

# NEW MARSUPIAL (MAMMALIA) FROM THE EOCENE OF ANTARCTICA, AND THE ORIGINS AND AFFINITIES OF THE MICROBIOTHERIA

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## ABSTRACT:

We describe and comment on an isolated upper molar belonging to *Woodburnodon casei* gen. et sp. nov. (Mammalia, Marsupialia, Microbiotheria, Woodburnodontidae fam. nov.), from the Eocene of the La Meseta Fm (TELM 5 or *Cucullaea* I Member), Marambio (Seymour) Island, Antarctic Peninsula. With a body mass estimated between 900 to 1,300 g (depending on the type of equation and the possible molar locus of the type specimen), it represents the largest known Microbiotheria, living or extinct. Besides its size, other diagnostic features include a proportionally large metacone, reduced or absent para- and metaconules, and an unusual labial notch between styler cusps C and D. *Woodburnodon casei* is an undoubted Microbiotheria; however, its reference to the Microbiotheriidae is discarded: almost all its morphological characters are plesiomorphic when compared with South American microbiotheriids, even with respect to the oldest representatives of this family. This suggests (a) a quite ancient and southern origin for *Woodburnodon* and its ancestors, and (b) that the origins and initial radiation of the Microbiotheria may have occurred from a generalized peradectoid. The new taxon, here referred to the new family Woodburnodontidae, constitutes the second microbiotherian known from these Antarctic levels and age; this confirms the association of representatives of this order within a common, Andean-Patagonian-Antarctic biogeographic region, already present since the Late Cretaceous. Microbiotherians stand as the plesiomorphic sister-group of Bonapartheriiform marsupials, the latter including *Glasbius* and allied taxa.

Keywords: *Antarctica, Eocene, La Meseta Fm., Marsupials, Microbiotheria.*

## RESUMEN: Nuevo marsupial (Mammalia) del Eoceno de la Antártida, y los orígenes y afinidades de los Microbiotheria.

Se describe y comenta un molar superior aislado perteneciente a *Woodburnodon casei* gen. et sp. nov. (Mammalia, Marsupialia, Microbiotheria, Woodburnodontidae fam. nov.), procedente de niveles eocénicos de la Fm. La Meseta (Miembro TELM 5 o *Cucullaea* I), Isla Marambio (Seymour), Península Antártica. Con una masa corporal estimada entre 900 y 1.300 g (dependiendo de la ecuación analizada y del locus molar posible), se trata del más grande microbiotherio, fósil o viviente, conocido hasta el momento. Además del tamaño, sus rasgos diagnósticos incluyen un metacono proporcionalmente grande, para- y metaconulo reducidos o ausentes, y una inusual muesca labial entre las cúspides estilares C y D. *Woodburnodon casei* es un indudable Microbiotheria, si bien su pertenencia a los Microbiotheriidae debe descartarse. Casi todos sus caracteres son plesiomorfos en comparación con los microbiotheriidos sudamericanos, incluso cuando se lo compara con los más tempranos representantes de la familia. Esto sugiere (a) un origen antiguo y austral para *Woodburnodon* y sus ancestros, y (b) que la evolución inicial de los Microbiotheria pudo haber tenido su origen a partir de un generalizado peradectoideo. El nuevo taxón, aquí asignado a la nueva familia Woodburnodontidae, constituye el segundo Microbiotheria conocido para los mismos niveles y edad de la Antártida, lo que confirma la asociación de los representantes de este orden con una región biogeográfica común, Andino-Patagónico-Antártica, ya existente desde por lo menos el Cretácico Tardío. Los Microbiotheria constituyen el grupo hermano plesiomorfo de los marsupiales Bonapartheriiformes, estos últimos incluyendo a *Glasbius* y taxones afines.

Palabras clave: *Antártida, Eoceno, Fm. La Meseta, Marsupiales, Microbiotheria.*

## INTRODUCTION

Extinct Antarctic mammals are exclusively known from several localities at different levels of the La Meseta Formation (Marambio/Seymour Island, Antarctic Peninsula; Early to Late Eocene; Reguero *et al.* 2002). Up to now the recognized taxa are unequi-

vocally related to South American native mammalian lineages: gondwanatherians (Goin *et al.* 2006); polydolopid, microbiotheriid, and didelphimorphian marsupials (Woodburne and Zinsmeister 1982, Goin *et al.* 1999); tardigrade xenarthrans, and astrapotherian and litoptern ungulates (Reguero *et al.* 2002 and literature cited; Bond *et al.*

2006). Additionally, an enigmatic, insectivore-like mammal represented by tiny isolated tooth, was lost after a brief description (Goin and Reguero 1993).

The first mention of an extinct Antarctic marsupial (and of extinct mammals at all) was that of Woodburne and Zinsmeister's (1982) description of a polydolopine poly-

dolopimorphian. After two decades of field prospecting, it is clear that polydolopines comprise the most abundant marsupials of this age in Antarctica. Successive discoveries led to the description of new polydolopines, as well as several fossils referable to microbiotheriids (Microbiotheria), derorhynchids (Didelphimorphia), and prepido-lopids (Polydolopimorphia; Goin *et al.* 1999). The first Antarctic microbiotherian to be described was an edentulous dentary (Goin and Carlini 1995). A few years later, Goin *et al.* (1999) described *Marambiotherium glacialis* on the basis of this and a new dentary bearing an m4. This taxon is a small-sized microbiotheriid with a few derived features suggesting affinities with the Late Pa-

leocene (Itaboraian age) *Mirandatherium alipioi* (Paula Couto 1952). The specimen first described by Goin and Carlini (1995) can be referred to *Marambiotherium glacialis*.

Here we describe a third specimen belonging to an Antarctic microbiotherian marsupial. Its large size and plesiomorphic dental features prevent any possible referral either to *Marambiotherium glacialis* or to any other member of the Microbiotheriidae. The new taxon sheds new light on the ancient origin (probably, late Cretaceous) of microbiotherians in former Gondwanan continents, on its extreme southern biogeographic range, and on the variously proposed affinities between microbiotherians, other australidelphians, and "polydolopi-

morphians".

#### Abbreviations, methods and terminology.

MLP, División Paleontología Vertebrados, Museo de La Plata; MPM-PV, Museo Regional Provincial "Padre Manuel Jesús Molina", Río Gallegos, IAA, Instituto Antártico Argentino, Dirección General del Antártico, Buenos Aires. Molar dimensions were obtained with a digital calliper. L, length; W, width; all measurements are in mm. Body mass estimations follow Gordon (2003); Y, ln body mass (in grams); X, ln molar area (in square millimeters); r, Pearson Correlation Coefficient;  $r^2$ , Determination Coefficient (for r and  $r^2$ , see Gordon 2003); g, grams. Molar nomenclature follows Goin *et al.* (2003).

## SYSTEMATICS

Infraclass METATHERIA Huxley, 1880  
 Supercohort MARSUPIALIA Illiger, 1811  
 Superorder AUSTRALIDELPHIA Szalay, 1982  
 Order MICROBIOTHERIA Ameghino, 1889

Family WOODBURNODONTIDAE nov.

**Etymology.** Derived from *Woodburnodon* gen. nov., only known genus of the family.

**Included genera.** *Woodburnodon* gen. nov.

**Distribution and diagnosis.** As for the type species.

*Woodburnodon casei*, gen. et sp. nov.

(Figure 1 a-e)

**Etymology.** Generic and specific names honour Drs. Michael Woodburne and Judd A. Case, respectively, pioneer researchers of Antarctic fossil mammals; the generic suffix -odon comes from the Greek *odontos*, tooth. Gender is masculine.

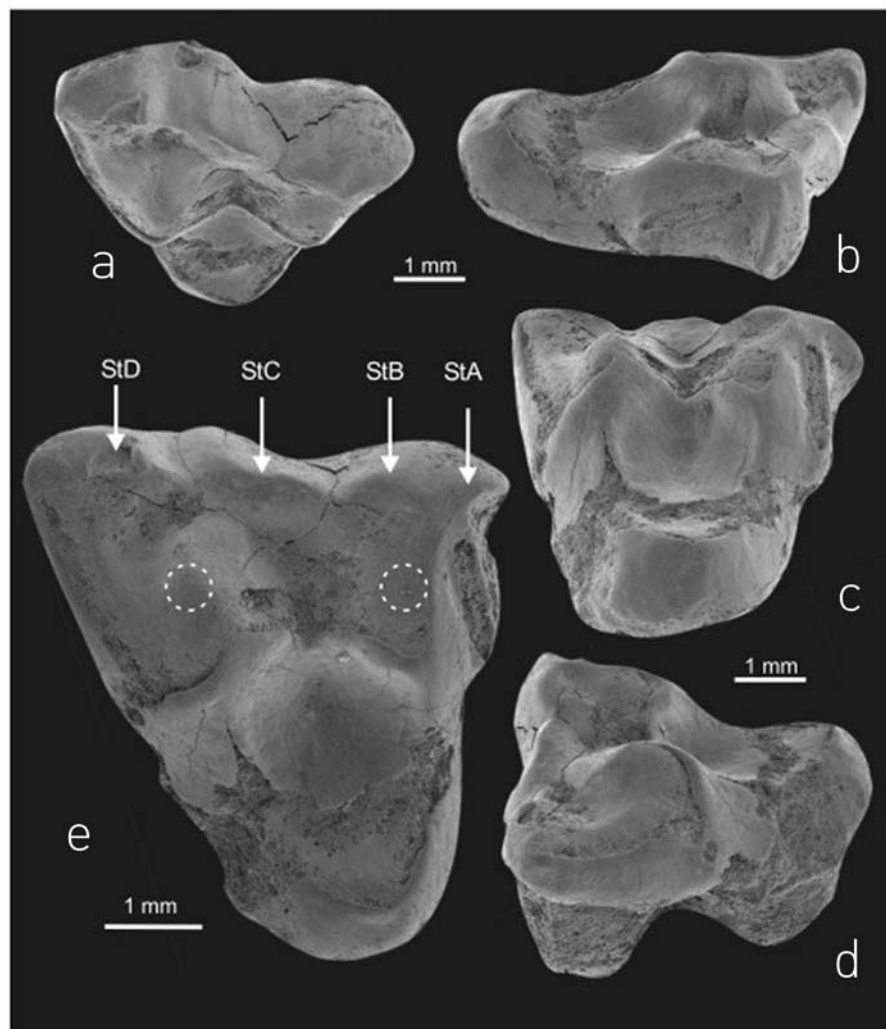
**Type (and only known) species.** *W. casei* sp. nov.

**Generic diagnosis.** As for the type species.

**Type specimen.** MLP 04-III-1-2, an isolated, worn upper right molar (M2 or M3).

**Hypodigm.** The type only.

**Locality, stratigraphy, and age.** Locality IAA 1/95 (Reguero *et al.* 2002), Seymour (Marambio) Island, Antarctic Peninsula. La Meseta Formation (Elliot and Trautman



**Figure 1:** *Woodburnodon casei* gen. et sp. nov. (Microbiotheria). a-e, MLP 04-III-1-2 (Type), an isolated upper right molar (M2 or M3) in labial (a), anterior (b), lingual (c), posterior (d), and occlusal (e) views. Scale: 1 mm.

1982); TELM 5 (Sadler 1988) or *Cucullaea* I Member (Marensi *et al.* 1998). Following Marensi (2006) and Dutton *et al.* (2002) we assign an early Middle Eocene age to the mammal-bearing levels at TELM 5.

**Measurements.** Length: 4.96 mm, width: 5.58 mm.

**Diagnosis** (for the type and only known species of the genus). Differs from all other microbiotherians in the following combination of features: very large size; metacone proportionally large; preparacrista comparatively longer and more perpendicularly oriented in relation to the molar axis; a labial notch is present between stylar cusps C and D.

**Description and comments.** The type specimen is quite worn and lacks enamel on the paracone, centrocrista and postmetacrista; the trigon area is very wide; accordingly, the protocone is stout and robust. The metacone is larger and higher than the paracone (Fig. 1a). The preparacrista seems to end not at the anterolabial corner of the tooth (as in most microbiotheriids) but at an intermediate point between stylar cusps A and B; as a consequence, it is more perpendicularly oriented with respect to the antero-posterior molar axis than in other microbiotherians. The anterobasal cingulum is short and shallow. The metacone is relatively large, high and has convex slopes on both its labial and lingual faces. The centrocrista is broken but its preserved portion indicates it was completely straight (Fig. 1 c, e). Because of its poor preservation at the lingual slopes of the paracone and metacone (Fig. 1 c, e), neither the paraconule nor the metaconule are observable; however, judging from the preserved structures, even if these cusps were present they must have been quite reduced. The postmetacrista is not shortened but moderately developed and straight. The stylar shelf is noticeably reduced, as are the stylar cusps, which are labio-lingually compressed. Notwithstanding, stylar cusps A, B, C and D are recognizable. Stylar cusp B is small, low, and is set immediately labial to the paracone, while stylar cusp D is much smaller, labio-lingually compressed, and located posterolabially to the metacone. Between these cusps, and anterolabial to the metacone, is a thickening of the enamel at the labial face

of the stylar shelf; three minute wear facets suggest that it was originally higher than the preserved structure, thus suggesting its homology with a very labio-lingually compressed stylar cusp C. The ectoflexus is very shallow; posterior to it there is a peculiar, obliquely set notch between stylar cusps C and D (Fig. 1 a, e).

## MOLAR LOCUS OF THE TYPE SPECIMEN

The molar locus of specimen MLP 04-III-1-2 cannot be certainly determined. For a microbiotherian, its postmetacrista is well-developed, suggesting that the specimen is not an M4. In turn, the preparacrista is not extremely short, as is characteristic of most first (and many second) upper molars of microbiotherians, and is not obliquely set but quite transversal to the antero-posterior molar axis, thus suggesting the tooth is an M3. As argued below, *Woodburnodon casei* is a generalized, non-microbiotheriid microbiotherian. Thus, it could be argued that the preparacrista is that of an M2. In short, we conclude that specimen MLP 04-III-1-2 could be either an M2 or an M3.

## WEAR FACETS

Even though specimen MLP 04-III-1-2 is partially broken and worn, it can be observed that the wear facet of the postmetacrista is well-developed -other cutting crests of this molar are not observable due to the strong wear of the whole tooth. However, the most conspicuous feature of this specimen is the important development of the grinding facet of the protocone (at its inner face). This, together with the proportionally large protocone and trigon basin, suggests that the grinding of food during mastication was a predominant feature of *Woodburnodon casei*. The extent of the wear facet at the inner face of the protocone in this species much resembles that of the upper molars of the living *Caluromys derbianus* (Caluromyidae), of frugivorous feeding habits.

## BODY MASS ESTIMATE

Body mass was estimated following procedures stated in Gordon (2003), basically

consisting of a simple least squares regression analyses. Measurements used for constructing all equations were taken from Gordon (2003). A complication is that the molar locus of specimen MLP 04-III-1-2 is uncertain (see above). Molar area (L x W) is 27.67 mm<sup>2</sup>.

Four equations were constructed to estimate the body mass of *Woodburnodon casei*. In the first two, the genus *Caluromys* was excluded of the regression; in the last two it was included (see Gordon 2003).

When *Caluromys* was excluded, the following equations were constructed:

a) Assuming the specimen as a M2, then  $Y = 1.708 X + 1.3478$   $r = 0.994$ ;  $r^2 = 0.989$ . In this case, body mass result is 1,118.08 g;

b) Assuming the specimen as a M3, then  $Y = 1.6356 X + 1.36$   $r = 0.993$ ;  $r^2 = 0.987$ , resulting in a body mass of 889.95 g.

When *Caluromys* was included, the following equations were constructed:

a) Assuming the specimen as a M2, then  $Y = 1.6908 X + 1.5432$   $r = 0.9707$   $r^2 = 0.9424$  resulting in a body mass of 1.283.9 g.

b) Assuming the specimen as a M3, then  $Y = 1.557 X + 1.7592$   $r = 0.9419$   $r^2 = 0.8872$  and the body mass estimation is 1.021.85 g.

Taking in account that microbiotheriids have a reduced M/m4, it is therefore probable that *Woodburnodon* also had its last upper molar reduced in size regarding the M3, a condition also present in *Caluromys*. For this reason we favor the last set of body mass estimations, i.e., that one including *Caluromys* in the equation. In short, our best estimate is that *Woodburnodon* had a body mass between 1,000 and 1,300 g.

The size of specimen MLP 04-III-1-2, and the inferred body mass of *Woodburnodon casei*, indicates that this species constitutes the largest known microbiotherian marsupial, extinct or living.

The second largest microbiotherians are referable to the genus *Pachybiotherium*. Up to very recently, upper molars for representatives of this genus were unknown. Work in progress by F. Goin, M. Tejedor, A. Abello and G. Martin will describe a new species of *Pachybiotherium*, for which an upper molar is known (MPM-PV 1806, a right M3). This new species is slightly larger than the type species of the genus, *P. acclinum* Ameghino, and much larger than *P. minor* Goin. Our

estimate of the body mass of this new species of *Pachybiotherium*, based on its upper molar, is 255.99 g using an equation lacking *Caluromys*, and 312.07 g if *Caluromys* is included in the equation. Thus, and taking into account their body mass estimates, we can conclude that *Woodburnodon casei* was no less than three, and probably four, times larger than the largest species of *Pachybiotherium*.

## DISCUSSION

### A new family of microbiotherian marsupials

*Woodburnodon casei* represents the second Microbiotheria known from the Eocene of the Antarctic Peninsula. Taking into account their poor representation in the fossil record, the currently known array of Middle Eocene Antarctic microbiotherians (two species) should be regarded as moderately diverse.

Three microbiotherian apomorphic features are present in specimen MLP 04-III-1-2, type of *Woodburnodon casei*: wide protocone, comparatively short postmetacrista, and reduced stylar shelf. Additionally, the persistence of a straight centrocrista is a generalized feature present in all known microbiotherians. The reduction or absence of para- and metaconules is also a derived feature present in microbiotherians with known upper molars.

Besides its microbiotherian affinities, it is not possible to refer the new species to the Microbiotheriidae, the only family previously known for this order: (1) microbiotheriids have upper molars with the stylar shelf even more labio-lingually reduced than in *Woodburnodon*. (2) Microbiotheriid stylar cusps are indistinguishable as such, because of their extreme reduction and labio-lingual compression. Actually, most microbiotheriid upper molars have a reduced, ridge-like structure labially bordering the stylar shelf, making impossible to make a secure identification of the stylar cusps. *Woodburnodon casei* is plesiomorphic in that its stylar cusps are still observable and placed in the plesiomorphic condition. (3) Finally, especially on M1-2, microbiotheriids have an extremely short preparacrista which

is oriented not perpendicular to the antero-posterior molar axis but oblique to it; in *Woodburnodon*, even though the preparacrista is worn, it is not significantly short or obliquely oriented. In short, *Woodburnodon casei* cannot be assigned to the Microbiotheriidae, as it lacks the basic synapomorphies that characterize this family. Therefore, we recognize the new family Woodburnodontidae for its inclusion.

### Origins of the Microbiotheria

When compared with the oldest known microbiotherian, *Khasia cordillerensis* (Muizon 1991), from the Early Paleocene of Tiupampa, Bolivia, it is striking that *Woodburnodon casei* is more plesiomorphic than this taxon concerning all of the above mentioned features. In fact, *Woodburnodon* appears to be more plesiomorphic than all other known microbiotherians. This suggests that woodburnodontid's upper molar morphology is close to, or represents the, ancestral microbiotherian molar pattern. The fact that this taxon comes from Paleogene levels of Antarctica is noteworthy, and is an indication that the very origin of microbiotherians could be tied to the southernmost regions of the Austral (biogeographic) Kingdom (*sensu* Morrone 2002), probably during Early Paleocene or even Late Cretaceous times (see below and Woodburne and Case 1996).

Previously (e.g. Marshall 1987, Marshall *et al.* 1990), microbiotheriids and North American pediomyids were grouped in a common clade, the Microbiotheria. Even though this taxonomic conclusion has been abandoned (see, e.g., Kielan Jaworowska *et al.* 2004, Case *et al.* 2005), it was reasonably based. Some advanced pediomyids (e.g. *Protolambda florencae*, from the Late Cretaceous; see Fox 1987: fig 5, and Davis 2007: fig 11) show derived features in common with microbiotheriids (upper molars with reduced stylar shelf, short and obliquely set preparacrista, robust protocone). The upper molar morphology of *Woodburnodon casei* sheds light on this topic, as it is more clearly derivable from a peradectoid-like pattern than from any pediomyid-like morphology. For instance, *Woodburnodon's* upper molar has a metacone that is larger than the

paracone. Pediomyids, as well as other basal metatherians (e.g., alphadontids), have paracones and metacones that are subequal in height and size. Another example is the reduction of the stylar shelf: while pediomyids have much reduced the anterior portion of the stylar shelf, in *Woodburnodon* this structure is equally reduced, both anteriorly and posteriorly. A third feature is the strong, winged conules of pediomyids, which are reduced or absent in *Woodburnodon* and all other microbiotherians. Finally, the preparacrista in *Woodburnodon* is more or less perpendicular to the molar axis, while in pediomyids is invariably oriented anteriorly. In short, these features suggest that some of the more derived microbiotherians convergently evolved a pediomyid-like morphology, i.e., a further reduction in the stylar shelf and cusps, and a more oblique orientation and shortening of the preparacrista. Thus, *Woodburnodon* adds empirical evidence of the independence of pediomyid and microbiotherian lineages. Two other, more radical, alternative inferences can be made on this topic: (1) *Woodburnodon* is indeed a Pediomyidae whose ancestors reached Antarctica from North America, via South America, by the Late Cretaceous; more modern microbiotheriids evolved from this pediomyid lineage. For the reasons stated above, we cannot favor this hypothesis. (2) At least some of the Late Cretaceous, North American taxa currently assigned to the Pediomyidae are actually advanced microbiotherians that arrived on that continent from Southern South America before the end of the Cretaceous. Testing this last hypothesis would need a phylogenetic analysis including all known microbiotherians together with peradectoids, early didelphoids, as well as more basal metatherians (e.g., alphadontids and allies). However, on the basis of *Woodburnodon's* upper molar morphology, as well as on the new evidence on the evolution of the Pediomyidae (Davis 2007), this last hypothesis seems even less probable.

Following Johanson (1996, see also Eaton 1993) Kielan Jaworowska *et al.* (2004) updated the dental diagnosis of the Peradectidae. Regarding the upper molars, they state that these molars have "... relatively smaller stylar cusp A placed close to stylar cusp B



and about on the same level on the stylar shelf; cusp B reduced in size and subequal to stylar cusp C; ectoflexus shallow on all upper molars, not becoming deeper posteriorly; metacone taller than paracone; postmetacingulum lost; preparacrista extends from paracone to a point anterior to cusp B, rather than terminating at that cusp; conules and conular cristae reduced, with postmetacingular crista lost." (Kielan Jaworowska *et al.* 2004: XX). [Note that this diagnosis was made as compared to the "Alphadontidae", also regarded as basal "didelphimorphians". Case *et al.* (2005), on the contrary, included *Alphadon*, *Peradectes* and allies within the Alphadelphia, a clade outside of, and basal to, the Didelphimorphia. While we still recognize the Alphadontidae as a basal clade -i.e., Case *et al.*'s (2005) Alphadelphia-we now accept the exclusion of the Peradectidae from the Alphadelphia, and, based on Kielan Jaworowska *et al.*'s (2004) arguments, we regard it as a ?Didelphimorphia (Goin 2007). Goin (2003, 2007) argued that peradectids, mayulestids, and caroloameghiniids belong to a natural group: the Peradectoidea]. It is clear from the above-mentioned diagnosis that the Microbiotheria were derived from a peradectoid-like ancestor; in turn, the reduction of stylar cusps and shelf, as well as the enlargement of the protocone in the upper molars, constitute derived features diagnostic of the Microbiotheria.

#### Affinities of the Microbiotheria

The new evidence provided by *Woodburnodon casei* is relevant for the interpretation of the affinities of several marsupial groups that have been variously referred as derived from, or related to, the Microbiotherians. Recent studies of metatherian phylogeny consistently relate microbiotherians with part, or all, the Australidelphian marsupial clades (see, e.g., Asher *et al.* 2004, and literature cited). Regarding South American marsupials, outstands the problem of polydolopimorphian relationships. Goin (2003), Goin and Candela (2004), and Oliveira and Goin (2006) argued that microbiotherians have a sister-group relationship with polydolopimorphians. According to Case *et al.* (2005) polydolopimorphians include the

Hatcheriiformes, the Bonapartheriiformes, and the Polydolopiformes (on the origin of the molar pattern of the Polydolopiformes, see Goin *et al.* 2003). Main derived features leading to polydolopimorphians include the enlargement of the metaconule, the pairing of StB and D with the paracone and metacone, respectively, and the further reduction of the stylar shelf. In fact, *Woodburnodon casei* fits quite well the pattern expected for an ancestor of Hatcheriiformes as well as of Bonapartheriiformes: reduced stylar shelf, large protocone, short preparacrista and postmetacrista -the true nature of *Woodburnodon*'s metaconule is unknown because of the poorly preserved type specimen of this species. However, a series of peculiar apomorphies of the Polydolopiformes (*Roberthoffstetteria*, polydolopids and allies), are definitely not derivable from *Woodburnodon*; this suggests now to us that these marsupials may belong to a different clade, with quite different origins than those of Hatcheriiformes + Bonapartheriiformes. Particularly, the lingual alignment of the paraconule and the metaconule with the protocone, the expansion of anterior and posterior cingula, and the persistence of a StC which is placed lingually with respect to other stylar cusps in the upper molars, seem to be contradictory with other previously related groups, as the bonapartheriiformes. New phylogenetic analyses should test these contrasting hypotheses, especially taking in account the new information provided by *Woodburnodon* and several other basal metatherians. We wonder, for instance, whether the inclusion in a future analysis of the North American, late Cretaceous *Albertatherium* could reveal an independent origin of polydolopines and allies, more closely related to a much more basal metatherian radiation than that of microbiotherians and bonapartheriiformes. Upper molars of *Albertatherium* have their para- and metaconules set quite lingual with respect to the paracone and metacone, respectively, as well as a lingual StC.

#### Ecology, biogeography, and the timing of the microbiotherian radiation.

*Dromiciops gliroides* Thomas is the only living representative of the Order Micro-

biotheria. Its range is restricted to the temperate forests of the Southern Andean Cordillera, from 36° to 43° South latitude. It is regarded as a strictly arboreal animal (Szalay 1994), with frugivorous-insectivorous feeding habits (Mann 1955, Amico and Aizen 2000). An interesting case of mutualism has been described by Amico and Aizen (2000) involving *Dromiciops* as a seed disperser of the parasite epiphyte *Tristerix corymbosus* (Loranthaceae). Seed dispersal of this plant requires not only effective ingestion and transport, but also an adequate placement on the living branches of its host tree (*Nothofagus dombeyi*). *Dromiciops* discards the exocarpium of *Tristerix* fruits and eats the remaining parts, including the seeds; the latter are transported throughout the intestine, and defecated later --up to 98% of the seeds ingested are deposited on the host tree. Passage through the digestive tract of *Dromiciops* is crucial for seed germination. Thus, *Dromiciops* is a highly effective seed disperser of this plant. To Aizen *et al.* (2002), the high dependence of *Tristerix* on its marsupial disperser could be a result of the antiquity of their co-evolutionary relationships (*Tristerix* is the oldest known Loranthaceae, being first recorded in the late Cretaceous, ca. 70 Ma).

The mutualistic relationship between *Dromiciops* and a plant related to the *Nothofagus* flora provides an interesting clue on the possible trophic relationships of extinct Antarctic microbiotheriids. Other microbiotheriid associations, such as one proportionally rich assemblage from the early Neogene of Central Patagonia, have also been related to the nearby presence of a *Nothofagus* flora (Goin *et al.* 2007). The upper molar morphology of *Woodburnodon casei* includes an enlarged, bulky protocone and a wide trigon basin indicative of frugivorous feeding habits. In turn, frugivory suggests an arboreal or semi-arboreal type of locomotion. In short, as already suggested for polydolopine polydolopimorphians (Woodburne and Case 1996), the origin, radiation, and dispersal of microbiotherians may be related to the origin, radiation, and dispersal of the *Nothofagus* flora. The distribution, locomotion, and feeding habits of the single living species of Microbiotheriidae, *Dromiciops gliroides*, strongly support this last

hypothesis. Hill and Dettmann (1996) identified several rapid evolutionary radiations following the appearance of *Notofagus* in the fossil record. The oldest of these occurred by the Late Campanian-Maastrichtian of southernmost Patagonia and the Antarctic Peninsula. This suggests a possible timing for the microbiotherian radiation. A recent phylogenetic review of metatherians addressed once again the question of the origins and early biogeography of the Australidelphian radiation. Discussing their results on *Dromiciops gliroides*, the authors stated that the "[n]esting of *Dromiciops* within Australidelphia implies either back-migration from Australia to South America or multiple dispersals into Australia" (Asher *et al.* 2004: 248). Our identification of *Woodburnodon casei* as the most generalized microbiotherians known up to now supports an alternative hypothesis: the origin of the Microbiotheria (and, probably, of other lineages of the Australidelphian radiation) in the Antarctic continent, or, also probable, in a very restricted biogeographic region including southernmost South America (i.e., Patagonia) and Antarctica. The consideration of South America as a homogeneous unit frequently hides a much more complex biogeographic scenario: the belonging of southern South America to a biogeographic kingdom (the Austral Kingdom *sensu* Morrone 2002), different from that of the Neotropical region (belonging to the Holotropical Kingdom), which includes most of the remaining portions of this continent.

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