. 4D), originally represented by an isolated tooth described by Russell *et al.* (1976). The presence of a double root in the latter species precludes assignment of the otherwise similar Santa Maria cynodont to *Meurthodon*. It is difficult to envisage the overall morphology of the dromatheriids (*sensu* Godefroit & Battail 1997), considering the conspicuous variations in tooth crown morphology, and especially taking into account the presence of taxa with and without divided roots.

Therioherpetidae is Battail's (1991) emendation of Bonaparte & Barberena's (1975) *nomen* Therioherpetontidae. The validity of the family has been alternately denied and supported by

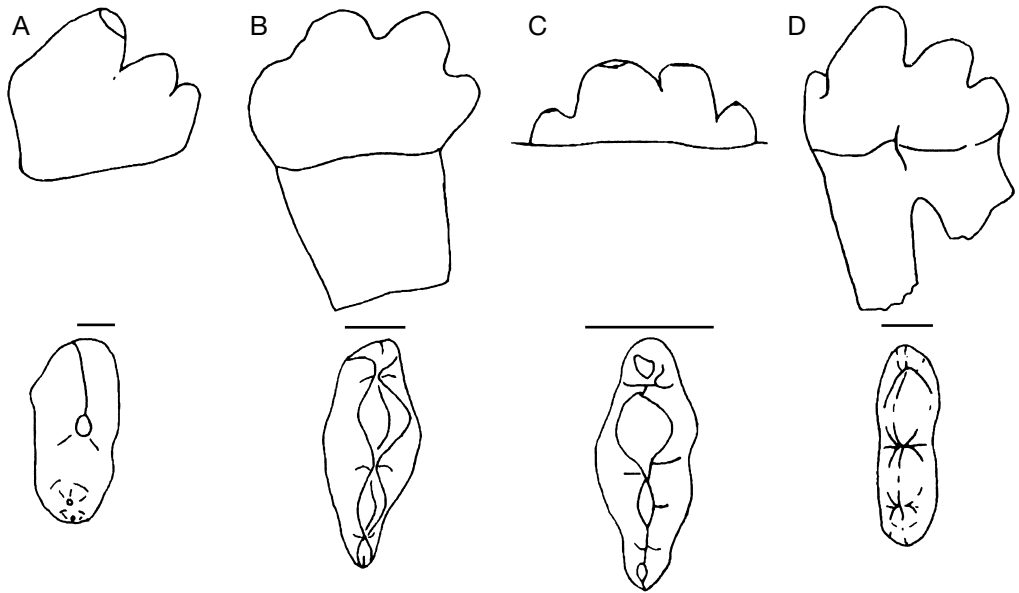


FIG. 4. — Lower postcanines in lateral (above) and crown (below) views; **A**, *Chiniquodon theotonicus* (sensu Abdala, 1996, PVL 4444); **B**, *Charruodon tetracuspoidatus* n. sp.; **C**, *Therioherpeton cargini* (from Bonaparte & Barberena 1975, Museu Histórico e Cultural Vicente Palloti, Santa Maria, Rio Grande do Sul, Brazil); **D**, *Meurthodon gallicus* (from Russell *et al.* 1976). Scale bars: 10 mm.

various authors. Hahn *et al.* (1984, 1994) and Godefroit & Battail (1997) assigned *Therioherpeton cargini* Bonaparte & Barberena, 1975 to the Dromatheriidae, whereas Sigogneau-Russell & Hahn (1994) recognized a Therioherpetidae that included *Therioherpeton* and *Meurthodon gallicus*. The holotype of *Therioherpeton cargini* (uncatalogued specimen in the Museu Histórico e Cultural Vicente Palloti, Santa Maria, Rio Grande do Sul, Brazil) preserves a series of broken upper postcanines, except the fifth tooth that retains some vestiges of the crown. Furthermore, there is a portion of the crown of the fifth lower postcanine (Fig. 4C). Upper and lower postcanines both possess four aligned cusps and lack a cingulum (although the lower postcanine crown is missing its base). The “a” and “c” cusps are the larger cusps, whereas the “b” and “d” are almost the same size (Bonaparte & Barberena 1975). Thus, it is noteworthy that the crown morphology of *Charruodon tetracuspoidatus* is similar to that of *T. cargini* in both the number

and the relative development of the cusps. Nevertheless, the latter species differs from the former in that the cusps do not seem to be recurved, and each root exhibits a longitudinal furrow, a feature that has been interpreted as an “incipient bifurcation of the root” (Bonaparte & Barberena 1975).

In addition to the above-mentioned cynodonts, strictly sectorial postcanines are known also in cynognathids and galesaurids. However, the differences are even more conspicuous in terms of crown pattern between these cynodonts and *Charruodon tetracuspoidatus*, and the late appearance of the Santa Maria form makes assignment to either family highly doubtful.

The new material presents, as it is clearly evident from the above comparisons, a number of similarities and differences with members of all groups of advanced cynodonts. We propose the provisional inclusion of *Charruodon tetracuspoidatus* within Therioherpetidae, pending further evidence for an alternative assignment.

A review of the phylogenetic interrelationships of advanced cynodonts is beyond the scope of our paper. Instead, we would like to propose a sequence of morphological changes in the sectorial postcanines of some advanced cynodonts (Fig. 4). At first, the chiniquodontid postcanines show the prominence of the central cusp sharply posteriorly directed. The condition in *Charruodon* is similar, but the accessory cusps are more developed and even retain some posterior curvature. In *Therioherpeton*, the morphology of the teeth is mostly similar to that of *Charruodon*, but the cusps are not directed posteriorly and the root features a prominent groove. Finally, the postcanine morphology of *Meurthodon* is similar to that of *Charruodon*, and possibly *Therioherpeton*, but the crown is narrower and the roots are completely divided (Russell *et al.* 1976; Sigogneau-Russell & Hahn 1994). The latter feature suggests a mammaliaforme evolutionary level for *Meurthodon*, judging from the recent phylogenetic proposals of Hopson & Barghusen (1986), Rowe (1988), Wible (1991), Crompton & Luo (1993) and Luo (1994).

The new sectorial-toothed cynodont *Charruodon tetracuspидatus* from the Santa Maria Formation confirms the high diversity of the Brazilian Triassic fauna. The association of cynodonts with sectorial teeth, the traversodontid *Exaeretodon*, and the basal archosaur *Proterochampsia* is recorded also from the Carnian age Ischigualasto Formation of Argentina (Rogers *et al.* 1993; Martinez *et al.* 1996), which suggests that the stratum in the Santa Maria Formation yielding *Charruodon tetracuspидatus* is approximately 228 my. old.

### Acknowledgements

We are especially grateful to D. Cargnin who showed us the locality of provenance. J. Bertoletti and M. Richter (Laboratório de Paleontologia, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica de Rio Grande do Sul, Brazil), J. Powell (Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina) and A. Brutti (Museu Histórico e Cultural Vicente Palloti, Santa

Maria, Rio Grande do Sul, Brazil) kindly let us examine specimens in their care. For comments and advice, we thank J. Ferigolo, M. Langer and L. Maciel, who also made suggestions for the name of the species. We particularly thank the reviewers, B. Battail (Laboratoire de Paléontologie, MNHN, Paris) and P. Godefroit (Institut des Sciences naturelles de Belgique), whose comments and suggestions greatly improved the final version of the paper. S. Modesto revised our English. Preparation of the material was performed by M. Isasi, then at the Museo Argentino de Ciencias Naturales Bernardino Rivadavia in Buenos Aires. This research was made possible by financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) of Brazil, the Museu de Ciências e Tecnologia, Pontifícia Universidade Católica de Rio Grande do Sul, Brazil and the Museu de Ciências Naturais da Fundação Zoobotânica de Rio Grande do Sul.

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Submitted on 17 August 1999;  
accepted on 23 March 2000.