

# Earliest South American paucituberculatans and their significance in the understanding of ‘pseudodiprotodont’ marsupial radiations

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We describe the oldest Paucituberculata marsupials, from the La Barda and Las Flores localities (Argentina; Late Palaeocene, and Early–Middle Eocene), as well as from the Itaboraí Basin (Brazil; Late Palaeocene). The new taxa are represented by very scarce, although well-preserved, dental remains. A parsimony analysis was performed in order to evaluate the phylogenetic affinities of these taxa. Representatives of both *Riolestes capricornicus* gen. et sp. nov. and *Bardalestes hunco* gen. et sp. nov. appear to be basal paucituberculatans, and their molar features give clues on the early evolution of the representatives of this order. Within the Paucituberculata we recognize two major clades: Caenolestoidea and Palaeothentoidea. We conclude that ‘pseudodiprotodont’ marsupials of the traditional literature (i.e. Polydolopimorphia + Paucituberculata) do not form a natural group. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 155, 867–884.

ADDITIONAL KEYWORDS: Argentina – Brazil – Caenolestidae – molar morphology – Paleogene.

## INTRODUCTION

Living paucituberculatans (Mammalia, Marsupialia) are restricted to the caenolestid genera, *Caenolestes*, *Lestoros*, and *Rhyncholestes*. However, the rich evolutionary history of the Paucituberculata includes a diverse array of extinct taxa, some of them remarkably derived (Marshall, 1980). The concept and relationships of the Paucituberculata are of particular interest as its living representatives have been included in many phylogenetic analyses of marsupial relationships in recent years (see, e.g. Kirsch, Lapointe & Springer, 1997; Jansa & Voss, 2000; Sánchez-Villagra, 2001; Horovitz & Sánchez-Villagra, 2003, 2007; Asher, Horovitz & Sánchez-Villagra, 2004; Baker *et al.*, 2004; Cardillo *et al.*, 2004; Phillips *et al.*, 2006; Ladevèze & de Muizon, 2007).

The antiquity of the Paucituberculata depends largely on the extent and content of this order as proposed by different authors. According to their criteria, no indisputable records of Palaeocene Paucituberculata have existed until now. In this paper we describe the oldest Paucituberculata yet found, coming from the Middle Chubut River Volcanic-Pyroclastic Complex (Argentina; Early–Middle Eocene), the Las Flores Formation (Argentina; Itaboraian Age, Late Palaeocene), and the Itaboraí Basin (Brazil; Itaboraian Age, Late Palaeocene). The new taxa are represented by a few isolated remains, mostly consisting of upper and lower molars; notwithstanding, their good preservation sheds light on the early evolution of the representatives of this order. Furthermore, the dental information derived from these new taxa provides new evidence on the very concept of Paucituberculata. We describe the new taxa and assess their phylogenetic relationships in the context of South American marsupials.

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## MATERIAL AND METHODS

### PROVENANCE OF THE STUDIED SPECIMENS

New specimens were recovered from the Late Palaeocene and Early–Middle Eocene sites of La Barda and Las Flores (Argentina), and from Late Palaeocene levels of Itaboraí (Brazil).

The La Barda locality is a recently discovered fossiliferous site located near the town of Paso del Sapo in north-western Chubut Province, Argentina (Fig. 1). The La Barda sediments consist of consolidated tuffs intercalated in the Volcanic-Pyroclastic Complex of the Middle Río Chubut. This Palaeocene–Eocene succession was reviewed by Aragón & Mazzoni (1997); previous studies of the regional geology, stratigraphy, geochemistry, petrogenesis, and palaeobotany were made by Petersen (1946), Archangelsky (1974), Volkheimer & Lage (1981); Lage (1982); Aragón & Romero (1984); Mazzoni & Aragón (1985); Aragón, Mazzoni & Merodio (1987); Rapela *et al.* (1988); Mazzoni, Aragón & Merodio (1989); and Wilf *et al.* (2003). This complex includes a variety of volcanoclastic, intrusive, pyroclastic, and effusive rocks deposited over several million years. Absolute datings of the over- and underlying rocks, stratigraphical relationships, and faunal content suggest a latest Early

Eocene to earliest Middle Eocene age (Ypresian–Lutetian boundary) for the mammal-bearing sediments (Tejedor *et al.*, 2005; in press).

Originally correlated with Banco Negro Inferior levels (Marshall *et al.*, 1981), the Las Flores Formation (Legarreta & Uliana, 1994; Fig. 1) was later referred to the Río Chico Group by Bond *et al.* (1995). Its type locality is exposed at the ‘Yacimiento Las Flores’, an oil-bearing field on the eastern slopes of the Southern Cliff of Lake Colhue Huapi (Sarmiento Department, Chubut Province, Argentina). The extremely rich diversity of marsupials recovered from these levels (Bond *et al.*, 1995) are presently being described (a preliminary note on this diversity was presented in Goin, Candela & Forasiepi, 1997). These marsupials show substantial identity with those of Itaboraí at the generic level, thus confirming their Itaboraian (Late Palaeocene) age (Oliveira & Goin, 2006).

The local fauna of São José de Itaboraí (State of Niterói, south-eastern Brazil; Fig. 1), conventionally assigned to the Late Palaeocene of South America (Marshall, 1985), shows a unique diversity of metatherians and several ‘ungulates’, as well as the oldest known *Xenarthra* (Bergqvist, 1996; Oliveira, 1998). Although the proposal of an Itaboraian Land-mammal Age has been a subject of controversy (e.g. Bonaparte, Van Valen & Kramartz, 1993), more recent studies on the stratigraphy and faunal content of the contemporary Las Flores Formation (central Patagonia, Argentina) supports its validity and use as biochronological reference (Bond *et al.*, 1995). The fossil marsupials of São José de Itaboraí comprise a great variety of specimens, most of them of small size, which were successively described by Simpson (1947); de Paula Couto (1952a, b, 1961, 1962, 1970); Marshall (1982a, b, 1984, 1987); Marshall & de Muizon (1984); Oliveira (1998); and Ladevèze (2004, 2007). Their diversity includes most major lineages of South American marsupials, such as microbiotherians, didelphimorphians, polydolopimorphians, and sparassodonts.



**Figure 1.** Map of South America indicating localities cited in the text.

### CLADISTIC ANALYSES

The dataset (Supporting Information Appendix S1) included 43 characters (Supporting Information Appendix S2) and 24 taxa pertaining to different clades of marsupials (see Taxon sample). The multi-state characters were treated as unordered. The data set was analysed by performing a heuristic search with parsimony under equal weights with TNT 1.1 (Goloboff, Farris & Nixon, 2003). The shortest trees were found by generating 500 Wagner trees, and then submitting them to the tree bisection-reconnection branch-swapping method, retaining ten trees per replication. State transformations were considered

synapomorphies for a given node only if they were unambiguous. Unambiguous character state optimizations and matrix and tree editions were obtained with the program WINCLADA (Nixon, 1999). Relative and absolute Bremer support (Goloboff & Farris, 2001) were calculated in order to assess clade support using TNT (Goloboff *et al.*, 2003) and performing heuristic searches.

#### TAXON SAMPLE

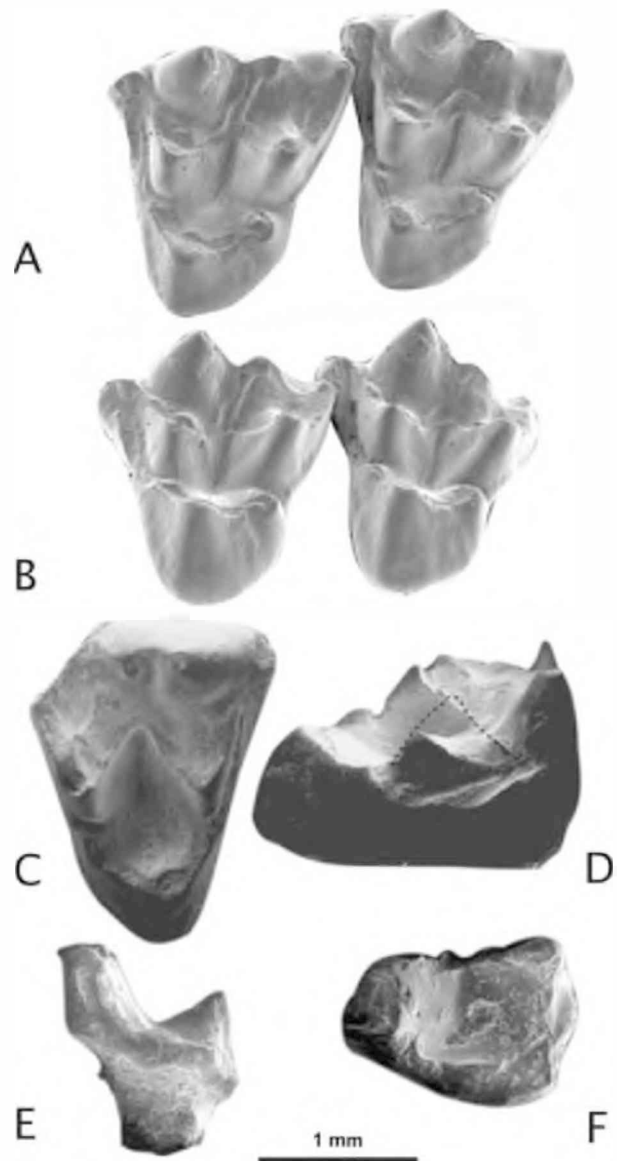
In order to establish the closer phylogenetic relationships of the new taxa described herein, *Bardalestes hunco* gen. et sp. nov. and *Riolestes capricornicus* gen. et sp. nov. (see below and Figs 2, 3), genera of the main lineages of South American Metatheria were included in these analyses. Within Didelphimorphia the genus *Pucadelphys* (Fig. 4D) was selected (Marshall & de Muizon, 1995, but see Rougier, Wible & Novacek, 2004). *Derorhynchus* (Fig. 4E) is an 'opossum-like' marsupial whose affinities are still being discussed (see de Paula Couto, 1952a; Goin, Oliveira & Candela, 1998a; Goin, 2003).

The extant Paucituberculata *Rhyncholestes* and *Caenolestes*, and the extinct *Stilotherium* (Fig. 5E), *Plioolestes*, *Phonocdromus* (Fig. 5C, D), and *Pichipilus* (Fig. 5A, B) were selected as representatives of the 'Caenolestidae' (*sensu* Marshall, Case & Woodburne, 1990). *Palaeothentes* and *Acestis* were selected as representatives of the Palaeothentidae, and *Parabderites* and *Abderites* as Abderitidae.

Within Microbiotheria *Microbiotherium* (Fig. 4G, H) was selected. *Glasbius* (Fig. 4F) was included as a basal polydolopimorphian (Goin, *et al.*, 1998b; Goin & Candela, 2004). *Prepidolops* (Prepidolopidae; Fig. 6A), *Bonapartherium* (Fig. 6B, C, F) *Epidolops* (Bonapartheriidae), *Polydolops* (Polydolopidae), *Roberthoffstetteria* (fam. indet.; see Goin, Candela & de Muizon, 2003), *Proargyrolagus* (Argyrolagidae; Sánchez-Villagra & Kay, 1997), and *Klohnia* (Argyrolagoidea, fam. indet.; Flynn & Wyss, 1999) were selected as representatives of Polydolopimorphia (*sensu* Goin & Candela, 2004). Specimens referable to *Klohnia* studied in this work (Fig. 6D, E) include a set of numerous, unpublished specimens exhumed at Early Oligocene levels in Gran Barranca, Chubut Province. In short, with the only exception of the carnivorous Sparassodonta, all major lineages (orders) of South American metatherians were represented in this analysis. To assess the polarity of characters, *Alphadon* (Fig. 4A–C) was taken as the root as this taxon is currently considered as a generalized Metatheria (Marshall *et al.*, 1990).

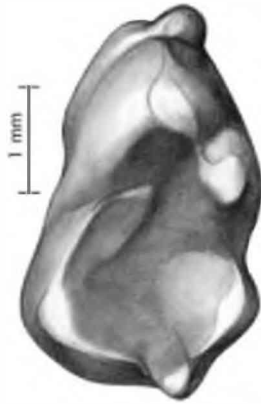
#### ABBREVIATIONS

CHU, Institut des Sciences de l'Évolution, USTL (Montpellier); LIEB, Laboratorio de Investigaciones



**Figure 2.** A, B, *Bardalestes hunco* gen. et sp. nov., specimen LIEB-PV 1135 (detail), left M2-3 (A, occlusal view; B, occlusal-lingual view). C–F, *Bardalestes* sp. C, D, specimen MLP 90-II-5-336, an isolated upper molar (M?) lacking the metastylar area (C, occlusal view; D, anterior view). The dashed line indicates the inferred profile of the paracone; E, F specimen MLP 90-II-5-300, an isolated right molar lacking most of the trigonid (E, lingual, and F, occlusal views).

en Evolución y Biodiversidad, Sede Esquel, Universidad Nacional de la Patagonia (Esquel); MCN-PV: Coleção de Paleovertebrados, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre); MLP, Departamento Paleontología Vertebrados, Museo de Ciencias Naturales de La Plata (La Plata); MMP: Museo Municipal de Ciencias



**Figure 3.** *Riolestes capricornicus* gen. et sp. nov. Occlusal view of specimen MCN-PV 1790, an isolated m1.

Naturales (Mar del Plata); MNRJ: Museu Nacional (Rio de Janeiro); PVL: Colección Paleozoología Vertebrados, Instituto Miguel Lillo (Tucumán); YPFB Pal, Colección de Paleontología, Yacimientos Petrolíferos

Fiscales de Bolivia, in Centro de Tecnología Petrolera (Santa Cruz). SALMA, South American Land-Mammal Age. The generalized metatherian dental formula is assumed to be:  $I/i$  5/4,  $C/c$  1/1,  $P/p$  3/3,  $M/m$  4/4. Molar nomenclature follows Goin *et al.* (2003).

#### SYSTEMATIC PALAEOONTOLOGY

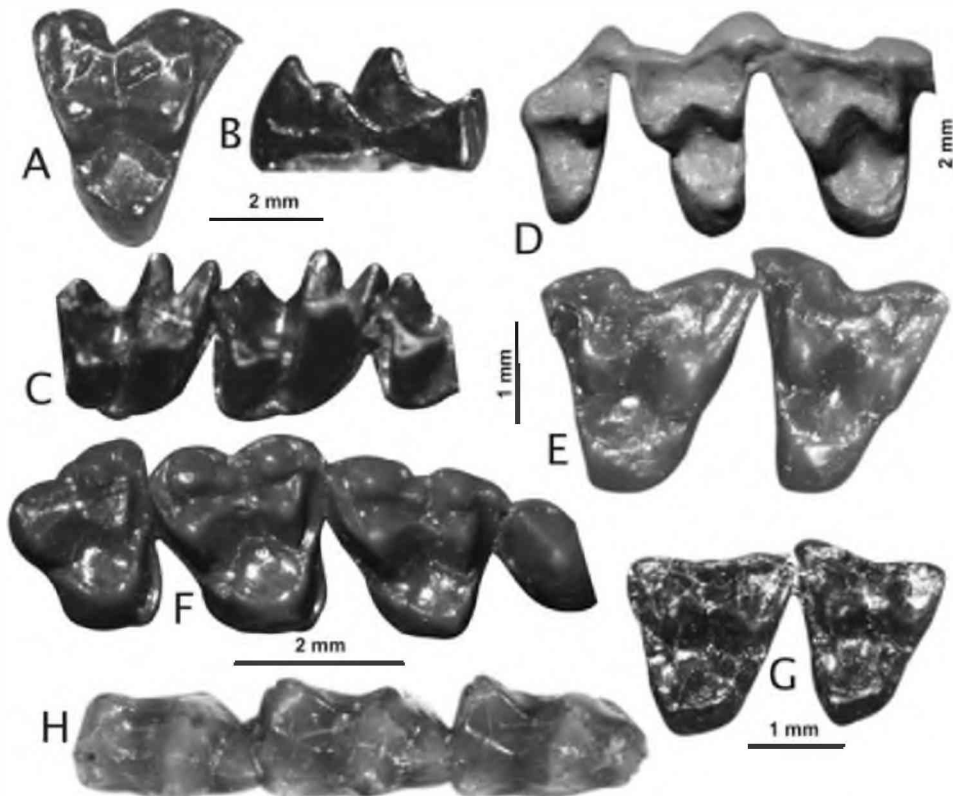
SUPERCOHORT MARSUPIALIA ILLIGER, 1811

ORDER PAUCITUBERCULATA AMEGHINO, 1894

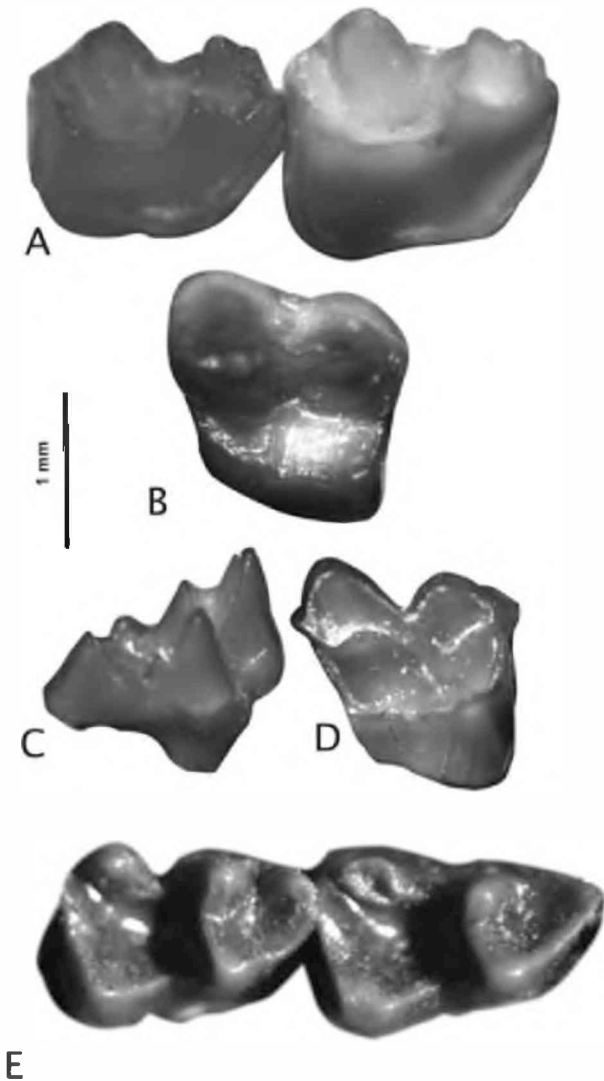
PLESION *BARDALESTES* GEN. NOV.

*Diagnosis:* Differs from all other paucituberculatans in that the upper molars lack an enlarged, 'hypocone-like', metacone; the paracone is less reduced; the paracone and the metacone are less twinned to StB and StC + StD, respectively; StB much larger than StC + StD; distal end of entocristid in m1–3 relatively high.

*Etymology:* *Barda*, from La Barda locality, where the type specimen of the type species of the genus was collected; *-lestes*, Latin for 'thief', 'pirate' and, by



**Figure 4.** A–C, *Alphasodon* sp. A, B, specimen MLP 87-I-4-31, right Mx in occlusal (A) and anterior (B) views. C, specimen AMNH 116632 (detail) showing the talonid of m1 and complete m2–3, occlusal–labial view. D, *Pucadelphys andinus*; specimen YPFB Pal 6472 (detail, cast) showing right M2–4, occlusal view. E, *Derorhynchus* sp., specimen MNRJ 2506-V (cast), left M2–3 in occlusal view. F, *Glasbius intricatus*, specimen UM VP 1593 (cast), right P3–M3 in occlusal view. G, H, *Microbiotherium tehuelchum*; G, specimen MLP 58-IX-3-4, left M2–3 in occlusal view; H, specimen MLP 11-35, left m1–3 in occlusal view.



**Figure 5.** A, B, *Pichipilus* sp.; A, specimen MLP 77-VI-13-15, right m2-3 in occlusal-labial view; B, specimen MPEF-PV 4804, right M2 in occlusal view. C, D, *Phonocdromus* sp., specimen MPEF-PV 4810, right M3 (C, anterior-labial; D, occlusal-lingual views). E, *Stilotherium dissimile*; MACN 8464 (part), right m1-2 in occlusal view.

extension, 'carnivorous' (*lestikos*), a term that characterizes the generic name of several fossil and living Paucituberculata.

*Type species:* *Bardalestes hunco* sp. nov.

*Distribution:* Late Palaeocene and Early-Middle Eocene, South America.

***BARDALESTES HUNCO* SP. NOV.**

(FIG. 2A, B)

*Type:* LIEB-PV 1135 (Fig. 2A, B), a fragment of left maxillary with M2-3, and roots and part of the crown of M4.

*Hypodigm:* The type only.

*Locality, horizon and age:* La Barda, Paso del Sapo (Chubut Province, Argentina). Andesitas Huancache Formation, Early-Middle Eocene.

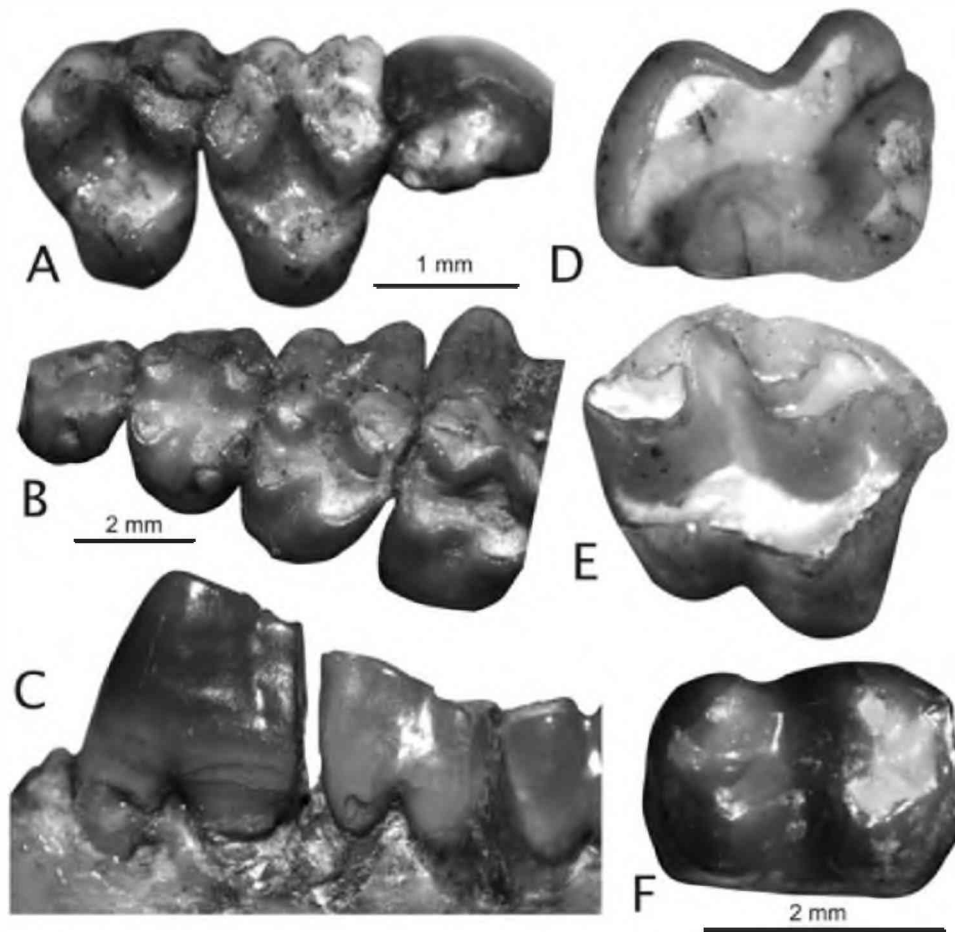
*Measurements:* See Table 1.

*Diagnosis:* Differs from all other paucituberculatans in that the upper molars lack an enlarged, 'hypocone-like', metaconule; the paracone is less reduced; the paracone and the metacone are less twinned to StB and StC + StD, respectively; StB much larger than StC + StD.

*Description* (Fig. 2A, B): The M2 and M3 of the type specimen are very similar to each other, the M3 being longer and wider than the M2. Although its crown is badly broken, it can be seen that the M4 (not shown in Fig. 2) was very short and narrow, and two-rooted. Its width is approximately half the width of M3. The protocone of M2 is comparatively wider than that of M3. In both molars the anterobasal cingulum is narrow and lingually connected with the preparacunar crest. The trigon is ample and transversely long; in the M2 the metacone is somewhat higher than the paracone, whereas in the M3 both cusps are subequal in height. In both molars the protocone is

**Table 1.** Dental measurement of *Bardalestes hunco* gen. et sp. nov., *Bardalestes* sp., and *Riolestes capricornicus* gen. et sp. nov. Measurements are in mm

Taxon	Specimen	LM2	WM2	LM3	WM3	Lm1	Wm1	Lmx
<i>Bardalestes hunco</i>	LIEB-PV 1135	1.42	1.68	1.41	1.78			
<i>Bardalestes</i> sp.	MLP 90-II-5-336	1.51	1.89					
<i>Dracolestes</i> sp.	MLP 90-II-5-300							1.05
<i>Riolestes capricornicus</i>	MCN-PV 1790					3.79	2.36	



**Figure 6.** A, *Prepidolops didelphoides*; MLP 81-XI-15-1, right P3–M2 in occlusal view; B, C, F, *Bonapartherium hinakusijum*; B, MMP 1408, detail of left M1–4 in occlusal view; C, F, specimen PVL 4018; C, detail of left dentary showing p3–m2 in labial view; F, detail of right dentary showing the m3 in occlusal view. D, E, *Klohnia* sp.; D, MPEF-PV 4291, left mx in occlusal view; E, MPEF-PV 4292, right Mx in occlusal view.

slightly eccentric, as in the upper molar here referred to *Bardalestes* sp. (see below), it is not in line with the tips of the StB and the paracone. StA is small and very low, StB is comparatively enormous, suboval in section and connected by means of a crest to the immediately posterior cusp (StC + STD; see below). This latter cusp is much smaller and lower than the StB and is even more reduced and close to StB in the M3 than it is in the M2. The postmetacrasta is longer than the preparacrasta and is orientated parallel to the postparacrasta. The apex of the centrocrista is deep and reaches externally the anterolingual slope of StC + StD. In both the M2 and M3 the metaconule is larger than the paraconule.

*Comments:* One of the most striking features of the upper molars of *Bardalestes hunco* is the morphology, position, and relative size of StB. This cusp is very large, high and is clearly facing the paracone,

even if it is slightly posteriorly shifted in comparison with other South American marsupials. The cusp immediately posterior to StB is much smaller and occupies an intermediate position between the StC and StD of other more generalized marsupials. Thus, it raises the question of the homology of this cusp in *Bardalestes*. Derorhynchid ‘didelphimorphians’ show some features that ‘anticipate’ the molar pattern of Paucituberculata: large (although not proportionally huge) StB, a deeply V-shaped centrocrista, winged metaconule that is larger than the paraconule, and molars with a salient hypoconid and, in some cases, a slightly labiolingually compressed entoconid. The morphology of the styler area of the representatives of this family is worth analysing. In this respect, some indeterminate Derorhynchidae from Itaboraí are suggestive: specimen MNRJ 2506-V exhibits, especially in the M1, some proximity of the paracone to the StB, no reduction of the latter cusp and the

reduction of the StC and StD, especially the latter. The same features can be seen in the indeterminate Derorhynchidae specimens MNRJ 2352-V and MNRJ-V 2894-V, DGM 813-M, and MNRJ 2894-V, all from the Itaboraí Basin. A morphological pattern similar to that occurring in the styler region of *Bardalestes* can be even more clearly appreciated in the derorhynchid *Pauladelphys*, from the Middle Eocene of Antarctica and Early Eocene of Paso del Sapo (Goin, Tejedor & Abello, 2000, 2001). In the only known upper molar of *Pauladelphys juanjoii* (MLP 96-I-5-45), an isolated left M1, a manifest closeness between the reduced StC and StD is observed, so that the latter cusp is relatively distant from the metastylar corner of the tooth. The same condition is seen in upper molars referable to *Pauladelphys* sp. from Eocene levels of Paso del Sapo (Tejedor *et al.*, in press). In some of these specimens (e.g. LIEB-PV 1116, LIEB-PV 1114), StC and StD are almost subequal and twinned, so that their bases are fused. This pattern suggests that the cusp posterior to the StB of the *Bardalestes* specimens studied here may have been the result of the fusion of the styler cusps StC and StD. The subsequent evolution of this cusp in the more derived Paucituberculata may have involved an increase in size and its setting apart from the StD. Interestingly, in caenolestids such as *Stilotherium dissimile*, the styler cusp posterior to the StB (which we homologize here with StC + StD) maintains its relative size in the upper molar series: it is larger than the StB in the M1, subequal to StB in the M2, and smaller and closer to the StB in the M3. Even though no M1s are known among the *Bardalestes* specimens described here, it can be seen that in the M3 of this taxon the StC + StD is smaller and closer to the StB than in the M2.

In brief, from the assemblage of Paleogene South American 'opossum-like' marsupials, the upper molar pattern that occurs in the derorhynchid *Pauladelphys* may be an indication of the process underwent by the earliest paucituberculatans. In the particular case of the styler area, the small cusp posterior to the StB seems not to be either the StC or the StD but rather the result of the fusion of both cusps.

#### *BARDALESTES* SP. (FIG. 2C–F)

*Referred specimens:* MLP 90-II-5-336, an isolated upper molar (M<sup>?</sup>2; Fig. 2C, D) lacking the metastylar area; MLP 90-II-5-335, an isolated left protocone; MLP 90-II-5-337, an isolated right protocone; MLP 90-II-5-300 (Fig. 2E, F), an isolated right talonid.

*Locality, horizon and age:* Easternmost part of the Southern Cliff of Colhué Huapi lake, Sarmiento Department, Chubut Province, Argentina. Las Flores

Formation, Río Chico Group; Late Palaeocene (Itaboraian Age).

*Measurements:* See Table 1.

*Description* (Fig. 2C, D): Even though broken and mostly missing the metastylar area, it is evident that MLP 90-II-5-336 is a wide molar (i.e. its labio-lingual diameter is larger than the mesio-distal one). The trigon basin is labio-lingually wide because of the deep centrocrista. The protocone is moderately developed; its tip is relatively centrally placed, that is, it is not aligned in a transverse axis with StB and the paracone. The preprotocrista is not symmetrical to the postprotocrista as the metaconule, larger than the paraconule, is posteriorly salient. Both the paracone and the metacone are worn down almost to their bases; from their respective sections it can be inferred that the paracone was only slightly smaller than the metacone. The preparacrista is subequal in length to the postparacrista and the premetacrista; it is almost transversally orientated with respect to the dental axis. The postparacrista and the premetacrista are subequal in length; they are not symmetrical to each other but instead the premetacrista is slightly more transverse to the dental axis. The postmetacrista has preserved only its proximal end which is parallel to the postparacrista; its preserved portion suggests that it was moderately developed. The paraconule is half the size of the metaconule; both cusps are 'winged', i.e. they have pre- and postconular cristae. The preparaconular crest continues labially in the anterobasal cingulum; the postparaconular crest is reduced or absent; in turn, and even though worn, the premetaconular crest seems to have been longer and more subhorizontal than the postmetaconular one, which descends abruptly downwards and posterolabially. The styler shelf is moderately developed and is deeply penetrated by the centrocrista at its central portion. The ectoflexus is almost undistinguishable; StB and StC + StD are very close together and have no labial emargination. A tiny cuspule which is very low and subcircular in section can be observed behind the labial apex of the centrocrista. This cuspule is not located near the labial face of the tooth, as are other styler cusps, but instead it is internally placed on the styler shelf. The most conspicuous feature of the remaining styler cusps is the very large size of StB, which occupies most of the anterior half of the styler shelf. StB is not only large but also very high; it is suboval in section, as it is slightly labiolingually compressed. Its labial and lingual slopes are steep; anteriorly it has a rounded edge, whereas the posterior one is crest-shaped, trenchant in aspect. The metastylar area is broken behind StC + StD. At the lingual slope of StB a minute wrinkle can be observed, just

posterior to the labial end of the preparacrista. Compared to other 'opossum-like' marsupials, it is evident that the lingual slope of StB and the labial slope of the paracone in *Bardalestes* are very close to each other relative to the total width of the upper molar (see the reconstruction of the paracone in Fig. 2D). The anterolabial corner of the tooth, poorly preserved, is rather small; a moderately developed but very low StA can be inferred from it. The anterior cingulum is poorly developed.

Three additional specimens are also referred to *Bardalestes* sp. Two of them (MLP 90-II-5-335 and MLP 90-II-5-337) consist of isolated protocones, one left and the other right; they are roughly similar, in size and morphology, to the protocone of the already described upper molar. The third specimen (MLP 90-II-5-300; Fig. 2E, F) consists of a fragmentary right molar preserving the talonid and part of the posterior wall of the trigonid. Judging from the preserved portion of the metacristid, the trigonid was much higher than the talonid. The latter has a salient hypoconid, a small, laterally compressed entoconid, and a reduced hypoconulid located posterior to the entoconid; the talonid basin is relatively deep; the cristid obliqua ends anteriorly near the labial base of the protoconid; the distal end of the entocristid in m1–3 is relatively high (Fig. 2F). There is a short postcingulum at the posterior face of the talonid; the posthypocristid is almost transverse to the dental axis.

One additional specimen can also be also referred to *Bardalestes* sp.: MLP 90-II-5-332. This specimen consists of an isolated talonid belonging to a mx. Its morphology resembles that of MLP 90-II-5-300. The specimen was polished in order to examine its enamel structure (specimen KOE 2991; Koenigswald & Goin, 2000). As in the upper and lower molars of the Caenolestidae, the enamel in *Bardalestes* shows prisms that are orientated more or less straight between the enamel–dentine joint and the outer enamel surface. A thick interprismatic matrix orientated at an angle with the prisms could be observed. This pattern is common among other generalized 'opossum-like' marsupials (Koenigswald & Goin, 2000: 149).

*Comments:* Among the 'opossum-like' marsupials collected from the Las Flores Formation, represented by more than 700 isolated teeth, there are a few taxa of very small size. The specimens here assigned to *Bardalestes* sp. are among the smallest of them. Specimen MLP 90-II-5-300 has the hypoconulid twinned to the entoconid, a synapomorphy of Late Cretaceous and younger marsupials (Kielan-Jaworowska, Cifelli & Luo, 2004). In addition, the laterally expanded hypoconid, and the labio-lingually compressed entoconid are features diagnostic of the Paucituberculata (see below). Specimens MLP 90-II-

5-335 and MLP 90-II-5-337 are almost identical in size and morphology. In turn, specimen MLP 90-II-5-300, an isolated lower molar fragment, matches in size and shape the expected pattern for an occlusal antagonist to the type specimen. In short, their size, morphology, and inferred occlusal relationships concur in assigning all specimens to the same taxon.

The size and morphology of specimen LIEB-PV 1135, type of *Bardalestes hunco*, are very similar to those of specimen MLP 90-II-5-336. The greatest differences between the latter and LIEB-PV 1135 are the following: StC + StD larger in the latter, which in addition lacks the cusplule posterior to the centrocrista apex, and, especially in M2, more posteriorly located with respect to the StB. Regarding their size, specimen MLP 90-II-5-336 is slightly larger than LIEB-PV 1135. In all other features, the M3 of LIEB-PV 1135 is indistinguishable from specimen MLP 90-II-5-336, for which reason we assume the latter to be an M3 as well. The finding of new material could prove that the small differences between them fall within the variability range of a single species, as the greatest difference is the increased size of the cusp posterior to the StB (which we consider homologous to the fusion of cusps StC+ StD).

#### **RIOLESTES GEN. NOV.**

*Diagnosis:* As for the type and only known species.

*Etymology:* *Rio-* for the state of Rio de Janeiro, Brazil, where are located the fossiliferous outcrops of the Itaboraí Basin; *-lestes*, Latin for 'thief', 'pirate' and, by extension, 'carnivorous' (*lestikos*), a term that characterizes the generic name of several fossil and living Paucituberculata.

*Type species:* *Riolestes capricornicus* sp. nov.

*Distribution:* Late Palaeocene, South America.

#### **RIOLESTES CAPRICORNICUS SP. NOV. (FIG. 3)**

*Etymology:* In reference to the geographic placement of the fossil locality, near the Southern Tropic of Capricorn.

*Locality, horizon, and age:* São José de Itaboraí, State of Rio de Janeiro, Brazil (22°44'51"S, 42°51'21"W); Itaboraí Basin, Late Palaeocene (Itaboraian Age).

*Type:* MCN-PV 1790 (Fig. 3), an isolated m1.

*Hypodigm:* The type only.

*Measurements:* See Table 1.



*Diagnosis:* Differs from the remaining Paucituberculata in the following combination of characters: large size, m1 with reduced paraconid, mesially placed; persistence of the paracristid notch, vestigial anterobasal cingulum, trigonid basin absent; metaconid well displaced posteriorly.

*Description:* The most distinctive features of this molar are its proportionally large size, reduced paraconid, high protoconid, backwardly placed metaconid, absent trigonid basin, labially salient hypoconid (i.e. laterally expanded), and wide talonid basin. The paraconid is poorly developed, much less than the metaconid; its anterior face is flat. The anterobasal cingulum, although vestigial, runs at a short distance below and labial to the paraconid. The metaconid is moderately developed and is set close to the protoconid but quite posterior to it. Thus, the metacristid (postprotocristid + postmetacristid) is short, high, and in occlusal view is obliquely placed with respect to the dental axis. The paracristid (preprotocristid + postparacristid) is sharp, trenchant, and runs steeply downwards, almost subvertical, from the protoconid to the paraconid. The paracristid notch is placed just posterior to the paraconid. The talonid is much wider than the trigonid; its basin is well bound by the pre-entocristid, the cristid oblique, and the posthypocristid. The hypoconid and the entoconid are subequal in height, the latter being laterally compressed; the hypoconulid is located posterolingually relative to the entoconid, and is projected backwards. The cristid obliqua reaches anteriorly up to a point below the notch of the metacristid; it is not parallel to the labial face of the tooth but instead narrows the talonid basin anteriorly. There is no postcingulum. Below the crown, the anterior root is smaller than the posterior one. The cristid obliqua is worn on its anterodorsal edge, as well as the posthypocristid near the hypoconulid and the entoconid at its labial face.

*Comments:* *Riolestes capricornicus* can be considered a marsupial on the basis of the pairing of the entoconid and the hypoconulid. Its most distinctive features agree well with those expected for a member of the Paucituberculata: labially projected hypoconid and laterally compressed entoconid (see below). An additional feature, the metaconid clearly posterior to the protoconid, occurs in the first molar in most Paucituberculata – except in *Stilotherium*, *Phonocdromus*, and *Pichipilus*. Finally, the paraconid of m1 is reduced in all paucituberculatans, as in the type of *Riolestes capricornicus*.

Although not frequent among more modern marsupials, the location of the metaconid somewhat posterior with respect to the protoconid appears not

only in the m1 but also in the dp3s of several different lineages, including some very generalized forms such as *Alphadon*. Cifelli (1994), referring to several deciduous molars tentatively referred to *Alphadon perexiguus*, pointed out that ‘... the trigonid is broadly open lingually, with the paraconid and metaconid more anteriorly and posteriorly placed, respectively, than on the permanent molars. The paraconid and metaconid are weakly developed (...) As usual among marsupial dP3s, the cristid obliqua extends anterolingually as a crest to the tip of the metaconid, resembling the distal metacristid (...) seen in permanent molars of primitive Tribosphenida’ (Cifelli, 1994: 124; Cifelli & de Muizon, 1998). The posterior placement of the metaconid with respect to the protoconid is also verified in the permanent molars of some Early Palaeocene South American taxa, such as the polydolopimorphian *Roberthoffletteria nationalgeographica*. Among the most primitive Sparassodonta, such as some Hathliacynidae, the reduction of the metaconid in m1 occurs together with its posterior placement in the trigonid. In some Microbiotheriidae, such as *Pachybiotherium acclinum*, *Eomicrobiotherium gaudryi*, and *Microbiotherium gallegosense*, the posteriorly ‘shifted’ metaconid in m1 occurs together with the mesial ‘shift’ of the paraconid, as in *Riolestes*. Some early Didelphimorphia, such as *Itaboraidelphys camposi*, also show a slight posterior displacement of the metaconid. Finally, among the Paucituberculata Caenolestidae and, especially, Palaeothentidae, the m1 metaconid also shows a displacement similar to that of *Riolestes*. In short, the posterior displacement of the metaconid is not exclusive to the marsupial dp3 but also occurs in several permanent molars in various lineages, noticeably in the m1 of most Paucituberculata. Luckett & Hong (2000) demonstrated that the dp3 is vestigial and extremely reduced in paucituberculatans, which is obviously not the case in MCN-PV 1790. Finally, the positions and relative sizes of the trigonid cusps in *Riolestes capricornicus* match well those of the m1 of paucituberculatans.

*Riolestes capricornicus* and *Bardalestes* sp. from Las Flores are contemporary paucituberculatans. Differences between them include the following features: *Riolestes capricornicus* triples *Bardalestes* sp. in size; its type specimen differs from the lower molar referred to *Bardalestes* sp. in that there is a less salient hypoconid, the entoconid is comparatively smaller, the hypoconulid is less proximate to the entoconid (in *Bardalestes* it is almost immediately posterior to the entoconid), it has a shallower talonid basin, and it lacks a posterobasal cingulum. All these differences warrant a generic distinction between these taxa.

## RESULTS OF THE PHYLOGENETIC ANALYSIS

Five most parsimonious trees of 116 steps in length (CI = 0.55; RI = 0.79) were obtained. The strict consensus tree, the unambiguous synapomorphies, and the values of relative Bremer support are shown in Fig. 7. Two main clades are recognized in the strict consensus tree. One of them shows a basal trichotomy formed by *Pucadelphys*, *Derorhynchus*, and the clade that contains the new genera *Riolestes* and *Bardalstes* plus the traditionally known Paucituberculata (see Discussion). Within the latter clade two major groupings emerge: the Palaeothentoidea clade (that includes Pichipilidae, Abderitidae, and Palaeothentidae) and the Caenolestoidea clade. It is the last that includes the extant paucituberculatan marsupials. The other main group contains *Microbioterium* and *Glasbius*, along with a large grouping that includes a traditionally considered Polydolopimorphia plus *Proargyrolagus* and *Klohnia*.

## DISCUSSION

As a result of our analyses two important issues concerning the phylogeny of South American marsupials can be addressed: the supposed monophyly of all 'pseudodiprotodont' marsupials, and the extension and content of the Paucituberculata. Both of these are discussed below.

### 'PSEUDODIPROTODONTS' IS NOT A NATURAL GROUP

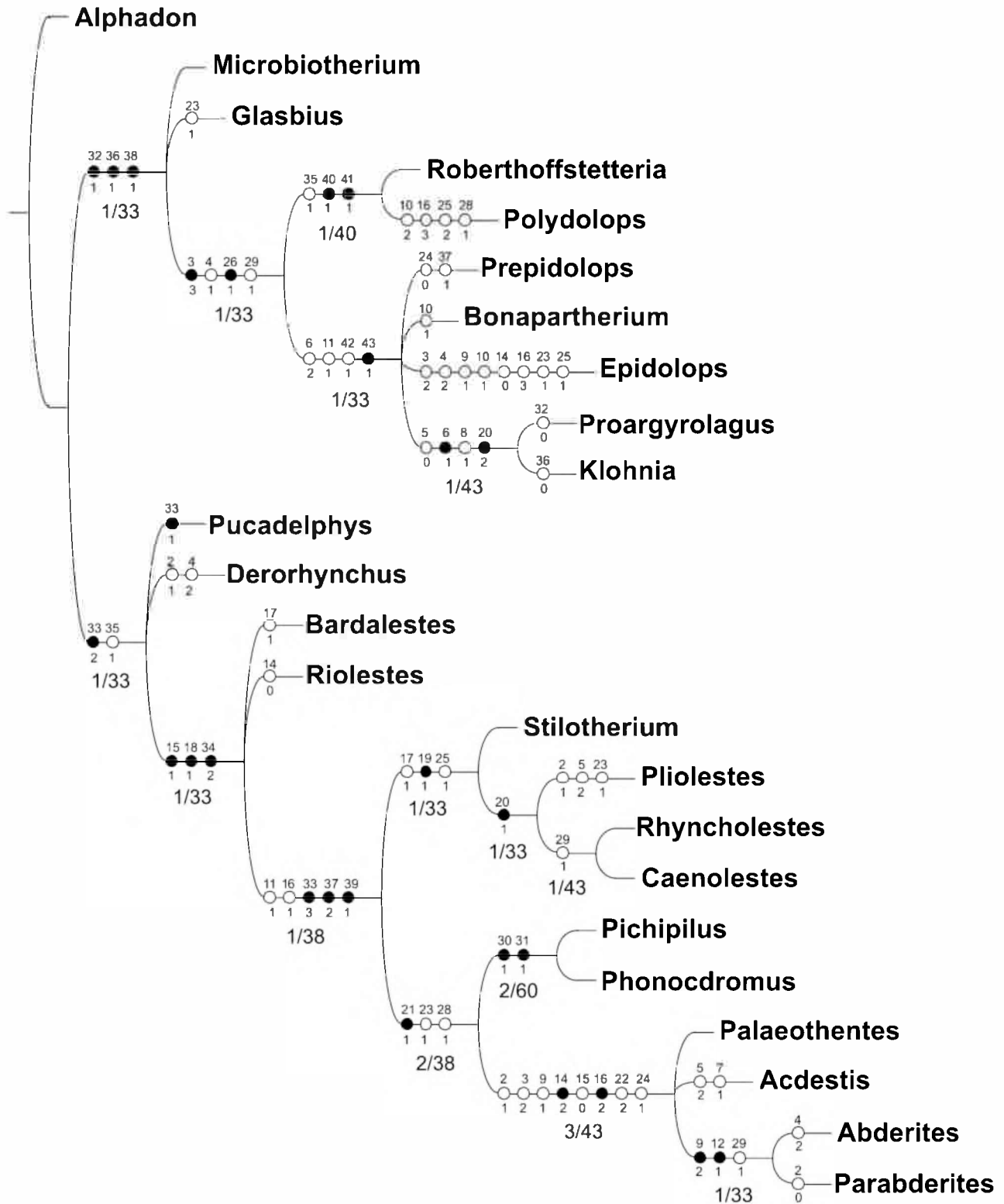
The term 'pseudodiprotodonts' is usually employed either as a formal or as an informal designation for several groups of (mostly extinct) South American marsupials possessing a hypertrophied and procumbent first incisor: Caenolestidae, Palaeothentidae, Abderitidae, Prepidolopidae, Bonapartheriidae, Polydolopidae, Argyrolagidae, Patagoniidae, and Groeberidae. Arguments as to whether these taxa represent a natural group are still under way (see below). According to Ride (1962) the pseudodiprotodonty of South American forms evolved convergently with that of kangaroos and similar Australasian forms that are grouped in the Order Diprotodontia. The fact that the hypertrophied procumbent incisor of the caenolestids and related forms derives from i1 or i2, whereas in Diprotodontia it derives from i3 or i4, was central to his arguments (see Ride, 1962: 295–300).

The history of the Paucituberculata concept is long and complex, as is the history of proposed phylogenetic relationships of paucituberculatans with other South American marsupial groups. Ever since Ameghino (1894) erected the Paucituberculata to

include the families Caenolestidae, Palaeothentidae, and Abderitidae, different 'pseudodiprotodont' groups have been considered as phylogenetically related, and those hypotheses were formalized in various classifications (see Table 2). One of the most enduring views was the proposal of Gregory (1910) and Simpson (1928) of closer relationships between Polydolopidae and Caenolestidae, which led to the long-lasting classification of both groups in the Superfamily Caenolestoidea (Simpson, 1930, 1945; de Paula Couto, 1952a, 1961; Reig, 1955). During the 1960s a significant change in the classification of marsupials occurred when Ride (1964) proposed a scheme that included orders. In this context, the name Paucituberculata was again adopted, but only to include Simpson's Caenolestoidea (i.e. Caenolestidae + Polydolopidae). Kirsch's (1977) scheme is among the classifications that followed this arrangement. During the decades since, different phylogenies of the Marsupialia have been proposed on the basis of molecular characters, anatomical characters, or both. Deeply rooted in these discussions is the issue of whether or not the 'pseudodiprotodonts' are regarded as a natural group. Three basic hypotheses have been advanced to date: (1) 'pseudodiprotodonts' are a natural group [Simpson, 1945; Ride, 1964; Aplin & Archer, 1987; Marshall, 1987; Marshall *et al.*, 1990 (in part); Kirsch *et al.*, 1997]; (2) Paucituberculata and Polydolopimorphia do not constitute a natural group, and the Argyrolagoidea are included within the former [Marshall *et al.*, 1990 (in part); Szalay, 1994]; (3) Paucituberculata and Polydolopimorphia do not form a natural group, and the Argyrolagoidea are included within the latter (Goin & Candela, 2004; Case, Goin & Woodburne, 2005). These proposals are expressed in the classification schemes shown in Table 2.

Although they were originally restricted to representatives of the genus *Polydolops* and allied forms, diverse findings during the second half of the 20<sup>th</sup> century resulted in a notable increase in our knowledge of the extent and diversity of the Polydolopimorphia (Goin & Candela, 1996, 2004; Case *et al.*, 2005). The current concept of Polydolopimorphia includes not only the Polydolopidae but also the prepidolopids, bonapartherids (Bonapartheriinae + Epidolopiinae), gashterniids, and an assemblage of taxa whose intraordinal relationships are not yet clearly established: *Hondonadia*, *Rosendolops*, *Wamradolops*, *Klohnia*, and *Roberthoffstteteria* (Goin & Candela, 1996, 2004; Goin *et al.*, 2003; Case *et al.*, 2005). All these authors also argued in favour of the inclusion of the Argyrolagoidea within the Polydolopimorphia.

The concept of Pseudiprotodontia was introduced by Kirsch *et al.* (1997) as a formal taxon including the



**Figure 7.** Strict consensus of five equally most parsimonious trees of ‘pseudodiprotodont’ marsupials. Numbers above each branch indicate character number, whereas those below are the character-states; absolute and relative Bremer support values are below each branch.

**Table 2.** Selected marsupial classifications. Those of Simpson (1945) and Ride (1964) include all metatherian lineages, whereas the remainder include only extinct and extant marsupials from the Americas. Classifications go down to family level only

Simpson, 1945	Ride, 1964	Aplin & Archer, 1987	Marshall, Case & Woodburne, 1990	Szalay, 1994	Kirsch, Lapointe & Springer, 1997
Order Marsupialia	Infraclass Metatheria	Supercohort Marsupialia	Infraclass Metatheria	Infraclass Metatheria	Infraclass Marsupialia
Superfamily Didelphidae	Superorder Marsupialia	Cohort Ameridelphia	Supercohort Marsupialia	Cohort Ameridelphia	Supercohort Boreoamericantheria
Family Didelphidae	Order Marsupialia	Order Didelphimorpha	Cohort Alphadelphia	Order Didelphida	Order Paradelphimorpha
Family Caroleomagnitidae	Superfamily Didelphoidea	Family Didelphidae	Order Peradectia	Suborder Archimetatheria	Family Peradectidae
Superfamily Borhyaenidae	Family Didelphidae	Family Sparassocynidae	Cohort Ameridelphia	Family Pedionymidae	Supercohort Neometatheria
Superfamily Dasypodidae	Family Stagodontidae	Order Paucituberculata	Order Didelphimorpha	Suborder Sudameridelphia	Cohort Didelphida
Family Dasypodidae	Family Pedionymidae	Superfamily Caroleomagnitoidae	Superfamily Didelphoidea	Infraorder Uaberaformes	Order Didelphimorpha
Family Notoryctidae	Family Borhyaenidae	Family Caroleomagnitidae	Family Didelphidae	Family Caroleomagnitidae	Family Didelphidae
Superfamily Paramakidae	Family Thyloacanthidae	Superfamily Caenolestidae	Family Sparassocynidae	Family Caroleomagnitidae	Cohort Pseudiprotodontia
Family Paramakidae	Family Necrolestidae	Family Caenolestidae	Order Polydolopimorpha	Infraorder Polydolopimorpha	Order Paucituberculata
Superfamily Caenolestidae	Superfamily Dasypodidae	Family Argrolagidae	Superfamily Polydolopidae	Family Prepidolopidae	Superfamily Caenolestidae
Family Caenolestidae	Family Dasypodidae	Family Croasidae	Family Prepidolopidae	Family Bonapartheriidae	Subfamily Caenolestinae
Family Polydolopidae	Family Thyloacanthidae	Family Argrolagidae	Family Prepidolopidae	Infraorder Sparassodonta	Subfamily Pichipilinae
Superfamily Phalangeroidea	Order Paucituberculata	Superfamily Polydolopidae	Family Prepidolopidae	Family Borhyaenidae	Subfamily Palaeobeniidae
Family Phalangeridae	Family Caenolestidae	Family Prepidolopidae	Order Sparassonta	Family Thyloacanthidae	Subfamily Alderitinae
Family Phalangeridae	Family Polydolopidae	Family Bonapartheriidae	Superfamily Borhyaenidae	Suborder Chirimetatheria	Subfamily Kolpaminae
Order Peramelina	Order Peramelina	Family Polydolopidae	Family Stagodontidae	Infraorder Poucituberculata	Superfamily Argrolagidae
Family Paramelidae	Family Paramelidae	Order Sparassonta	Family Stagodontidae	Infraorder Poucituberculata	Family Argrolagidae
Order Diprotodontia	Order Diprotodontia	Family Borhyaenidae	Family Hondadolopidae	Family Caenolestidae	Family Patagoniidae
Family Phalangeridae	Family Phalangeridae	Family Thyloacanthidae	Family Hondadolopidae	Subfamily Sternberginae	Family Patagoniidae
Family Wynyardidae	Family Wynyardidae	Order Australidelphia	Family Borhyaenidae	Subfamily Caenolestinae	Superfamily Groeberidae
Family Vombatidae	Family Vombatidae	Order Microbiotheria	Family Proborhyaenidae	Subfamily Palaeobeniinae	Family Groeberidae
Family Diprotodontidae	Family Diprotodontidae	Family Microbiotheriidae	Family Thyloacanthidae	Subfamily Alderitinae	Order Polydolopimorpha
Family Macropodidae	Family Macropodidae	...	Order Paucituberculata	Infraorder Simpsontheria	Superfamily Polydolopidae
Marsupialia <i>levinae</i> <i>sedis</i>	Marsupialia <i>levinae</i> <i>sedis</i>	...	Superfamily Caenolestidae	Family Gashternidae	Family Polydolopidae
Family Notoryctidae	Family Notoryctidae	...	Family Kolpaminae	Family Groeberidae	Family Propitobolidae
?Marsupialia	?Marsupialia	...	Family Caenolestidae	Family Argrolagidae	Family Bonapartheriidae
Family for <i>Gashternia</i>	Family for <i>Gashternia</i>	...	Family Alderitidae	Family Patagoniidae	Family Protodelphidae
		...	Superfamily Argrolagoidae	Suborder Didelphimorpha	Superfamily Caroleomagnitoidae
		...	Family Groeberidae	Family Didelphidae	Family Caroleomagnitidae
		...	Order Australidelphia	Family Sparassocynidae	Family Caroleomagnitidae
		...	Order Microbiotheria	Family Argrolagidae	Family Caroleomagnitidae
		...	Superfam. Microbiotheroidea	Family Groeberidae	Cohort Eumetatheria
		...	Family Pedionymidae	Order Condwanidelphia	Order Microbiotheria
		...	Family Microbiotheriidae	Suborder Microbiotheria	Family Microbiotheriidae
		...	...	...	...

**Table 3.** A proposed classification of the Paucituberculata

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Order Paucituberculata Ameghino, 1894
Plesion <i>Dracolestes</i> gen. nov.
Plesion <i>Riolestes</i> gen. nov.
Superfamily Caenolestoidae Trouessart, 1898
Family Caenolestidae Trouessart, 1898
<i>Stilotherium</i> Ameghino, 1887
<i>Pliolestes</i> Reig, 1955
<i>Rhyncholestes</i> Osgood, 1924
<i>Caenolestes</i> Thomas, 1895
Superfamily Palaeothentoidea, new rank
Family Pichipilidae (Marshall, 1980), new rank
<i>Pichipilus</i> Ameghino, 1890
<i>Phonocdromus</i> Ameghino, 1894
Family Palaeothentidae Sinclair, 1906
<i>Palaeothentes</i> Ameghino, 1887
<i>Acdestis</i> Ameghino, 1887
<i>Abderites</i> Ameghino, 1887
<i>Parabderites</i> Ameghino, 1902

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Paucituberculata (Caenolestoidae + Argyrolagoidea) and the Polydolopimorphia as a natural group. With some variations, a similar concept was supported by Simpson (1945); Ride (1964) and other more modern authors.

The results of our analysis (see also Abello *et al.*, 2004) argue against this grouping. On the one hand, *Microbiotherium*, *Glasbius* plus the Polydolopimorphia (including the Argyrolagoidea within the latter) form a monophyletic group supported by three synapomorphies (Fig. 7): large, bulbous protocone (32<sup>1</sup>), nonwinged metaconule (36<sup>1</sup>) and reduced styler shelf (38<sup>1</sup>). Taking into account recent proposals favouring close relationships between microbiotheriids and the diprotodontian radiation (e.g. Kirsch *et al.*, 1997; Horovitz & Sánchez-Villagra, 2003), the hypothesis of a grouping between Microbiotheria and Polydolopimorphia as part of a more comprehensive concept of Australidelphia deserves further research (not attempted here). On the other hand, Didelphimorphia and Paucituberculata analysed here represent a lineage supported by two features: deeply V-shaped centrocrista (33<sup>2</sup>) and metacone larger than the paracone (35<sup>1</sup>). Three synapomorphies support the Paucituberculata clade including all the remaining taxa, with the exception of *Pucadelphys* and *Derorhynchus*: labially salient hypoconid (15<sup>1</sup>), laterally compressed entoconid (18<sup>1</sup>), and StB or StB and StC + StD larger than the paracone and metacone, respectively (34<sup>2</sup>). Summing up, according to the results of our analysis, we will hereafter restrict the concept of order Paucituberculata to that of the 'Caenolestidae' *sensu* Marshall (1980) plus the new taxa described here (Table 3).

*RIOLESTES* AND *BARDALESTES*  
AS PAUCITUBERCULATA

Among the overwhelming diversity of South American Palaeocene marsupials, known mainly from remains found at Tiupampa (Bolivia; see Marshall & de Muizon, 1988; de Muizon, 1991) and Itaboraí (Brazil; see de Paula Couto, 1952a, b, 1962, 1970; Marshall, 1987), most marsupial lineages that evolved during the Cenozoic in this continent were already present: Didelphimorphia, Microbiotheria, Sparassodonta, Polydolopimorphia, and Paucituberculata. The new taxa *Riolestes capricornicus* and *Bardalestes hunco* constitute the oldest evidence of undoubted Paucituberculata in South America. Note that the three synapomorphies (labially salient hypoconid, laterally compressed entoconid, and StB or StB and StC + StD larger than the paracone and metacone, respectively) that nested *Bardalestes*, *Riolestes* and the remaining Paucituberculata (i.e. Palaeothentoidea + Caenolestoidae), are coincident with those features previously considered as distinctive of this group (Abello, 2007). This agrees with the definition of the Paucituberculata as the clade stemming from the most recent common ancestor of *Riolestes*, *Bardalestes*, and the Palaeothentoidea + Caenolestoidae clade. Within Paucituberculata, *Bardalestes* and *Riolestes* are the most basal and primitive members of the order, showing the plesiomorphic condition for each feature present in the remaining Paucituberculata. *Riolestes* and *Bardalestes* are informative on the early evolution of the molar pattern in the Paucituberculata. Among them, five features support the Caenolestoidae + Palaeothentoidea clade: paracristid of m1 lacking a notch (11<sup>1</sup>); hypoconulid somewhat reduced and anteroposteriorly compressed (16<sup>1</sup>); open centrocrista, with the postparacrista and premetacrista fused to the lingual slopes of the STB and STD, respectively (33<sup>3</sup>); metaconule much larger than the paraconule; and labiolingually compressed (39<sup>1</sup>) styler cusps which are lingually expanded, but not reaching the lingual face of the protocone (37<sup>2</sup>). Taking into account the plesiomorphic conditions of *Riolestes* and *Bardalestes*, the inferred ancestral molar pattern of the Paucituberculata is characterized by the presence of a paracristid notch in the m1, a well-developed hypoconulid, uncompressed styler cusps, a closed and deeply V-shaped centrocrista, and a metaconule larger than the paraconule but not enlarged or 'hypocone'-like. This latter feature gives to the upper molar a subtriangular occlusal design that differs from the typical quadrangular pattern of the remaining Paucituberculata.

*Bardalestes* and *Riolestes* not only shed light on the phylogenetic relationships of the remaining Paucituberculata (see below) but also give some hints on the

very origin, and timing, of this marsupial clade. Meredith *et al.* (2008) have recently reviewed the relationships and timeline of all major marsupial clades. Their results, applying MULTIDIVTIME and BEAST analyses for the divergence estimates, conclude that the 'All marsupials but Didelphimorphia' clade (i.e. the Paucituberculata plus the Australidelphia of their phylogeny in Meredith *et al.* 2008, fig. 2) split between 71.3 and 85.6 Mya (see their table 5). That is, the late (but not latest) Cretaceous. In sharp contrast, their divergence estimates for the Paucituberculata are stated to be between 9.2 and 14.1 Mya. The empirical evidence here provided on the fossil record of the Paucituberculata supports none of these estimates. The oldest known Paucituberculata is the Late Palaeocene *Riolestes capricornicus*. Derorhynchids, which stand as a probable sister group of paucituberculatans, have their oldest record in the latest early Palaeocene (the latest Danian Banco Negro deposits; Bond *et al.*, 1995). The much better known, earliest Palaeocene fauna of Tiupampa, lacks any record not only of paucituberculatans but also of derorhynchids.

#### CLADISTICS OF THE PAUCITUBERCVLATA

The present analysis yielded several unexpected results regarding the traditional systematic concepts for Paucituberculata marsupials: (1) the exclusion of *Pliolestes* from the 'Pichipilinae' (*sensu* Marshall *et al.*, 1990) and their grouping together with the Caenolestidae *Stilotherium*, *Caenolestes*, and *Rhyncholestes*; and (2) the grouping of *Pichipilus* and *Phonocdromus* as sister taxa to Palaeothentidae + Abderitidae clade. These conclusions are discussed separately.

1. In his original description of *Pliolestes tripotamicus*, Reig (1955) pointed out the close affinities of this genus with *Phonocdromus* (see also Pascual & Herrera, 1973). Subsequently Marshall (1980), in his review of the South American Caenolestidae, included *Pliolestes* in the new tribe Pichipilini, together with *Phonocdromus* and *Pichipilus*. Finally, Marshall *et al.* (1990) raised this taxon to a subfamilial rank: Pichipilinae (Caenolestidae).

The results of our analysis support the hypothesis that *Pliolestes* does not form a monophyletic group with *Pichipilus* and *Phonocdromus*, but instead with the 'Caenolestini' *sensu* Marshall (1980). Actually, the concept of Caenolestidae proposed in this paper is restrained to the following genera: *Caenolestes*, *Pliolestes*, *Rhyncholestes*, and *Stilotherium*, and is characterized by the following synapomorphies (see Fig. 7): high entocristid in m1–3 (17<sup>1</sup>), curved entoc-

ristid in m1–3 (19<sup>1</sup>), m4 single-rooted and greatly reduced in relation to m3 (25<sup>1</sup>). *Stilotherium* is the sister taxon to (*Pliolestes* (*Caenolestes* + *Rhyncholestes*)). The latter group is supported by the synapomorphy: entoconid posteriorly located (20<sup>1</sup>). *Rhyncholestes* plus *Caenolestes* share one synapomorphy: very shallow metaconid in m2–3 (29<sup>1</sup>). *Pliolestes* shows one homoplastic character shared with the representatives of the Palaeothentoidea (see below): para- and metaconids of m3 very close or fused (23<sup>1</sup>).

Note that neither the living caenolestid *Lestoros* nor the extinct *Pseudhalmarhiphus* were considered in this paper. The holotype (and only known remain) of the Deseadan species *Pseudhalmarhiphus guaraniticus* Ameghino (1899) (only species of the genus) has disappeared from Argentinean collections, so almost nothing can be said of its affinities. Marshall (1976, 1980), based on illustrations of the holotype published by Ameghino (1894), said that '... *Pseudhalmarhiphus* is structurally similar to and is probably ancestral to *Stilotherium dissimile*' (Marshall, 1980: 35). Finally the generic validity of *Lestoros inca* (Thomas, 1917) – the only species of this genus geographically restrained to the Andean region south of Peru – has been discussed (e.g. Simpson, 1970). Marshall (1980) stated that *Caenolestes* and *Lestoros* can hardly be distinguished.

2. Another result of this analysis is the exclusion of *Pichipilus* and *Phonocdromus* from the Caenolestidae and their grouping as sister taxa of palaeothentids + abderitids. The features that, according to Marshall (1980), justify regarding the 'Caenolestinae' – including *Stilotherium*, *Pseudhalmarhiphus*, *Caenolestes*, *Lestoros*, *Rhyncholestes*, *Pliolestes*, *Phonocdromus*, and *Pichipilus* – as a monophyletic group, are the following: (1) double-rooted and functional p2; (2) p3 large, double-rooted and subequal or higher than the trigonid of m1; (3) M/m 1–4 tuberculo-sectorial, without lophs in unworn molars; (4) m1 with prominent metaconid; (5) nonmodified talonid and trigonid areas; (6) m2–3 with differentiated trigonids and talonids; (7) talonid much larger than trigonid in occlusal view; (8) M1–3 with metacone ('intermediate conule' *sensu* Marshall, 1980) labially orientated; (9) M1 quadritubercular; (10) neither P3 nor M1, p2 or m1 are modified as sectorial teeth; (11) presence of an antorbital vacuity between the nasal, maxillary, and frontal. However, none of these features are synapomorphies within the Paucituberculata, nor are present in all 'Caenolestinae' taxa: (1) a double-rooted and functional p2 is the generalized condition in all marsupials; (2) p3 is quite small compared with the development of this tooth in the Palaeothentidae and Abderitidae – and, in any case,

its development is only moderate with respect to other marsupial groups; (3) the molars of the Palaeothentidae are also tuberculo-sectorial and lack lophs; (4) in the Palaeothentidae the metaconid is also prominent; (5) the statement that that the trigonid and talonid areas in the m1 of 'Caenolestidae' are 'non-modified' was not verified in our study: in *Caenolestes*, as well as in *Rhyncholestes*, *Stilotherium*, and *Pliolestes*, the para- and metaconids are separated and the trigonid lacks a basin; (6) trigonids and talonids are differentiated in all the Paucituberculata and, besides, both *Pichipilus* and *Phonocdromus* share the same differentiation between both regions as the Palaeothentidae; (7) talonid wider than trigonid is not an exclusive feature of 'Caenolestidae' *sensu* Marshall (1980); rather, as it has been pointed out, it is already present in a generalized form of Paucituberculata: *Riolestes capricornicus*; (8) the metacone, when present, is always labially orientated, adjacent to the stylar cusp D; (9) M1 is quadritubercular in all Paucituberculata – although with slight variants; see Character Analysis; (10) 'P3, M1, p2, and m1 not differentiated in sectorial teeth' is the generalized condition in all marsupials; (11) finally, the presence of the vacuities cannot be verified in *Pichipilus* or *Phonocdromus* (see Character Analysis). This latter character is important because, as Marshall (1980: 127) himself recognized, despite the other features listed in his diagnosis, this one would be actually the only synapomorphy in common with his 'Caenolestinae' ('Caenolestini' + 'Pichipilini'). As mentioned above, the only specimen of 'Pichipilini' in which a skull has been preserved, with the rostrum area, is MLP 66-I-17-204, assignable to *Pichipilus centinelus*; however, the presence or absence of antorbital vacuities cannot be determined because of the damage to the material (*contra* Marshall & Pascual, 1977). Thus, *Pichipilus* and *Phonocdromus* do not show derived features in common with the 'Caenolestinae' *sensu* Marshall *et al.* (1990), but with the Palaeothentidae and Abderitidae, with which they form a monophyletic group. Both genera, here included within the family Pichipilidae (new rank) do not show affinities with *Pliolestes*, a caenolestid related to the *Rhyncholestes* + *Caenolestes* clade. The Pichipilidae are the sister group of palaeothentids + abderitids. In turn, pichipilids, palaeothentids, and abderitids, here included within the Superfamily Palaeothentoidea nov., are the sister group of the Caenolestoidea. In our concept, this last taxon includes a single family: Caenolestidae, containing the following genera: *Stilotherium*, *Pseudhalmarhiphus*, *Caenolestes*, *Lestoros*, *Rhyncholestes*, and *Pliolestes*.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Data matrix

**Appendix S2.** Morphological characters used for phylogenetic analysis

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