



## ABSTRACT

*Carolocoutoia ferigoloi* gen. et sp. nov. is the largest of protodidelphid marsupials, known from Middle Paleocene levels at Itaboraí Formation, southeastern Brazil. It differs from other members of this family in having molars with low cusps which are basally inflated, rounded crests without cutting edges, and a thick enamel layer which is wrinkled, specially at the labial half. A comparative analysis among representatives of this family led us to recognize only three genera undoubtedly assignable to it: *Protodidelphis* PAULA COUTO, 1952, *Robertbutleria* MARSHALL, 1987, and *Carolocoutoia* gen. nov. Protodidelphids lack the basic derived features diagnostic of Polydolopimorphian marsupials, while most of its derived features agree with its belonging to the Didelphimorphia. Protodidelphids comprise a specialized clade of opossum-like marsupials adapted to frugivorous or frugivore-omnivorous feeding habits. They differ from other didelphimorphians in having very large, spire-like entoconids, reduced and antero-posteriorly compressed paraconids, absence of styler cusp C and of para- and metaconules, large styler cusps B and D which are proximate to each other, short postmetacristae, eccentric protocones, and molars that increase rapidly in size from M/m1 to M/m3.

## RESUME

*Carolocoutoia ferigoloi* n. gen. et sp. (Protodidelphidae), un nouveau "marsupial opossum-like" du Brésil. *Carolocoutoia ferigoloi* n. gen. et sp. est le plus grand marsupial protodidelphidé connu des niveaux du Paléocène moyen de la Formation Itaboraí, Sud-est du Brésil. Il diffère des autres membres de cette famille par des molaires avec des couronnes très courtes, des cuspides basses gonflées à la base, des crêtes arrondies sans bords coupants, une grosse couche d'émail labialement rugueuse. Une analyse comparative des représentants de cette famille nous a permis de reconnaître seulement trois genres: *Protodidelphis* PAULA COUTO, 1942, *Robertbutleria* MARSHALL, 1987, et *Carolocoutoia* n. gen. Les protodidelphidés n'ont pas les caractères diagnostiques dérivés des marsupiaux polydolopimorphes, tandis que la majorité de ses caractères dérivés s'accordent avec son appartenance aux Didelphimorphia. Les protodidelphidés constituent un clade spécialisé de marsupiaux adaptés à un régime alimentaire frugivore ou frugivore-omnivore. Ils diffèrent d'autres didelphimorphes par de très grands entoconides, des paraconides réduits et comprimés antéro-postérieurement, l'absence de la cuspidé styler C et des para- et métaconules, des cuspides styleres B et D grandes et proximales, postmétacrista courte, protocône excentré, et des molaires qui augmentent rapidement de taille, des M/m1 vers M/m3.

## INTRODUCTION

Protodidelphids were recently recognized as a family of South American marsupials (Marshall *et al.*, 1990); however, both its intra- and interfamilial relationships have been subject of different interpretations (cf. Paula Couto, 1952; Aplin and Archer, 1987; Reig *et al.*, 1987; Marshall, 1987; Marshall and Muizon, 1988; Marshall *et al.*, 1990; Szalay, 1994; Goin and Candela, 1996). Judging by their molar structure (low crowns, bunoid cusps, poorly developed cristae), these medium to large-sized opossum-like marsupials had omnivorous or frugivore-omnivorous feeding habits. Their known distribution, according to the taxonomic concept of the Protodidelphidae followed in this work (see below), was restricted to South America during middle

Paleocene times (Itaboraian Age; but see Marshall *et al.*, in press).

In this report we describe a new genus and species of protodidelphid which represents the largest known member of this family. We discuss its affinities, as well as the diagnostic features of the family among didelphimorphian marsupials.

**Abbreviations:** MCN-PV, Paleontología Vertebrados, Museo de Ciencias Naturales, Fundação Zoobotânica de Rio Grande do Sul, Porto Alegre, Brazil; DGM, Divisao de Geologia e Mineralogia do Departamento Nacional da Producao Mineral, Ríó de Janeiro, Brazil; MLP, Departamento Paleontología Vertebrados, Museo de La Plata, Argentina. M1, M2, M3, M4, upper molars.

## SYSTEMATICS

Supercohort MARSUPIALIA ILLIGER, 1811

Order DIDELPHIMORPHIA GILL, 1872

Family PROTODIDELPHIDAE (MARSHALL, 1987)

**New diagnosis:** protodidelphids differ from other didelphimorphians in their large size, with very low-crowned molars having bunoid cusps; lower molars have the hypoconulid posteriorly oriented; the entoconid is very large, conical, spire-like, and circular in section, with its base occupying most of the lingual half of the talonid; paraconids are anteroposteriorly compressed and somewhat reduced; upper molars lack StC, as well as para- and metaconules; the postmetacrista is poorly developed (except in *Guggenheimia*); StB and StD are well developed, proximate to each other, and connected by a zigzag crest (except in *Guggenheimia*); the centrocrista is more "U"-shaped than "V"-shaped (except in *Guggenheimia*); the long axis of StD is not parallel to the molar line but clearly oblique to it; upper and lower molars increase markedly in size from M/m1 to M/m3.

**Included genera:** *Guggenheimia* PAULA COUTO, 1952 (?), *Protodidelphis* PAULA COUTO, 1952, *Robertbutleria* MARSHALL, 1987, and *Carolocoutoia* gen. nov.

**Comments:** on the position of *Guggenheimia*, see the Discussion.

### *CAROLOCOUTOIA* gen. nov

**Etymology:** in memory of Dr. Carlos de Paula Couto (1930-1982), for his numerous contributions on fossil mammals from Brazil.

**Type species:** *Carolocoutoia ferigoloi* sp. nov.

**Distribution:** Middle Paleocene (but see Marshall *et al.*, in press), South America.

**Diagnosis:** as for the type species.

*Carolocoutoia ferigoloi* sp. nov.

(plate 1, fig. 1a)

**Etymology:** honouring Dr. Jorge Ferigolo, researcher of the Museo de Ciencias Naturais, Fundação Zoobotânica de Rio Grande do Sul, Porto Alegre, in recognition to his contributions on the evolutionary biology of South American mammals.

**Holotype and only known specimen:** MCN-PV 1802, an isolated upper left molar (M<sup>3</sup>; see Comments).

**Horizon and Locality:** Sao José de Itaboraí, Niteroi, state of Rio de Janeiro, Brazil. Itaboraí Formation, Middle Paleocene (Itaboraian Age; but see Marshall *et al.*, in press).

**Measurements:** length: 7.2 mm; width: 6.8 mm.

**Diagnosis:** differs from other protodidelphids in its larger size; upper molars with very low crown, low cusps which are basally inflated, rounded crests without cutting edges; thick enamel layer wrinkled labially and at the antero-labial and postero-labial corners.

**Description**

The holotype is notable for its large size and bunoid, sharpless, and basally inflated cusps. The molar is subequal in length and width (see Measurements and plate 1, fig. 1). The enamel layer is thick and wrinkled mostly at the labial face and at the parastylar and metastylar corners. There is very few difference in height between the stylar shelf and the shallow trigon basin. In occlusal view it is apparent that the lingual and labial faces of the tooth are not limited by cusps -protocone and stylar cusps, respectively- but that the crown faces extend smoothly outwards, thus enlarging its transverse diametre. Three stylar cusps are present: StA -small but clearly visible-, StB -the largest one-, and StD -smaller than StB. The ectoflexus is poorly developed. All stylar cusps are connected by sharpless crests. From StB a short crest connects with the posterolabial slope of StA. Linking StB and StD there is a very low, irregular crest that describes a zigzag trajectory in occlusal view. Behind StD two crests are developed: one of them is labially oriented, curved, and ends at the metastylar corner; the other one is very short and extends shortly behind this cusp. There are no traces of StC or StE. After StA, the paracone is the lowest cusp. The preparacrista is short and although points towards StA, it ends on the anterior slope of StB. The centrocrista is very feeble, more "U"-shaped than "V"-shaped, and closes smoothly the trigon basin at its labial margin. The metacone is higher than the paracone, lower than StB, and subequal to StD, as in *Robertbutleria*. The postmetacrista is very short; in occlusal view is not straight but slightly curved from the metacone up to the metastylar corner. The protocone is very wide and its cusp is forwardly oriented, being almost in line with a transverse axis connecting StB and the paracone. A short preprotoconal cingulum is present. There are no traces of the para- and metaconule. All cusps show moderately developed wear facets at their points, were the thick enamel layer is evident. The three roots of the tooth are strong and wide, being the lingual one stronger than the two labial ones.

## Comments:

Compared with specimen DGM 303-M of *Protodidelphis vanzolinii* -the only known protodidelphid with a complete upper molar series preserved- the holotype of *Carolocoutoia ferigoloi* shows, in overall shape and proportions, more correspondences with the M3 of that species. These include the relative sizes of the cusps, shape of the metastylar corner, and relative length of the postmetacrista.

## DISCUSSION

### Affinities of the Protodidelphidae

Protodidelphids were firstly regarded as a subfamily (Protodidelphinae MARSHALL, 1987) of Caroloameghiniidae, then considered as basal polydolopimorphians. In Marshall's (1987: 145) original concept, protodidelphids included the following genera: *Bobbschaefferia* PAULA COUTO, 1970, *Guggenheimia* PAULA COUTO, 1952, *Protodidelphis* PAULA COUTO, 1952, *Reigia* PASCUAL, 1983, and *Zeusdelphys* MARSHALL, 1987. Posteriorly Marshall *et al.* (1990) recognized them at family rank, regarding it as the plesiomorphic sister group of all remaining Polydolopoidea (Order Polydolopimorphia). This time, Marshall *et al.* (1990) excluded *Zeusdelphys* and *Reigia* from the Protodidelphidae, including instead two additional genera: *Procaroloameghinia* MARSHALL, 1982, and *Robertbutleria* MARSHALL, 1987. More recently, Goin and Candela (1996) argued in favour of the didelphimorphian affinities of the Protodidelphidae, as was already done by Aplin and Archer (1987).

The notable diversity of Paleocene opossum-like marsupials bearing bunoid dentitions has complicated speculations on the affinities of the Protodidelphidae, mainly due to several convergences in their molar morphology. The concept of Protodidelphidae followed here is restricted to the following genera: *Protodidelphis*, *Guggenheimia* (?), *Carolocoutoia*, and *Robertbutleria*, and considers this family as a derived clade of Didelphimorphian marsupials. This implies the exclusion of *Procaroloameghinia*, *Zeusdelphys*, *Reigia*, and *Bobbschaefferia*, whose affinities are discussed below:

1. *Procaroloameghinia pricei* MARSHALL, 1987 was recognized on the basis of two mandibular remains belonging to the same individual – DGM 805-M and DGM 924-M– with complete p3-m4. Additionally, several lower molars and at least one upper, belonging to a new – still innominate – species of *Procaroloameghinia*, have been recently recovered from beds at Yacimiento Las Flores, in Central Patagonia (Chubut province, Argentina; Itaboraian Age; Goin *et al.*, 1997). A review of the holotype of *P. pricei* and of the new Patagonian specimens led us to the following conclusions: (a) as stated by Marshall (1982, 1987), *Procaroloameghinia* is an ideal structural ancestor of *Caroloameghinia* AMEGHINO, 1901, and (b) the Caroloameghiniidae were peradectoid marsupials of bunoid dentitions convergent to, but with no direct affinities with, the Protodidelphidae. It is worthy to comment briefly the main features of specimen MLP 90-II-5-122 (plate 1, fig. 1d), an upper molar of

*Procaroloameghinia* sp. from Patagonia; this specimen is interesting not only because is the only known upper tooth assignable to this genus, but also because of its generalized pattern: straight centrocrista, para- and metaconule moderately developed and subequal, StC present, well developed postmetacrista, and very wide protocone. Except this last feature, exclusive of caroloameghiniids, the rest of them is common among peradectoids; on the contrary, among protodidelphid didelphimorphians several derived features are clearly opposed to them (see the diagnosis of Protodidelphidae). Even though some of these features appear convergently in other marsupial lineages – e.g., in primitive Polydolopi-morphians; see Goin and Candela (1996) –, the combination of them is diagnostic of the Protodidelphidae.

2. The genus *Bobbschaefferia* PAULA COUTO, 1970 [= *Schaefferia* PAULA COUTO, 1952: 12, nec *Schaefferia* ABSOLON, 1900: 265 (Collembola), nec *Schaefferia* HOULBERT, 1918: 421 (Lepidoptera)] includes only one species: *B. fluminensis* (PAULA COUTO, 1952). Its holotype consists of a fragmentary left mandible with the two last molars preserved (MNRJ 1350-V). Paula Couto also assigned specimen DGM 314-M as paratype (Paula Couto, 1952) or hypodigm (1962) of this species. However, as already suggested by Crochet (1980) both specimens do not belong to the same taxon. Although *B. fluminensis* can be referred to a didelphimorphian, it lacks most of protodidelphid synapomorphies: the paraconid is not reduced or antero-posteriorly compressed, the entoconid is not spire-like but labio-lingually compressed, and the cristid obliqua is more labially placed at the anterior end. On the contrary, the "paratype" DGM 314-M, as well as several other DGM and MNRJ specimens previously assigned to *B. fluminensis* (see Paula Couto, 1970; Marshall, 1987), are clearly assignable to the Protodidelphidae, and probably to a new species, of *Guggenheimia* (Goin & Oliveira, unpublished data).

3. Regarding *Reigia punae* PASCUAL, 1983, a recent review by Goin and Candela (1996) excluded it from the Polydolopimorphia. The authors concluded that "...even though we are confident in considering *Reigia punae* a didelphimorphian its autapomorphies prevent us from referring it to any of the known families of this order (Goin and Candela, 1996: 295). Even though its somewhat bunoid shape superficially resembles protodidelphids, known remains of *Reigia punae* – a fragmentary maxillary with M3-M4 – lack most of protodidelphid synapomorphies, e. g. absence of StC and para- and metaconule, StB and StD very well developed and connected by a zigzag crest, poorly developed postmetacrista in M3. Finally, several features present in *Reigia* – and in many other didelphimorphians – are not present in proptodidelphids: absence of pre- and postprotoconal cinguli, anteroposteriorly compressed M4, preparacrista pointing to StA (except in *Guggenheimia*), etc. For this reason, we consider *Reigia punae* not a protodidelphid but a Didelphimorphia *incertae sedis*.

4. *Zeusdelphys complicatus* was originally regarded by Marshall (1987) as a polydolopimorphian of his subfamily Protodidelphinae. Previously, the same author (Marshall, 1984) referred the specimen DGM 896a-M – holotype of *Z. complicatus* – to

the didelphimorphian *Eobrasilia coutoi*, one of the largest opossum-like marsupials known from Itaboraí. Later, Marshall *et al.* (1990) assigned *Zeusdelphys* to the Kollpaniidae, in their opinion the more generalized group of Paucituberculata marsupials. Even though it was originally referred to a M3, it could be argued that the holotype of *Z. complicatus* corresponds to a first upper molar, thus explaining several features of it otherwise common in the M1's of other Didelphimorphians: small postmetacrista, StB close to the paracone, large, subequal StB and StD. On one hand, *Z. complicatus* shares some derived features with protodidelphids: lack of StC and of para- and metaconules, eccentric protocone, and large StB and StD -this last feature also being present in the Polydolopimorphia and the Paucituberculata. On the other hand, some very peculiar features of this taxon are autapomorphic: almost flat labial surfaces of styler cusps, StB and StD subdivided by lateral grooves, open centrocrista, presence of a vertical groove at the anterior face of the protocone, and presence of a very peculiar, flat cusp lingual to and between StB and StD. On the whole, and in spite of several similarities with the Protodidelphidae, *Zeusdelphys complicatus* is so extremely derived, and its known remains so scarce, as to preclude its precise affinities. In absence of other materials of this taxon, we regard it as a Didelphimorphia *incertae sedis*. It wouldn't be discarded the original suggestion by Marshall (1984) that it may represent an upper molar of *Eobrasilia coutoi*, a peculiar non-protodidelphid didelphimorphian known only from Itaboraí, Brazil.

In conclusion, we propose here a restricted concept of the Protodidelphidae that includes only the four genera already mentioned (but see below for the assignment of *Guggenheimia*). It is interesting to point out that none of the earlier (e. g., Tiupampian) South American marsupial faunas known up to date includes taxa referable to, or showing at least some features in the line of, the Protodidelphidae.

Protodidelphids are didelphimorphians, not polydolopimorphians; in their description of the primitive polydolopimorphian *Rosendolops primigenium*, from Casamayoran levels of Patagonia, Goin and Candela (1996) proposed a concept of the Polydolopimorphia that explicitly excludes the Protodidelphidae. "Most of protodidelphid 'polydolopimorphian' features are, in fact, related to the development of bunoid molars compatible with more frugivorous feeding habits: brachyodont molars, large cusps B and D, similar in height to the paracone and metacone, reduced cristae. None of them, however, are synapomorphies diagnostic of polydolopimorphian marsupials" (Goin and Candela, 1996: 294). On the contrary, the amount of features present in the Protodidelphidae agree with their assignation to the Didelphimorphia. In some of these features -e. g., metacone only slightly higher than the paracone, rounded centrocrista, which is more "U"-shaped than "V"-shaped- protodidelphids comprise the plesiomorphic extreme of a gradient, whose more derived expression is present in other didelphimorphian lineages. However, in other features -e. g., complete absence of StC, para- and metaconules, bunoid cusps, large size- they are derived among other groups of the order.

### Affinities of *Carolocoutoia*

Compared to the other taxa here referred to the Protodidelphidae: *Protodidelphis*, *Guggenheimia*, and *Robertbutleria*, *Carolocoutoia* seems to be more directly related

to *Robertbutleria*. In fact, when confronted with specimen MCN-PV 1806 of *R. mastodontoidea*, the holotype of *C. ferigoloi* seems to represent, in several aspects, an inflated, wrinkled, and larger version of it. In both species the metastylar corner of the M3 show characteristic creases, and on the posterior slope of StD it can be observed a small crest -though much less developed in *R. mastodontoidea*- that extends to the posterior end and near the base of this cusp. A new specimen belonging to this species, MCN-PV 1806 (plate 1, fig. 1b), deserves further comment: even though it is clearly larger than the other two known upper molars of this species (see Marshall, 1987), it should be noted that a rapid increase in size from M/m1 to M/m3 is precisely a diagnostic feature of the Protodidelphidae. In his original description of *R. mastodontoidea*, Marshall (1987) assigned specimen DGM 896A-M to a M1 and specimen DGM 896B-M to a M2. We agree with this and assign specimen MCN-PV 1806 to a M3 of the same species. Apart from its larger size, the only differences that this specimen has with the DGM specimens are gradient-related. For instance, in DGM 896A-M (a M1) a preprotoconal cingulum continues posteriorly to connect directly with the postprotoconal cingulum; in specimen DGM 896B-M (a M2) the pre- and postprotoconal cinguli are not connected to each other but are interrupted at the lingual face of the protocone; finally, in specimen MCN-PV 1806 (a M3) both cinguli are much shorter and more clearly separate from each other. The postmetacrista of this last specimen also maintains the same proportions in length with respect to the those of the DGM specimens as that of the M3 of *Protodidelphis vanzolinii*: all of them are subequal in length, although that of M2 is, in proportion to the size of the tooth, slightly larger.

In turn, *Carolocoutoia* represents a more derived pattern than that of *Robertbutleria*: larger size, much more bunoid cusps basally inflated, shorter cristae, lower crown. All these features warrant its generic identity despite the basic morphological pattern shared by both.

*Robertbutleria* and *Carolocoutoia* seem to be, in turn, more closely related to *Protodidelphis* than to *Guggenheimia*. Even though upper molars of *G. brasiliensis* were unknown until now, there have been recently collected many upper and lower molars of this and of a new species of *Guggenheimia* at Itaboraian levels in Yacimiento Las Flores, Central Patagonia (see Goin *et al.*, 1997). Additionally, there is at least one isolated upper molar in DGM collection that is referable to this genus; it consists of an uncatalogued specimen (see plate 1, fig. 1c) whose structure, together with that of the Patagonian specimens, suggest that *Guggenheimia* could even not be a protodidelphid: molars are less bunoid, stylar cusps B and D are very proximate to each other (much more than in *Carolocoutoia*, *Protodidelphis*, and *Robertbutleria*), StD is more labiolingually compressed, the postmetacrista is well developed, the zig-zag crest connecting stylar cusps B and D does not exist, the protocone is much more excentric (anteriorly placed) and the preparacrista points to StA. All these features but the first one are derived ones, and most of them suggest that *Guggenheimia* could represent an early offshoot of differently specialized didelphimorphians.

In conclusion, *Carolocoutoia ferigoloi* is one of the largest known didelphimorphian marsupials, fossil or living. Its very low crown, reduction of cristae, and inflated cusps, suggest that this species developed extreme adaptations towards



frugivorous feeding habits. Among the Protodidelphidae, *Carolocoutoia* seems to be more closely related to *Robertbutleria* than with any other member of this family. In turn, *Protodidelphis vanzolini* is in several features ancestral to the more specialized pattern present in species of these two genera. Finally, *Guggenheimia* may prove to belong not to protodidelphids but to a different clade of didelphimorphian opossums.

It is difficult, in view of our present state of knowledge, to precise the affinities of the Protodidelphidae among the Didelphimorphia. Its more probable affinities will arise after a thorough phylogenetic analysis including most of Paleogene South American opossum-like marsupials, including several enigmatic taxa as *Reigia punae* and *Zeusdelphys complicatus*.

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#### EXPLANATIONS OF PLATE

Figure 1.— Occlusal views of **a**: *Carolocoutoia ferigoloi* gen. et sp. nov., holotype MCN-PV 1802, an isolated upper left M?3; **b**: *Robertbutleria mastodontoidea*, specimen MCN 1806, an isolated upper left M3; **c**: *Guggenheimia brasiliensis*, uncatalogued DGM specimen, an isolated upper left M1; **d**: *Procaroloameghinia* sp., specimen MLP 90-II-5-122, an isolated upper right M?1. Scale: 1 mm.

