



## Analysis of dental homologies and phylogeny of Paucituberculata (Mammalia: Marsupialia)

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The Paucituberculata is an endemic group of South American marsupials, recorded from the early Cenozoic up to the present. In this report, the most comprehensive phylogenetic analysis of Paucituberculata to date is presented. Fifty-seven terminal species were scored for 74 new and re-examined characters. Homologies of dental characters used in previous systematic studies were critically reviewed to evaluate their inclusion in the analysis. Phylogenetic results corroborated two major paucituberculatan clades, Palaeothentoidea and Caenolestoida, and the main palaeothentoid groupings: Pichipilidae, Palaeothentidae, and Abderitidae. Taxon sampling and reinterpretations of molar cusp and crest homologies played an important role in the generation of new phylogenetic hypotheses. The main differences with respect to previous phylogenies were focused on palaeothentoid relationships: *Palaeothentes boliviensis* and *Pilchenia lucina* are not members of Palaeothentidae but instead clustered with *Pilchenia intermedia* and *P. antiqua*, forming the sister-group of a Palaeothentidae + Abderitidae clade, and *Titanothentes simpsoni*, previously considered a palaeothentine, is nested within the Adestinae clade. Based on the time-calibrated phylogeny, the following stages in the paucituberculatan evolutionary history are suggested: origin of the group, in the Paleocene to early Eocene at the latest, split of Caenolestoida and Palaeothentoidea clades during the late early to middle Eocene, evolutionary radiation of palaeothentid and abderitid lineages near the Oligocene–Eocene boundary, and decreased diversity and extinction of palaeothentoids during the middle Miocene. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 109, 441–465.

ADDITIONAL KEYWORDS: Abderitidae – Caenolestidae – Caenozoic – Palaeothentidae – South America.

### INTRODUCTION

The Paucituberculata is a metatherian clade endemic to South America. Among the diverse metatherians that have evolved in this continent, the paucituberculatans, along with Didelphimorphia and Microbiotheria, are the few lineages that have left living relatives (Goin, Abello & Chornogubsky, 2010). The extant paucituberculatans, grouped in the Caenolestidae, are the so-called *ratones runchos* or ‘shrew opossums’ and include six described species among the genera *Caenolestes*, *Lestoros*, and *Rhyncholestes*. Living caenolestids are small insectivorous species that inhabit several cold and wet habitats of the Andes, in three disjunct areas ranging from Ven-

ezuela to Chile and Argentina (Kirsch & Waller, 1979; Bublitz, 1987; Patterson & Gallardo, 1987; Albuja & Patterson, 1996).

Since the Paucituberculata was named by Ameghino (1904), the definition and content of this group has changed along with the increased knowledge of South American extinct marsupials (for a review see Goin *et al.*, 2009). Nowadays the consensus is that Paucituberculata is restricted to the Caenolestidae and three extinct groups: Pichipilidae, Abderitidae, and Palaeothentidae (Goin & Candela, 2004; Abello, 2007; Goin *et al.*, 2009). Thus, several metatherian lineages previously considered as paucituberculatans, e.g. the extinct Polydolopidae, Epidolopidae, and Argyrolagidae, are currently excluded from the Paucituberculata (Goin *et al.*, 2009; Chornogubsky, 2010).

In the context of Marsupialia, most phylogenetic studies based on molecular, morphological, or

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combined data (e.g. Horovitz & Sánchez-Villagra, 2003; Asher, Horovitz & Sánchez-Villagra, 2004; Nilsson *et al.*, 2004; Beck, 2008; Meredith *et al.*, 2008) place the paucituberculatans as the sister group of Australidelphia (i.e. Microbiotheria + Australasian marsupials, see Szalay, 1982). On the other hand, some morphological analyses that included several lineages of extinct South American metatherians show that they may be most closely related to some 'Didelphimorphia' (Goin *et al.*, 2009), or to the Australian Peramelemorphia (Ladevèze & de Muizon, 2010). According to this latter hypothesis paucituberculatans may be regarded as part of the australidelphian radiation.

In contrast to their poor modern representation, paucituberculatans were highly diverse in the past, including about 50 species (Abello, 2007). Considering their dietary niches, extinct paucituberculatans were not just insectivorous shrew-like forms such as the extant caenolestids, but the clade also included species, such as the abderitids, which are thought to have been very similar to the frugivorous Australian burramyids and phalangerids (Dumont, Strait & Friscia, 2000; Ortiz Jaureguizar, 2003; Abello, Ortiz-Jaureguizar & Candela, 2012). Paucituberculatans are first recorded in the early Eocene of Brazil and Argentina (Goin *et al.*, 2009), and throughout the Cenozoic reached a wider distribution, occurring in many South American fossil localities (Abello, 2007). However, they are mainly known from Patagonian fossil assemblages (Marshall, 1980; Bown & Fleagle, 1993; Goin *et al.*, 2009).

The paucituberculatan fossil record is largely fragmentary. About 10% of the species are known by relatively complete cranial remains, and only two specimens referred to palaeothentid species (*Palaeothentes minutus* and *P. lemoinei*) have an associated cranial and postcranial skeleton (Abello & Candela, 2010). The majority of the fossil evidence consists of teeth, either isolated or associated in incomplete jaws and maxillary bones. Because of this preservation bias, systematic studies have been mainly based on tooth morphology.

After Ameghino's studies (e.g. Ameghino, 1889, 1891, 1894, 1900–1902), the most important contribution to the knowledge of paucituberculatan evolution is Marshall's (1980) revision. More recently, Bown & Fleagle's (1993) work focused on systematics of Palaeothentidae, and several other contributions have described new paucituberculatan taxa in the context of faunal assemblage studies (e.g. Goin & Candela, 2004; Goin *et al.*, 2009). Since Marshall's (1980) contribution, the number of known extinct paucituberculatan species has roughly doubled. In part, this was the result of the implementation of screen-washed prospecting methods that have led to

increased specimen collection (Bown & Fleagle, 1993; Goin & Candela, 2004; Abello, 2007; Goin *et al.*, 2010). To date, only two cladistic analysis of Paucituberculata have been performed (Goin *et al.*, 2007, 2009) and both included selected genera as terminal taxa.

In view of the current state of knowledge of Paucituberculata species diversity, the aim of the present contribution is to explore their phylogenetic relationships through a cladistic analysis. To reconstruct the phylogeny of this group, it was necessary to revise paucituberculatan dental homologies, which resulted in a new vision with respect to the previous identifications of molar structures and dental series homologies. A fairly large number of specimens, some exceptionally well preserved, have become available in recent decades. These new materials allow a detailed revision of morphological characters, an analysis that is critical given that primary homology assessment is among the main determinants of the outcome of any phylogenetic analysis (Bryant, 1989; Hawkins, Hughes & Scotland, 1997).

#### INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MPEF-PV, Museo Paleontológico Egidio Feruglio (palaeovertebrate collection), Trelew, Argentina; PU, Princeton University collection, now at Yale Peabody Museum, USA.

#### DENTAL NOMENCLATURE

a, alveolus corresponding to a double-rooted tooth; abc, anterobasal cingulum; ac, anterobasal cuspule; act, anterior crest of m1 trigonid; alac, anterolabial crest; alic, anterolingual crest; anc, anterior cingulum; as, simple alveolus corresponding to a single-rooted tooth; atc, anterolabial trigonid cusp; C/c, upper and lower canine, respectively; co, cristid obliqua; eda, entocristid; Ent, entoconid; Hyp, hypococonid; Hypd, hypoconulid; I/i, upper and lower incisor, respectively; laca, labial crest of the anterobasal cuspule; lc, labial crest; lica, lingual crest of the anterobasal cuspule; mc, main cusp on p3; mdpc, metaconid posterior crest; M/m, upper and lower molar, respectively; Me, metacone; Med, metaconid; mel, metaconule; P/p, upper and lower premolar, respectively; Pa, paracone; pac, parastylar cusp; Pad, paraconid; pal, paraconule; parad, paracristid; pc, premetaconulid cusp; pent, postentocristid; plac, posterolabial crest on p3; plic, posterolingual crest on p3; pmd, postmetacristid; pmec, premetaconular crest; poc, postcristid; pome, postmetacrista; pomec, post-

metaconular crest; popc, postparaconular crest; popr, postprotocrista; poprd, postprotocristid, ppa, postparacrista; ppad, postparacristid; Pr, protocone; Prd, protoconid; prdpc, protoconid posterior crest; prepa, preparacrista; prepr, preprotocrist; preprd, preprotocristid; prme, premetacrista; prod, protocristid; prpc, preparaconular crest; StA, stylar cusp A; StB, stylar cusp B; StC, stylar cusp C; StC+D, fused stylar cusps C and D; StD, stylar cusp D.

## MATERIAL AND METHODS

### MATERIAL

Multiple specimens and casts (listed in Abello, 2007) belonging to described extinct species, new unnamed extinct species (recognized in Abello, 2007), and species representative of extant genera were examined. A list of the paucituberculatan studied in this contribution, including their provenance and main references, is included in Table 1.

### DENTAL HOMOLOGIES ANALYSIS

Dental series and tooth morphology were analysed following a comparative approach. Special attention was paid to molar crown morphology because most of the morphological variability of paucituberculatan is expressed therein. In this context, comparable features were identified among taxa and then primary homologies (*sensu* de Pinna, 1991) were assessed using a topographical correspondence criterion (see Rieppel, 1988).

To clearly illustrate the homology proposals and nomenclature used in this work, drawings of the plesiomorphic molar pattern of Metatheria (Marshall, Case & Woodburne, 1990: fig. 3) and representative molar morphologies of the main paucituberculatan groups are provided in Figures 1–4. Molar serial homologies and position of the molar/premolar boundary follow Luckett (1993).

### PHYLOGENETIC ANALYSIS

#### *Taxon sampling*

Fifty-seven species were used as terminal taxa. Most of the species previously referred to Paucituberculata were selected as ingroup (listed in Table 1). The species belonging to *Propalaeothenes* erected by Bown & Fleagle (1993) were excluded because *Propalaeothenes lepidus* and *Propalaeothenes hatcheri* are considered junior synonyms of *Palaeothenes intermedius* and *Palaeothenes minutus*, respectively (a detailed morphological comparison between type specimens and a discussion of the synonymy are offered in Abello, 2007). Four species were omitted from the ingroup for different reasons: (1) *Pseudhal-*

*mariphus guaraniticus* because its holotype, and only known specimen, is at present lost, (2) *Adestoides praecursor* because it is based on a mandible fragment with a molar so poorly preserved that much of its morphology is unknown, (3) *Hondathentes cazador* and (4) *Palaeothenes smeti*, both because the respective type specimens could not be examined directly and the illustrations provided by Dumont & Bown (1997) and Flynn *et al.* (2002) were inadequate for comparative purposes. The stem-metatherians *Pucadelphys andinus* and *Alphadon clemensi*, the ‘ameridelphian’ *incertae sedis* *Derorhynchus singularis* (Oliveira & Goin, 2011), and the didelphid *Didelphis albiventris* were used as outgroups. A previous phylogenetic analysis that evaluated the relationships of representative genera of the main South American lineages (e.g. Paucituberculata, Microbiotheriidae, Polydolopidae, and Argyrolagidae) indicated that *Derorhynchus* as a close outgroup to Paucituberculata (Goin *et al.*, 2009). In other analyses of the phylogenetic relationships of marsupials, the didelphids were found to be the closest outgroups of paucituberculatan (Horovitz & Sánchez-Villagra, 2003; Beck, 2008). On the other hand, *Pucadelphys* and *Alphadon* are more distant paucituberculatan outgroups (Luo *et al.*, 2003; Rougier, Wible & Novacek, 2004). *Alphadon clemensi* was used to root the analysis.

#### *Character sample*

Taxa were scored for 74 characters. Because of the fragmentary condition of paucituberculatan fossils, the selected characters mainly involve dental morphology and a few (two characters) refer to features of cranial bones. Forty-one of the characters are new, 33 were used in previous studies, and ten of the latter were modified from original definitions. The list of characters and a complete description and discussion of each one are provided in Appendix S1.

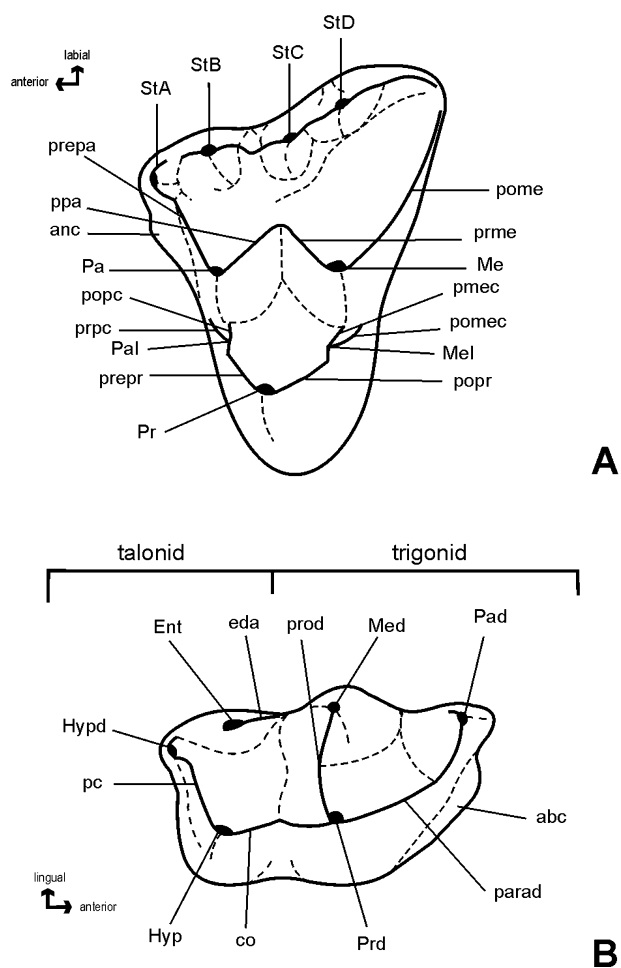
#### *Missing data*

The selected ingroup includes several poorly known species that are based on fragmentary materials; hence, the absence of evidence is reflected by multiple missing entries in the taxon-character matrix. For phylogenetic inferences derived from such data sets, missing data could be a problem involving an increase in the number of equally most-parsimonious trees (MPTs) and highly unresolved consensus trees. Several solutions have been proposed to deal with the effects of missing data, including deleting characters or taxa that have a certain proportion of missing entries, or use of consensus methods other than the strict consensus (for critical reviews see Kearney & Clark, 2003; Wiens, 2003; Prevosti & Chemisquy, 2011). An alternative approach, the ‘*Safe Taxonomic Reduction*’ method (STR) proposed by Wilkinson

**Table 1.** Geographical and temporal data for paucituberculatan species included in the phylogenetic analysis

Species	Occurrence	Age	Main reference
<i>Riolestes capricornicus</i>	São José de Itaboraí, Br.	early Eocene (Itaboraian)	Goin <i>et al.</i> , 2009
<i>Bardalestes hunco</i>	La Barda, Chubut, Arg.	early Eocene	Goin <i>et al.</i> , 2009
<i>Bardalestes</i> sp.	Las Flores, Chubut, Arg.	early Eocene (Itaboraian)	Goin <i>et al.</i> , 2009
<i>Evolestes hadrommatos</i>	Salla, Loaza, Bol.	late Oligocene (Deseadan)	Goin <i>et al.</i> , 2007
<i>Evolestes</i> sp.	La Cantera, Chubut, Arg.	late early Oligocene (pre Deseadan)	Goin <i>et al.</i> , 2010
<i>Perulestes fraileyi</i>	Santa Rosa, Ucayali, P.	late Eocene-early Oligocene	Goin & Candela, 2004
<i>Perulestes cardichi</i>	Santa Rosa, Ucayali, P.	late Eocene-early Oligocene	Goin & Candela, 2004
<i>Sasawatsu mahaynaq</i>	Santa Rosa, Ucayali, P.	late Eocene-early Oligocene	Goin & Candela, 2004
<i>Quirogalestes almagaucha</i>	Valle Hermoso, Chubut prov., Arg.	middle Eocene (Casamayoran)	Goin & Candela, 1998
<i>Pilchenia antiqua</i>	La Cancha, Chubut prov., Arg.	early Oligocene (Tinguirirican)	Goin <i>et al.</i> , 2010
<i>Pilchenia intermedia</i>	La Cantera, Chubut prov., Arg.	late early Oligocene (pre Deseadan)	Goin <i>et al.</i> , 2010
<i>Pilchenia lucina</i>	Cabeza Blanca, Chubut prov., Arg.	late Oligocene (Deseadan)	Marshall, 1980
<i>Stilotherium dissimile</i>	Santa Cruz and Neuquén prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Pliolestes tripotamicus</i>	Tres Arroyos, Buenos Aires prov., Arg.	early Pliocene (?Chapadmalalan)	Reig, 1955
<i>Pliolestes venetus</i>	La Pampa prov., Argentina	late Miocene (Huayquerian)	Goin <i>et al.</i> , 2000
<i>Pichipilus riggsi</i>	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Marshall, 1980
<i>Pichipilus centinelus</i>	Cerro Centinela, Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Pichipilus osborni</i>	?Karaiquen, Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Pichipilus halleuxi</i>	Alto Río Cisnes, Aisén, Chile	middle Miocene (Friasian)	Marshall, 1990
<i>Phonodromus gracilis</i>	Santa Cruz prov. Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Acdestodon bonapartei</i>	Cabeza Blanca, Chubut prov., Arg.	late Oligocene (Deseadan)	Bown & Fleagle, 1993
<i>Acdestis owenii</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Acdestis lemairei</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Bown & Fleagle, 1993
<i>Acdestis maddeni</i>	Quebrada Honda, Bol.	middle Miocene (Laventan)	Goin <i>et al.</i> , 2003
<i>Trelewthentes rothi</i>	Gaiman, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Bown & Fleagle, 1993
<i>Titanothentes simpsoni</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Rae <i>et al.</i> , 1996
<i>Palaeothentes pascuali</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Bown & Fleagle, 1993
<i>Titanothentes</i> sp.	Chubut and Santa Cruz prov., Arg.	early Miocene	Kramarz <i>et al.</i> , 2010
<i>Palaeothentes minutus</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Palaeothentes intermedius</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Palaeothentes lemoini</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Palaeothentes aratae</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Marshall, 1980
<i>Palaeothentes primus</i>	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Marshall, 1980
<i>Palaeothentes marshalli</i>	Gaiman, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Bown & Fleagle, 1993
<i>Palaeothentes migueli</i>	Gaiman, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Bown & Fleagle, 1993
<i>Palaeothentes boliviensis</i>	Salla, Bol.	late Oligocene (Deseadan)	Bown & Fleagle, 1993
<i>Carlothentes chubutensis</i>	Cabeza Blanca, Chubut prov., Arg.	late Oligocene (Deseadan)	Bown & Fleagle, 1993
<i>Abderites meridionalis</i>	Santa Cruz prov., Arg.	late early Miocene (Santacrucian)	Abello & Rubilar-Rogers, 2012
<i>Abderites crispus</i>	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello & Rubilar-Rogers, 2012
<i>Abderites aisenense</i>	Neuquen prov., Arg., and Aisén, Ch.	middle Miocene (Friasian)	Abello & Rubilar-Rogers, 2012
<i>Parabderites bicrispatus</i>	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Marshall, 1980
<i>Parabderites minusculus</i>	Cabeza Blanca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Marshall, 1980
<i>Pitheculites minimus</i>	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Marshall, 1980
<i>Pitheculites chenche</i>	La Venta, Col.	late Miocene (Laventan)	Dumont & Bown, 1997
<i>Pitheculites rothi</i>	Alto Río Cisnes, Ch.	middle Miocene (Friasian)	Marshall, 1990
sp. nov. 1	Gaiman, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello, 2007
sp. nov. 2	Gaiman, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello, 2007
sp. nov. 3	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello, 2007
sp. nov. 4	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello, 2007
sp. nov. 5	Gran Barranca, Chubut prov., Arg.	early Miocene (Colhuehuapian)	Abello, 2007
<i>Caenolestes fuliginosus</i>	Andes of Colombia and Ecuador	Recent	Bublitz, 1987
<i>Rhyncholestes raphanurus</i>	Valdivian region of Argentina and Ch.	Recent	Bublitz, 1987
<i>Lestoros inca</i>	Andes of Peru and Bol.	Recent	Bublitz, 1987

Arg, Argentina; Bol, Bolivia; Br, Brazil; Co, Colombia; Ch, Chile; P, Peru.



**Figure 1.** Plesiomorphic molar pattern of Metatheria showing dental terminology. A, upper molar in occlusal view. B, lower molar in occlusal view. For dental abbreviations see Dental Nomenclature.

(1995, 2003), seeks to enhance the resolution of consensus trees by identifying and a priori removing taxonomic equivalents. These taxa do not contribute with any unique information and can be excluded from the analysis without modifying the inferred relationships among the remaining taxa. For the current analysis, and in order to obtain more resolved summaries of the strictly supported relationships, the STR method was applied and taxonomic equivalents were identified using the TAXEQ3 program (Wilkinson, 2001).

#### Data matrix analysis

Two taxon-character matrices were constructed, the complete matrix (CM, see Appendix S1) including all ingroup and outgroup taxa detailed above, and the reduced matrix (RM) based on CM but excluding taxonomic equivalents (see results). The data sets

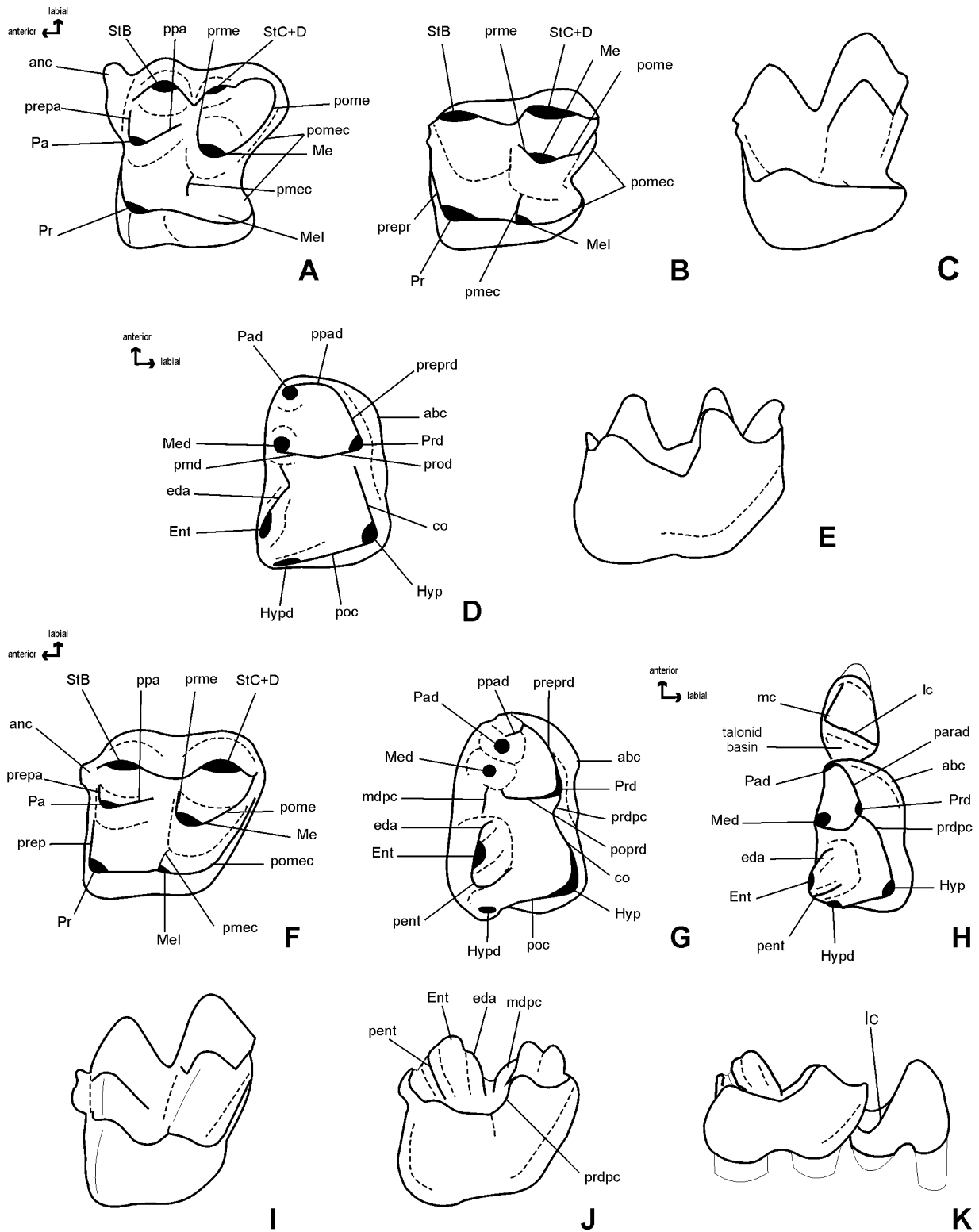
were analysed performing heuristic searches with parsimony with TNT 1.1 (Goloboff, Farris & Nixon, 2003). The shortest trees were found by generating 500 Wagner trees, and then subjecting them to the tree bisection-reconnection branch-swapping method (TBR), retaining ten trees per replication. All multi-state characters were treated as unordered because all hypotheses regarding the evolutionary relationships among the character states were assumed as equally probable. Polymorphic characters were coded as such, as implemented in TNT. To explore clade sensitivity, analyses implementing equal weights and the implied weighting method (Goloboff, 1993; Goloboff *et al.*, 2008) were conducted. For the character weighting method, values of the *K* constant of concavity ranged from 1 to 100. As part of the present study the following analyses were carried out: (1) CM analysis under implied weights, (2) RM analysis under equal weights, and (3) RM analysis under implied weights.

The strict component consensus method was applied to summarize the relationships that are common to multiple MPTs. Two algorithms for character optimization, accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN), were used to explore alternative reconstructions for some ambiguous character optimizations. As the presence of characters with weights or costs can lead to incorrect conclusions with regard to support when using Bootstrap and Jackknife (Goloboff *et al.*, 2003), support for the clades was measured by means of the symmetric resampling method (1000 replicates;  $P = 0.33$ ), reporting the results as absolute and GC (Group present/Contradicted) frequencies.

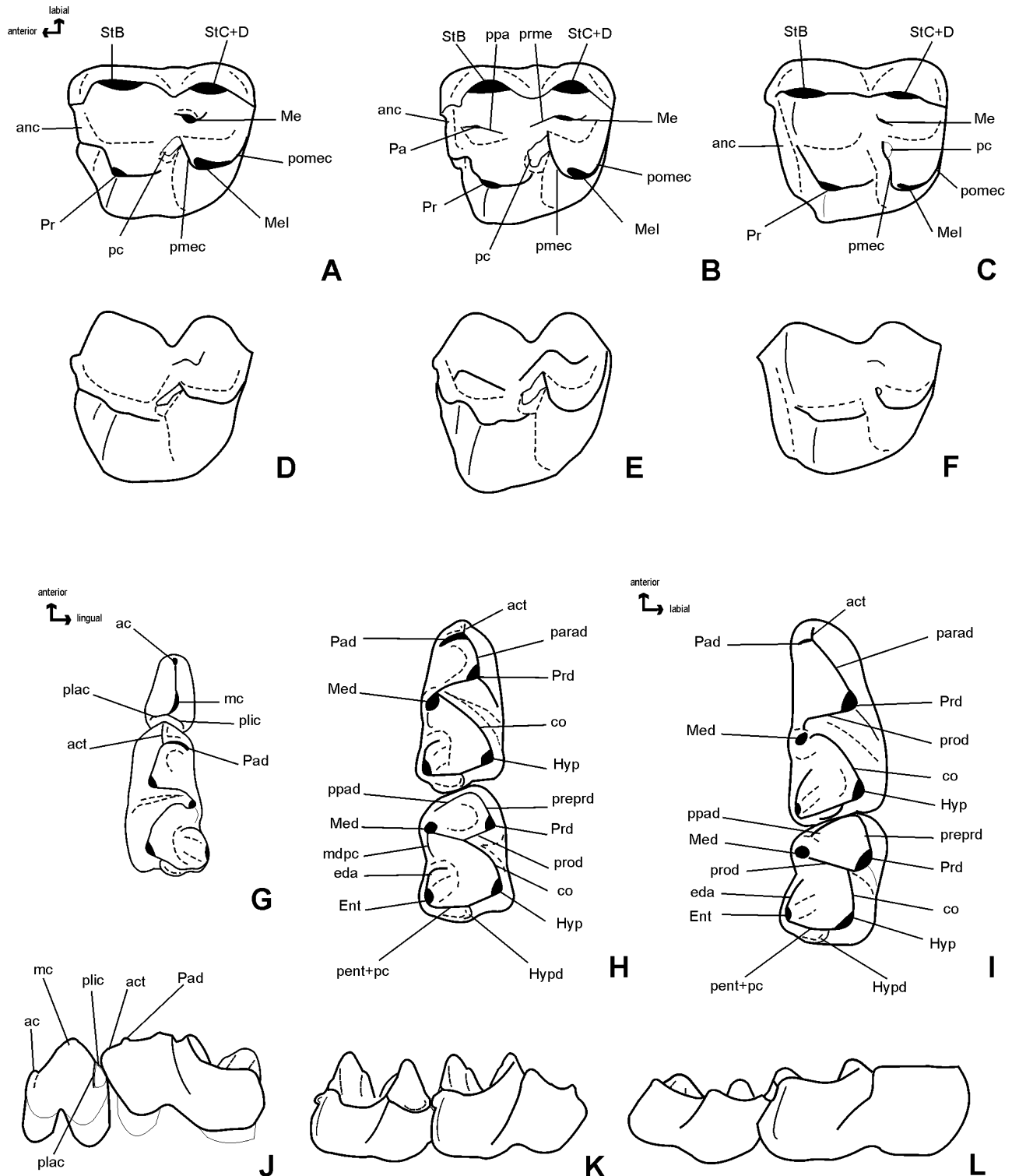
## DENTAL HOMOLOGIES

### HISTORICAL BACKGROUND

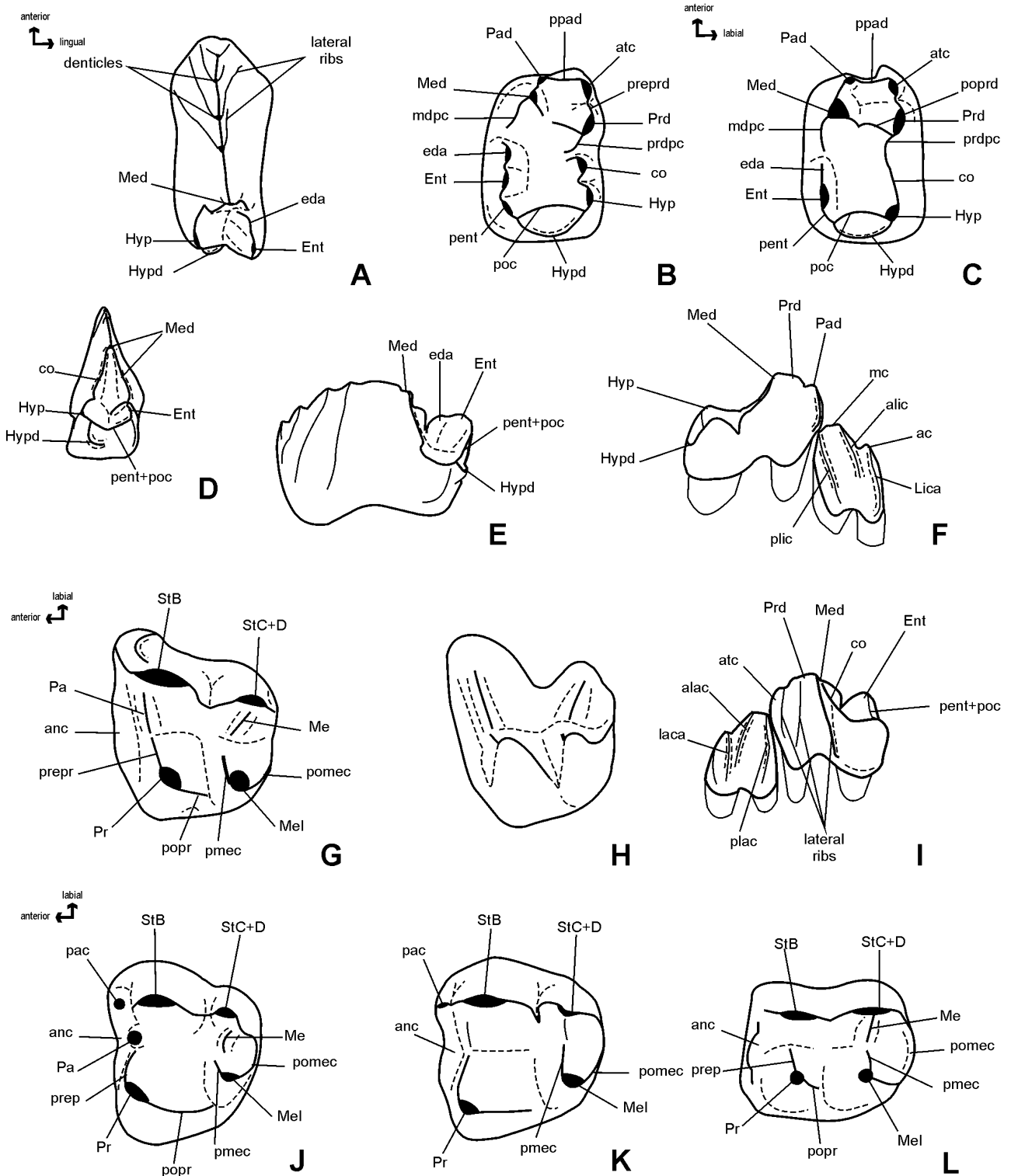
The lower dentition of paucituberculatans is characterized by a hypertrophied and procumbent numerical first lower incisor, reduction in number and crown simplification of the antemolar teeth, with some of them being peg-like (Fig. 5), and presence of four molars. Among representatives of the four main clades (Caenolestidae, Pichipilidae, Abderitidae, and Palaeothentidae) and basal paucituberculatans, the molars have quite distinct patterns of cusps and crests. Basal taxa, such as *Bardalestes hunco* (Goin *et al.*, 2009), have relatively unspecialized triangular upper molars with the complete set of cusps and crests that characterize the plesiomorphic molar pattern of Metatheria (Marshall *et al.*, 1990; Fig. 1). In contrast, the highly derived abderitids, such as *Abderites meridionalis*, have quadrangular upper molars, with enlarged posterolingual metaconule,



**Figure 2.** Schematic drawings showing dental morphology and terminology of upper and lower molars of *Evolestes hadrommatos* (A), *Stilotherium dissimile* (B–E) and pichipilids (F–K). *Evolestes hadrommatos*: M2 in occlusal view (A). *Stilotherium dissimile*: M1 in occlusal (B) and lingual (C) views; m2 in occlusal (D) and labial (E) views. Pichipilidae: M1 in occlusal (F) and lingual (I) views; m2 in occlusal (G) and labial (J) views; p3–m1 in occlusal (H) and labial (K) views. For dental abbreviations see Dental Nomenclature.

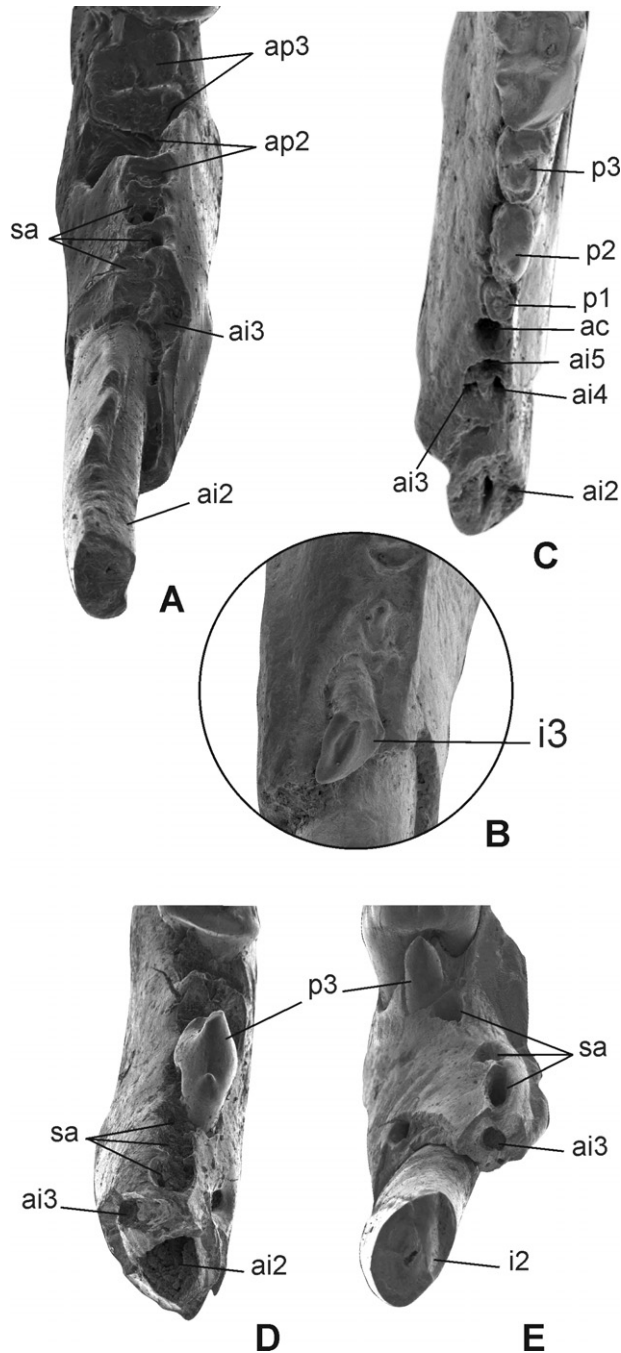


**Figure 3.** Schematic drawings showing dental morphology and terminology of palaeotheniid upper and lower teeth. *Palaeothenites minutus*: M1 in occlusal (A) and lingual (D) views; p3–m1 in occlusal (G) and labial (J) views; m1–2 in occlusal (H) and labial (K) views. *Palaeothenites primus*: M1 in occlusal (B) and lingual (E) views. *Acestis owenii*: M1 in occlusal (C) and lingual (F) views; m1–2 in occlusal (I) and labial (L) views. For dental abbreviations see Dental Nomenclature.



**Figure 4.** Schematic drawings showing dental morphology and terminology of abderitid upper and lower teeth. *Pitheculithes minimus*: m1 in occlusal (A), posterior (D), and labial (E) views; m2 in occlusal view (B); M1 in occlusal (G) and lingual (H) views; M2 in occlusal view (J). *Abderites crispus*: m2 in occlusal view (C); M2 in occlusal view (K). *Parabderites bicrispatus*: p3–m1 in lingual (F) and labial (I) views; M1 in occlusal view (L). For dental abbreviations see Dental Nomenclature.





**Figure 5.** Paucituberculatan antemolar series. *Stilotherium dissimile*: right mandible (MACN 8466) in antero-occlusal view (A), detail of left mandible (PU 15238) showing the staggered i3 in occlusal view (B). C, sp. nov. 4: left mandible (MLP 82-V-2-113) in occlusal view. D, *Palaeothenes primus*: left mandible (MLP 92-X-10-13) in antero-occlusal view. E, *Abderites meridionalis*: right mandible (MLP 55-XII-13-145) in antero-occlusal view. For dental abbreviations see Dental Nomenclature.

fusion of the para- and metacone to the styler cusps, and lower molars with neomorphic cusps present. Additionally, another derived dental morphology that evolved among abderitids is the plagiaulacoid dentition (see Simpson, 1933), characterized by highly modified m1 and P3 that are transformed into shearing structures.

Most paucituberculatan with a well-preserved antemolar portion of the dentary show reduction in the number of antemolar teeth with respect to that of generalized metatherians (Marshall, 1980). Taking into account that the traditionally accepted ancestral dental formula proposed for Metatheria is I5/4, C1/1, P3/3, M4/4 (Marshall, 1979; Hershkovitz, 1995; Cifelli & de Muizon, 1997), the reduction of up to five lower, and six upper antemolar teeth has engendered several hypotheses of serial homologies for the paucituberculatan antemolar teeth. Likewise, modifications of molar morphology with respect to the plesiomorphic molar pattern of Metatheria (Marshall *et al.*, 1990; Fig. 1), as was exemplified above, have led to different interpretations of the dental structures. The previous proposals are detailed below.

#### *Antemolar dental series*

Hypertrophy and procumbency of the anteriormost lower incisor evolved in both paucituberculatan and diprotodontians, and was originally viewed as supporting their phylogenetic affinity (Ameghino, 1889, 1890, 1891, 1893; Thomas, 1895; Sinclair, 1905, 1906; Osgood, 1921) rather than as a convergence (Dederer, 1909; Gregory, 1910; Simpson, 1928). From the results of several phylogenetic analyses it becomes clear that this character actually evolved several times in the Marsupialia, i.e. in the Paucituberculata, Diprotodontia, and in the South American extinct Polydolopimorphia (Springer, Kirsch & Case, 1997; Goin *et al.*, 2009). However, the serial homology of this first lower incisor is still controversial. Ride (1962) was the first to explicitly propose a homology hypothesis for the anteriormost lower incisor of paucituberculatan and diprotodontians. Based on embryological grounds for the diprotodontians and on the number of antemolar teeth for the extinct and extant paucituberculatan, he concluded that the procumbent and enlarged incisor is not homologous in both groups, being the i3 (or possibly the i4) in the case of diprotodontians and the i1 or i2 in the paucituberculatan. Therefore, Ride (1962) designated the condition present in the paucituberculatan and polydolopids as 'pseudodiprotodonty', as opposed to the 'true' diprotodonty of Australasian marsupials.

Based on arguments different from those of Ride (1962), Hershkovitz (1995) proposed the i2 homology of the more anterior lower incisor of paucituberculatan (Fig. 5). Following Winge (1893), Hershkovitz

(1982, 1995) stated that the first lower incisor in marsupials was phylogenetically lost and that other changes, throughout marsupial phylogeny, led to the crowded disposition of the remaining incisors (i2–5) and the wedged position of the i3 root between and behind the adjacent teeth. This ‘staggered’ condition of the i3 was observed in extant and extinct caenolestids (Sinclair, 1906: 420; Hershkovitz, 1995), and implied the i2 homology of the procumbent incisor of paucituberculatan as deduced from its relative position in the incisor row (Hershkovitz, 1995: 158). However, more recently Voss & Jansa (2009: 55) stated that for extant caenolestids there is no suggestion of staggered alveolus for any of the lower incisor loci, and Luckett & Hong (2000) pointed out that the homology of the paucituberculatan procumbent incisor is uncertain considering the absence of dental development data. Regarding the remaining antemolar teeth, the most accepted serial homologies, as expressed in dental formulae indicating each incisor, canine, and premolar tooth family, were those proposed by Marshall (1980) for the following paucituberculatan groups: Caenolestinae, I4/4, C1/1, P3/3; Palaeothentinae, I3/2, C1/1, P3/2–3; and Abderitinae, I?/2, C?/1, P?/3.

#### *Molar dental series*

Two patterns of tooth replacement have been proposed for metatherians. The most widely accepted view, evidenced in both living and extinct taxa (e.g. Luckett, 1993; Cifelli & de Muizon, 1997), considers a dp3–p3 replacement and the following serial homology of molars: m1, m2, m3, and m4. This molar series was the most used in the dental description of paucituberculatan (e.g. Marshall, 1976, 1980; Bown & Fleagle, 1993; Goin *et al.*, 2009). Alternatively, a replacement of m1–p3 was proposed by Archer (1978), implying a molar series formed by m2, m3, m4, m5. Archer’s hypothesis has been occasionally mentioned for paucituberculatan dentition (Marshall, 1990). It is important to note that paucituberculatan were previously suggested to lack a deciduous tooth (Archer, 1978; Marshall, 1980). However, as Luckett & Hong (2000) demonstrated, caenolestids are characterized by the presence of a small deciduous third premolar and a late p3 eruption with respect to that of m4. In the particular case of the P3–M4 series of abderitids, homologies were recently reviewed by Abello & Rubilar-Rogers (2012). Their proposals are in agreement with those of Marshall *et al.* (1990) and differ from those of Marshall (1976, 1980). Accordingly, the shearing teeth that form the abderitid plagiaulacoid complex are the P3/m1 in *Abderites* and *Pitheculites*, and the P3/p3–m1 in *Parabderites* (Fig. 4).

#### *Upper molars*

Most paucituberculatan have quadrangular upper molars with four main cusps: two labial and two lingual ones (Figs 2B, 3A–F, 4K–L). The interpretation of the labial cusps as stylar ones was first made by Osgood (1921: 123) and followed by several authors (e.g. Marshall, 1987; Marshall *et al.*, 1990; Goin & Candela, 2004; Goin *et al.*, 2009). However, in the same study, when describing the upper molars of *Caenolestes*, Osgood (1921: 120) designated the labial cusps as para- and metacone, and the lingual ones as protocone and hypocone; in addition, he identified an ‘intermediate conule’ basal and lingual to the metacone. These latter cusp names were adopted by Marshall as cusp homologies (1980: fig. 5b) leading him to conclude that the absence of the stylar shelf was a derived character of the Caenolestidae (= Paucituberculata; Marshall, 1980: 126). In the same way, several phylogenetic analyses including *Caenolestes* as a paucituberculatan representative also considered that this taxon lacks stylar cusps and that the labial cusps are homologous to the para- and metacone of the metatherian plesiomorphic molar pattern (e.g. Springer *et al.*, 1997; Sánchez-Villagra, 2001; Ladevèze & de Muizon, 2010). More recently, the labial cusps of *Caenolestes* were scored as representing stylar cusps in the phylogenetic analyses of Abello & Candela (2010) and Beck (2012).

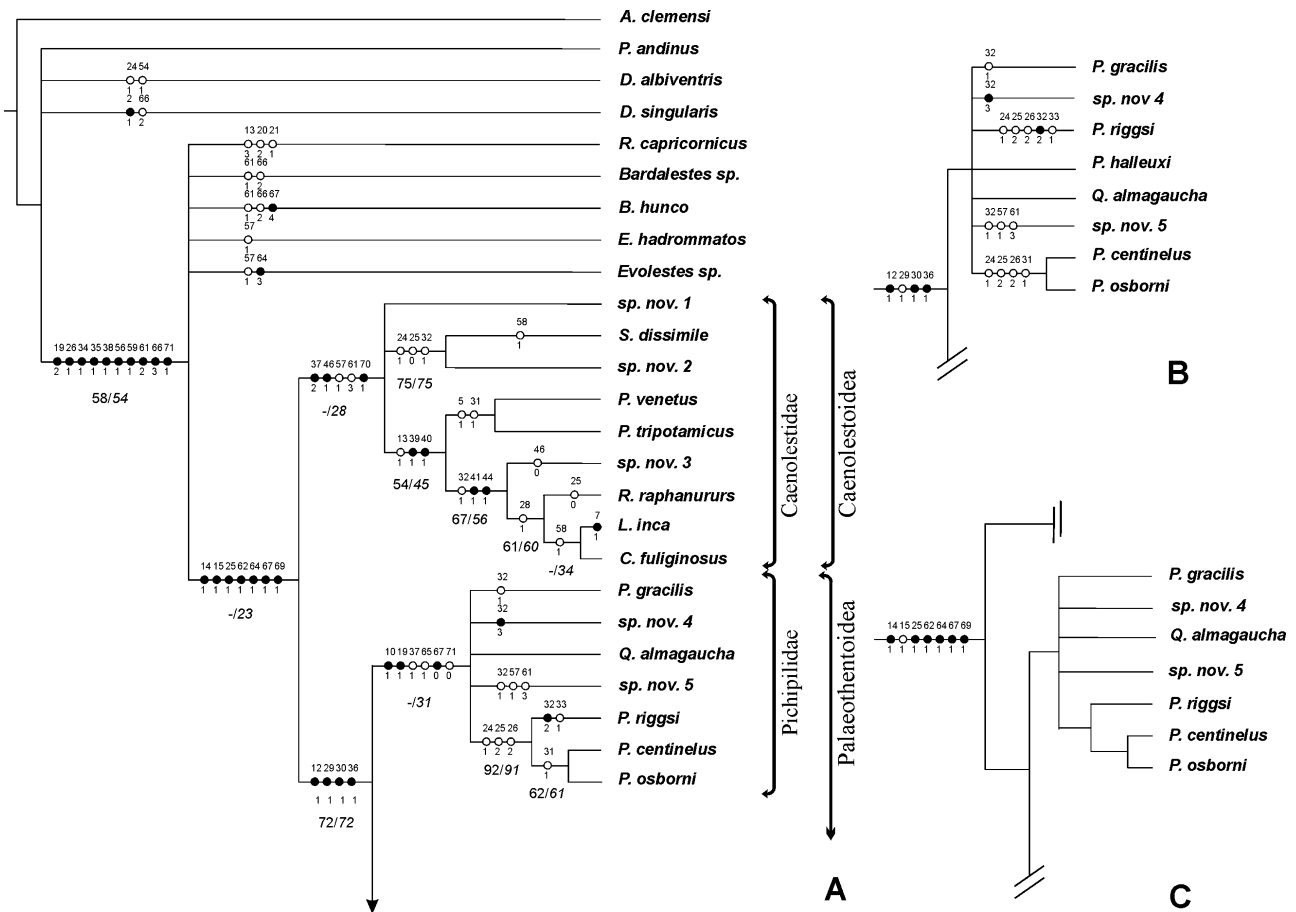
#### *Lower molars*

The lower molar pattern of caenolestids and pichipilids (Caenolestinae *sensu* Marshall, 1980) was considered as primitive in relation to that of palaeothentids and abderitids (Marshall, 1980; Marshall *et al.*, 1990; Bown & Fleagle, 1993). On m1–4 of caenolestids and pichipilids, Marshall (1980) and subsequent authors (Abello, 2007) identified the complete set of cusps and crest present in the plesiomorphic molar pattern of marsupials (Fig. 1). Several derived characters were identified for the lower molars of palaeothentids and abderitids (Marshall, 1980; Marshall *et al.*, 1990; Bown & Fleagle, 1993), particularly for the specialized m1 of abderitids; among these, the following characters are worth mentioning: absence of the paraconid on m2–3 in palaeothentids and abderitids (Marshall, 1980: 43; Marshall *et al.*, 1990: 440), presence of lophos on m2–4, and m1 with the metaconid absent and trigonid modified into a shear-blade in abderitids (Marshall, 1980: 43), and bifurcated paraconid on m1 of palaeothentinae (Marshall, 1980: 52; Bown & Fleagle, 1993: 49).

#### HOMOLOGY PROPOSALS OF THIS WORK

##### *Antemolar series*

As a result of the present study, the staggered i3 was identified in all extinct paucituberculatan with



**Figure 6.** Results of phylogenetic analyses. A, strict consensus cladogram of 252 most parsimonious trees (MPTs) arising from analysis of the reduced matrix (after safe taxonomic reduction) under implied weights with  $K = 3$  ( $L = 204$ ,  $CI = 0.54$ ,  $RI = 0.86$ ; continued in Fig. 7); symmetric resampling values above 50 (roman) and GC frequency differences (italic) are given below branches. B, strict consensus cladogram of 1780 MPTs produced by the analysis of the total matrix under implied weights with  $K = 3$  ( $L = 210$ ,  $CI = 0.53$ ,  $RI = 0.85$ ). C, strict consensus cladogram of 2040 MPTs produced by the analysis of the reduced matrix under equal weights ( $L = 214$ ,  $CI = 0.52$ ,  $RI = 0.84$ ). Only the topologies that differ from that of A are shown in B and C. Filled circles represent non-homoplasious characters; open circles indicate homoplasies. Numbers above circles represent characters, numbers below represent character states.

well-preserved alveoli or teeth of the antemolar series (Fig. 5); hence, and following Hershkovitz (1995), the hypertrophied lower incisor is considered to be the i2. The extinct taxa with verified staggered i3 are representatives of the main paucituberculatan clades: Caenolestidae, Pichipilidae, Abderitidae, and Palaeothentidae. Thereby, the staggered condition of the i3 could be seen as a generalized morphology for the paucituberculatans. As was mentioned before, none of the lower incisive loci has a wedged morphology in recent caenolestids (Voss & Jansa, 2009), but it is remarkable that *Stilotherium dissimile*, a caenolestid closely related to the extant members of the Caenolestidae clade (Fig. 6A), has a staggered i3. A possible explanation for this character distribution is that the staggered condition of the i3 could have been

lost in the lineage of extant caenolestids. Concerning the homology of the remaining antemolar teeth, the presence of eight teeth (or the corresponding alveoli) was verified in specimens of the most generalized paucituberculatan groups: Caenolestidae and Pichipilidae. If no supernumerary teeth were developed, as was suggested by Luckett & Hong (2000) and Martin (2007) for extant caenolestids, then a dental formula of 4i, 1c, and 3p may be assumed. Eight antemolar teeth are present in two specimens of *Stilotherium dissimile* (MACN 8467 and PU 15238), one of *Phonocdromus gracilis* (AMNH 9593), and two pichipilids (MLP 82-V-2-113 and MPEF-PV 4877; Fig. 5C). The remaining caenolestids and pichipilids, with complete antemolar series (six specimens), have seven antemolar alveoli or teeth. In this case, it is impossible to

know which tooth was lost, but it is certainly not the i2, i3, p2, or p3. The i2 is the hypertrophied first incisor, the i3 is the *staggered* second incisor, and the p2 and p3 are both two-rooted teeth (premolars) that are placed anterior to m1. The single-rooted and peg-like teeth between i3 and p2 are indistinguishable, so the lost teeth may be the i4, i5, c, or p1.

Palaeothenids have a general antemolar series formed by six teeth (Fig. 5D), occasionally reduced to five in some *Acdestis* specimens. As in caenolestids and pichipilids, i2, i3, and p3 are distinguishable, but the remaining antemolars are very similar peg-like teeth (Rae, Bown & Fleagle, 1996: fig. 9). As an exception (e.g. MACN 8318 and MACN 8347-8354c referred to *Palaeothenes minutus*) the tooth located just anterior to the p3 has its single alveolus divided by an osseous trabecula, thus denoting fused roots and thus a probable premolar locus. In relation to the maximum of eight antemolars, two or three lost teeth may correspond to a combination of i4, i5, c, p1, and p2.

Abderitids have six antemolar teeth (Fig. 5E). As in palaeothenids, i2, i3, and p3 are distinct, unlike the remaining peg-like antemolars. Only one specimen referred to *Abderites crispus* (MPEF-PV 5847) has a probable p2 just anterior to the p3 (Abello & Rubilar-Rogers, 2012). As in the case of palaeothenids, the loci of lost teeth are not certain.

The upper antemolar series of extant caenolestids comprises eight teeth: 4I, 1C, 3P. Incisors are distinct from each other. The more anterior one (I1) is vertical and all the following (I2–4) are slightly procumbent and longer than the I1, becoming smaller and anteroposteriorly shorter from the I2 to the I4. The canine is relatively large and double-rooted in *Lestoros inca* and females of both *Caenolestes* and *Rhyncholestes*, but single-rooted in males of *Caenolestes* and *Rhyncholestes* (see Voss & Jansa, 2009 and references therein). Premolars are two-rooted (except P1 of *L. inca*, see Bublitz, 1987), increasing in size from the P1 to the P3. Complete upper antemolar series are unknown for most extinct paucituberculatans. However, from the partially preserved type specimen of *Acdestis maddeni* (Goin *et al.*, 2003) and some specimens referred to *Palaeothenes minutus* (Abello, 2007) it is possible to reconstruct the upper series of these palaeothenids. Both species have seven antemolar teeth: 3I, C, and 3P. Considering the morphology of the incisors, it is possible to homologize them with the I1–3 of extant caenolestids.

Summing up, in this work the antemolar formula for most paucituberculatans is considered to be uncertain. However, in agreement with Hershkovitz (1995), two lower anterior incisors of paucituberculatans are homologized with the i2–i3 of generalized marsupials. In paucituberculatans with complete lower antemolar

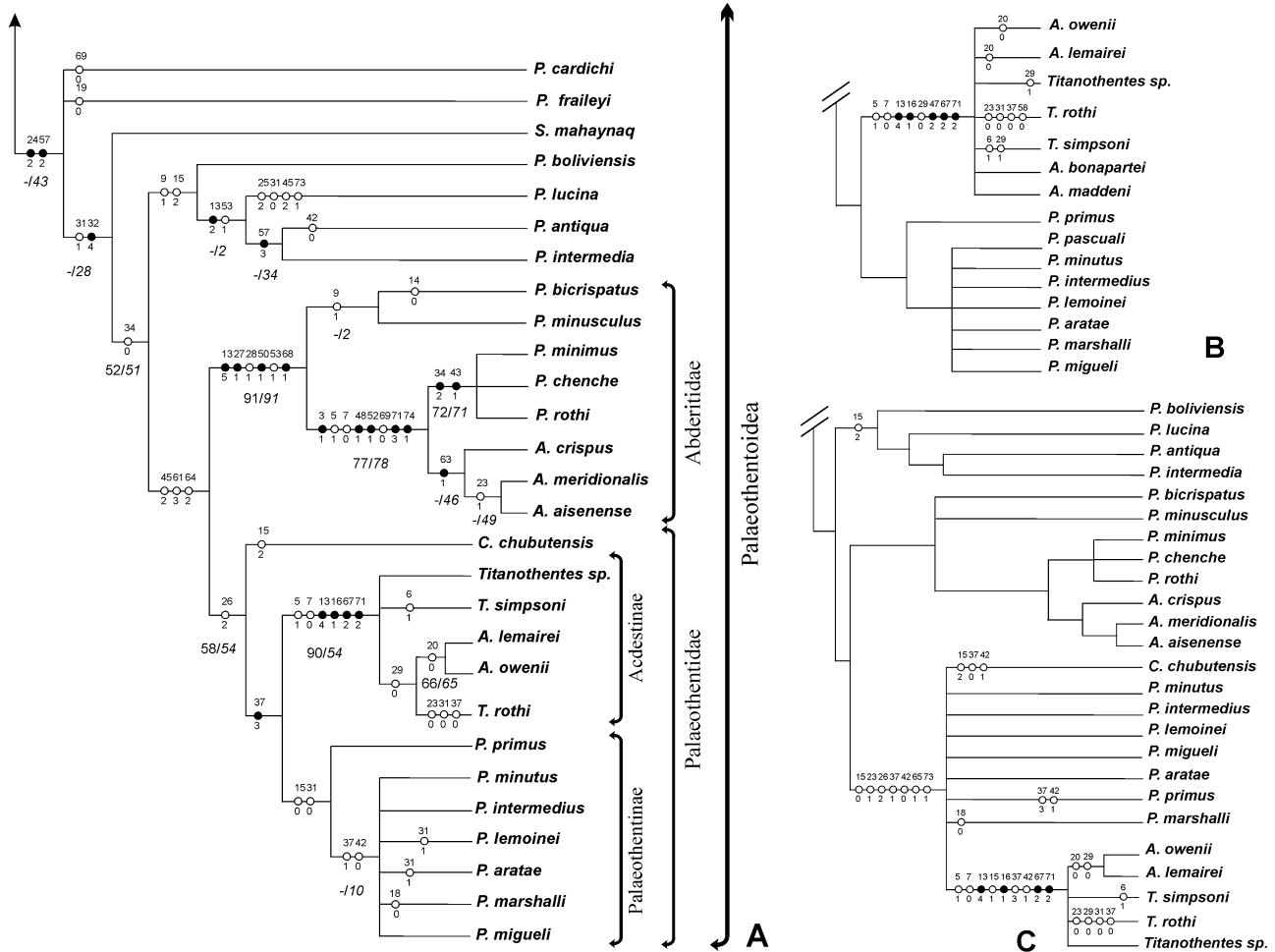
series, such as some caenolestids and pichipilids, the teeth present are the i2, i3, i4, i5, c, p1, p2, and p3. Other paucituberculatans have seven (some caenolestids and pichipilids), six (abderitids and most palaeothenids), or five (some acdestine specimens) antemolar teeth. In these reduced lower antemolar series, the lost tooth/teeth are of uncertain loci. Complete antemolar upper series are only known for living species; the teeth present are the I1, I2, I3, I4, C, P1, P2, and P3. Reconstructed upper antemolar series of palaeothenids indicates a reduction to seven teeth; based on morphological comparisons with the antemolars of caenolestids, the lost tooth is, most probably, the I4.

#### Upper molars

In agreement with the scheme of cusp homology originally proposed by Osgood (1921: 123) here the labial cusps are considered to correspond to styler cusps, and the antero-lingual cusp to the protocone (Figs 2A, B, 3A–F, 4K–L). The postero-lingual cusp originally considered a hypocone by Osgood (1921) is interpreted to be homologous to the metaconule, as proposed by previous authors (e.g. Goin & Candela, 2004; Goin *et al.*, 2009). The ‘intermediate conule’ (Osgood, 1921; Marshall, 1980) is reinterpreted here as the metacone. The para- and metacone are set lingually to the styler cusps. The paracone, when present, is smaller than the metacone (Figs 2A, 3B). A metacone is usually present (except in *Abderites* species; Fig. 4K) and variably reduced among paucituberculatans. In summary, the nomenclature and homology of cusps and crests adopted here is based on those of Osgood (1921) and Goin *et al.* (2009). The topological correspondence is as follows: anterolabial cusp = StB, posterolabial cusp = StC+D, anterolingual cusp = protocone, posterolingual cusp = metaconule, cusp lingual to the StB = paracone, cusp lingual to the StC+D and labial to the metaconule = metacone.

#### Lower molars

The homologies of several molar structures have been here reinterpreted from those proposed in previous studies; some of these reinterpretations are: presence of metaconid on the m1 of abderitids vs. absence of metaconid on the m1 of palaeothenids (Marshall, 1980: 123), ‘bifurcated paraconid’ on m1 of palaeothenids (Bown & Fleagle, 1993: 49) = paraconid plus anterior crest on m1 of palaeothenids, presence of paraconid on m2 of palaeothenids and abderitids vs. absence of paraconid on m2 of palaeothenids and abderitids (Marshall, 1980: 131; Marshall *et al.*, 1990: 440), and presence of postentocristid on m1–3 of palaeothenids and abderitids vs. absence of postentocristid on m1–3 of palaeothenids and abderitids (Goin *et al.*, 2009). These and other reinterpretations of cusp and crest



**Figure 7.** Results of phylogenetic analyses. A, strict consensus cladogram of 252 most parsimonious trees (MPTs) arising from analysis of the reduced matrix (after safe taxonomic reduction) under implied weights (continued from Fig. 6); symmetric resampling values above 50 (roman) and GC frequency differences (italic) are given below branches. B, strict consensus cladogram of 1780 MPTs produced by the analysis of the total matrix under implied weights. C, strict consensus cladogram of 2040 MPTs produced by the analysis of the reduced matrix under equal weights. Only the topologies that differ from that of A are shown in B and C. Filled circles represent unique character changes; open circles indicate homoplastic changes. Numbers above circles represent characters, numbers below represent character states.

homologies are discussed in detail in the character descriptions of the Phylogenetic Analyses (see Appendix S1).

**PHYLOGENETIC ANALYSIS**  
RESULTS (FIGS 6, 7)

The application of STR revealed seven potential taxonomic equivalents that could be safely removed: *P. pascuali*, *A. maddenii*, *P. osborni*, *P. halleuxi*, *A. bonapartei*, *P. rothi*, and *A. aisenense*; thus, an RM was constructed following the safe deletion rules proposed by Wilkinson (1995). However, *P. osborni*, *P. rothi*, and *A. aisenense* were retained in the RM because their exclusion would not improve the resolutions of the

clades that include them (see their phylogenetic positions in the strict consensus trees, Figs 6B, 7).

Analyses I, II, and III resulted in 1780, 2040, and 252 MPTs, respectively; in the analyses I and III the same consensus topologies were obtained with *K*-values from 3 to 100. The strict consensus and support values of analysis III are given in Figures 6A and 7A. Consensus trees of the analyses differ in the degree of resolution of some clades, particularly the Pichipilidae and Palaeothentidae (cf. Fig. 6A–C; cf. Figure 7A–C). Paucituberculata is highly supported in the three analyses. Within Paucituberculata there is a large basal polytomy formed by *R. capricornicus*, *E. hadrommatos*, *Evolestes* sp., *Bardalestes* sp., *Bardalestes hunco*, and a clade grouping the remaining

paucituberculatans. This latter clade groups most paucituberculatan species in two main clades. One of them includes extant caenolestids (*C. fuliginosus*, *L. inca*, *R. raphanurus*) and closely related extinct species: sp. nov. 1, sp. nov. 2, sp. nov. 3, *P. venetus*, *P. tripotamicus*, and *S. dissimile*. The second is the large clade Palaeothentoidea, which groups Pichipilidae (sp. nov. 4, sp. nov. 5, *P. gracilis*, *Q. almagaucha*, *P. riggsi*, *P. osborni*, *P. centinelus*, and *P. halleuxi*) as sister of the clade grouping palaeothentids and abderitids of the traditional literature. As result of the exclusion of *P. halleuxi* from analyses II and III, the monophyly of *Pichipilus* was recovered. The clade of non-Pichipilidae palaeothentoids has a basal trichotomy formed by *P. fraileyi*, *P. cardichi*, and the clade that includes the remaining taxa. This latter clade comprises *S. mahaynaq*, *Pilchenia* (including *P. boliviensis*, *P. lucina*, *P. intermedia*, and *P. antiqua*) and the clade formed by the sister groups Abderitidae (*Parabderites* + (*Pitheculites* + *Abderites*)) and Palaeothentidae (*C. chubutensis*, *T. pinturinus*, *A. owenii*, *A. lemairei*, *A. maddeni*, *T. rothi*, *T. simpsoni*, *A. bonapartei*, *P. primus*, *P. pascuali*, *P. minutus*, *P. intermedium*, *P. lemoinei*, *P. aratae*, *P. marshalli*, and *P. migueli*). For the Abderitidae clade, implied-weights analyses recovered the monophyly of *Parabderites*, absent from the results of analysis II (equally weighted). Within Palaeothentidae, Decastinae was the only group recovered in the three analyses (see clade discussion); the resolution of decastine relationships was improved by STR application and the recovery of *Acdestis-Trelewthentes rothi* monophyly. Relationships among the rest of the palaeothentids were largely unresolved in analysis II. As compared with the equal-weights analysis, implied-weights analyses yielded a higher number of nodes. *Carlothentes chubutensis* was sister to palaeothentines plus decastines and, among palaeothentines, *P. primus* was sister to the remaining *Palaeothentes* species (except *P. boliviensis* and *P. lucina*, see clade discussion).

#### CLADE DISCUSSION

Discussion of clades and systematic conclusions are based on the results of analysis III because its consensus tree yielded a higher number of nodes than those of analyses I and II, thus providing more information about the evolution of paucituberculatans. As noted above, the high number of recovered nodes resulted from the application of STR and implied-weights methods, which had their main impact in the resolution of relationships among palaeothentids.

*Paucituberculata*: The monophyly of Paucituberculata is corroborated by ten unambiguous synapomorphies

and relatively high support (58/54 absolute and GC frequencies; Fig. 6A). As in the results of Goin *et al.* (2009), the quite developed and salient hypoconid on m2–3 (34<sup>1</sup>) and a laterally compressed entoconid on m1–3 (35<sup>1</sup>) were recovered as paucituberculatan synapomorphies. Another feature considered a paucituberculatan synapomorphy by Goin *et al.* (2009), the larger size of the StB, or StB and StC+StD with respect to para- and metacone, was not recovered in this work. In the present analysis the character ‘relative sizes of the paracone and metacone with respect to the styler cusps’ was modified from character 34 in Goin *et al.* (2009), and reinterpreted in the characters 61 and 64 (see Appendix S1); thus, the paracone reduced and coalescent to StB (61<sup>2</sup>) was diagnostic of Paucituberculata and the metacone slightly reduced and coalescent to StC+D was a synapomorphy of a less inclusive clade (Caenolestoidea + Palaeothentoidea).

Relationships among basal paucituberculatans were ambiguous, resulting in a large polytomy that grouped *R. capricornicus*, *Bardalestes* sp., *B. hunco*, *Evolestes* sp., and *E. hadrommatos*. Several characters were scored as missing data in these taxa and so eight additional paucituberculatan synapomorphies were recovered under ACCTRAN (2<sup>2</sup>, 4<sup>1</sup>, 11<sup>1</sup>, 45<sup>1</sup>, 49<sup>1</sup>, 54<sup>1</sup>, 55<sup>1</sup>, 72<sup>2</sup>); among them is the hypertrophied and procumbent i2 (2<sup>1</sup>), one of the most distinctive morphological features of this group (Fig. 5; see Introduction). *Bardalestes hunco* and *Bardalestes* sp. on the one hand, and *Evolestes hadrommatos* and *Evolestes* sp. on the other, were not resolved as sister taxa; therefore, the generic assignments of *Bardalestes* sp. (Goin *et al.*, 2009) and *Evolestes* sp. (Goin *et al.*, 2010) are taxonomic decisions not completely supported by the present phylogenetic results. Excluding basal taxa, the remaining paucituberculatans are grouped in a large clade with a low support (–/23 absolute and GC frequencies). This grouping comprises two main clades: Caenolestoidea and Palaeothentoidea.

*Caenolestoidea*: Caenolestidae includes the Caenolestini *sensu* Marshall, 1980 (= Caenolestinae of Marshall *et al.*, 1990), *Pliolestes*, and the new species sp. nov. 1, sp. nov. 2, and sp. nov. 3. These result are in agreement with those of Goin *et al.* (2009) and differ from Marshall’s (1980) and Marshall *et al.*’s (1990) hypotheses in the inclusion of *Pliolestes*, and the exclusion of *Pichipilus* and *Phonocdromus* from the Caenolestidae clade.

Five unambiguous synapomorphies (37<sup>2</sup>, 46<sup>1</sup>, 57<sup>1</sup>, 61<sup>3</sup>, 70<sup>1</sup>), and one further synapomorphy revealed under ACCTRAN (1<sup>1</sup>), support Caenolestidae monophyly. Of the caenolestid synapomorphies proposed here, two have been suggested previously by Goin

*et al.* (2009): curved entocristid in m1–3 (37<sup>2</sup>; Fig. 2D) and single-rooted m4 (46<sup>1</sup>). Another synapomorphy proposed by these authors, high entocristid on m1–3 (39<sup>1</sup>), was recovered here supporting a less inclusive clade that groups *Pliolestes*, sp. nov. 3, and living caenolestids. The diagnostic characters of the Caenolestidae considered by Marshall (1980) and Marshall *et al.* (1990) have been extensively discussed in Goin *et al.* (2009), so this issue will not be further analysed here.

At the base of Caenolestoidea there is a trichotomy consisting of: (1) a clade comprising the sister-taxa *Stilotherium dissimile* and sp. nov. 2, (2) a group including the living Caenolestidae, sp. nov. 3, and *Pliolestes*, and (3) sp. nov. 1. All branches, except for the *C. fuliginosus* – *L. inca* clade, have high support values. This analysis revealed some interesting results regarding the cladistics and taxonomic composition of the Caenolestidae. In the first place, three new species may be referred to this group: sp. nov. 1, sp. nov. 2 and sp. nov. 3. On the other hand, according to the topology of the first clade, sp. nov. 2 may be considered a new *Stilotherium* species, which would extend the temporal range of this genus from the Santacrucian age (temporal provenance of *S. dissimile*; 16.3 Mya, Bown & Fleagle, 1993), back to the Colhuehuapian age (20 Mya, Madden *et al.*, 2010). Within the second group, the living caenolestids form a clade that has *C. fuliginosus* and *L. inca* as terminal monophyletic group, and *R. raphanurus* as its sister taxon. Up to now, both *Stilotherium* and *Pliolestes* have been considered the closest extinct relatives to living caenolestids (Goin *et al.*, 2009), but as was demonstrated in this analysis it is sp. nov. 3, from the Colhuehuapian of Patagonia (Abello, 2007), which now occupies this phylogenetic position. Outside the described clade is the sister-group *P. venetus* – *P. tripotamicus*. These results confirm the monophyly of *Pliolestes* species, as previously proposed by Goin, Montalvo & Visconti (2000), and the condition of *Pliolestes* as a member of Caenolestidae (Goin *et al.*, 2009).

**Palaeothentoidea:** The palaeothentoids encompass Pichipilidae and its unnamed sister group that clusters *Perulestes*, *Sasawatsu*, *Pilchenia*, abderitids, and palaeothentids. The results of the present study confirm previous hypotheses about the close phylogenetic relationships of pichipilids to palaeothentids and abderitids (Goin *et al.*, 2009), and reject the ‘Caenolestidae’ concept (i.e. Caenolestini + Pichipilinae) as proposed by Marshall (1980) and Marshall *et al.*, (1990). Palaeothentoidea is supported by high support values (72/72 absolute and GC frequencies) and four unambiguous synapomorphies (12<sup>1</sup>, 29<sup>1</sup>, 30<sup>1</sup>, 36<sup>1</sup>). Two of these were previously considered by Goin *et al.*

(2009): presence of a crest-like expansion posterior to the metaconid in m1–3 (29<sup>1</sup>; Fig. 2G) and markedly different thickness between the lateral and occlusal molar faces (12<sup>1</sup>). Another diagnostic character of Palaeothentoidea in Goin *et al.* (2009), namely the metaconid anteriorly placed with respect to the protoconid in m3, was not recovered in the present analysis. The relative position of the metaconid and protoconid was considered here for m2 and m3 conjointly (character 22). Among palaeothentoids, two character states were identified: metaconid anteriorly placed on m2–3 (22<sup>1</sup>), present in Pichipilidae (Fig. 2D), *P. cardichi*, and Abderitidae (except *P. bicrispatus*; Fig. 4B, C), and metaconid not anteriorly placed on m2, but anteriorly placed on m3 (22<sup>2</sup>), present in *Pilchenia*, *P. bicrispatus*, and Palaeothentidae (Fig. 3H, I). The character state 22<sup>1</sup> was recovered as a synapomorphy of Palaeothentoidea, but only under DELTRAN.

Excluding Pichipilidae, the remaining palaeothentoids are clustered in a large clade with *Perulestes*, *Sasawatsu*, and *Pilchenia* as successive sister-taxa to the Palaeothentidae + Abderitidae clade. The monophyly of Palaeothentidae + Abderitidae was assessed by several previous authors (Marshall, 1980; Marshall *et al.*, 1990; Abello, 2007; Goin *et al.*, 2009); this clade is here supported by three unambiguous synapomorphies.

**Pichipilidae:** Pichipilidae groups most of the ‘traditional’ pichipilids: *Pichipilus osborni*, *P. centinelus*, *P. riggsi*, *P. halleuxi*, *Quirogalestes almagaucha*, *Phonocdromus gracilis* (Marshall & Pascual, 1977; Marshall, 1980, 1990; Goin & Candela, 1998), and the new species: sp. nov. 4 and sp. nov. 5. The monophyly of this taxon is supported by six unambiguous synapomorphies (10<sup>1</sup>, 19<sup>1</sup>, 37<sup>1</sup>, 65<sup>1</sup>, 67<sup>0</sup>, 71<sup>0</sup>) and is relatively well supported in terms of GC frequency differences (GC = 31).

As mentioned above, the topology recovered in the present analysis does not support the inclusion of *Pliolestes* in the Pichipilidae. The close phylogenetic relationships among *Pliolestes*, *Pichipilus*, and *Phonocdromus* were originally proposed by Marshall (1976; see also Marshall & Pascual, 1977). Subsequently, Marshall (1980) reasserted these hypotheses by proposing a Pichipilini tribe (= Pichipilinae of Marshall *et al.*, 1990) which encompassed all these genera. Different taxa have been proposed as the phylogenetically closest relatives of *Pliolestes*; first, *Pichipilus osborni* (Marshall, 1976; Marshall & Pascual, 1977), and subsequently, *P. halleuxi* (Marshall, 1990; Ortiz Jaureguizar, 1997). However, these proposals were refuted by more recently phylogenetic analyses that demonstrated the caenolestid affinities of *Pliolestes* (Abello, 2007; Goin *et al.*, 2009).

A large basal polytomy was here found in the Pichipilidae clade. The poor resolution of pichipilid relationships was partially due to the poorly known species *Pichipilus halleuxi*, a taxonomic equivalent to most of the pichipilids. The exclusion of *P. halleuxi* from analyses II and III improved the phylogenetic resolution by recovering the *P. riggsi* (*P. osborni* + *P. centinelus*) clade; consequently, the monophyly of *Pichipilus* species was corroborated as originally proposed by Marshall & Pascual (1977). *Pichipilus halleuxi* was another species previously included in this genus (Marshall, 1990), but the result of the present analysis does not support this taxonomic assignation. However, as shown in Figure 6B, *P. halleuxi* is still a member of the Pichipilidae clade.

*Perulestes*, *Sasawatsu*, and *Pilchenia*: The sister group of Pichipilidae is a clade supported by two synapomorphies (24<sup>2</sup>, 57<sup>2</sup>) and relatively well supported in terms of GC frequency differences (GC = 43). The most basal taxa of this clade are *Perulestes*, *Sasawatsu*, and *Pilchenia*. In its original description, *Perulestes* was referred to the Caenolestidae (*sensu* Marshall, 1980) and two species were recognized, *P. cardichi* and *P. fraileyi* (Goin & Candela, 2004). However, in this analysis, these two species were not recovered as a monophyletic group and, on the contrary, both were positioned in a basal trichotomy with a clade that grouped the remaining non-Pichipilidae palaeothentoids. In view of these phylogenetic relationships, the assignation of *P. fraileyi* to *Perulestes* is not completely supported by the present phylogenetic results. Additionally, it is important to note that *Perulestes* species are recovered as palaeothentoids rather than members of Caenolestidae, as previously proposed (Goin & Candela, 2004). In agreement with Goin & Candela's (2004) observations, *Perulestes* species are considered to represent morphological intermediates between caenolestids, on the one hand, and palaeothentids and abderitids, on the other; some plesiomorphic characters (e.g. metaconid anteriorly placed relative to the protoconid on m2–3, well-developed anterobasal cinguli) are shared by *Perulestes* and pichipilids while some derived characters (e.g. metaconule higher than protocone, very reduced paraconid) place it closer to the palaeothentids and abderitids. Better knowledge of the dentition of *P. fraileyi* and *P. cardichi* will probably reveal a sister-group relationship between them. For example, an autapomorphic character of *P. cardichi*, the presence of parastylar cusp on M2 is entered as missing data in *P. fraileyi*, while an autapomorphy of *P. fraileyi*, namely the moderately deep protocristid, is entered as missing data in *P. cardichi*.

*Sasawatsu mahaynaq* was originally considered as a highly derived paucituberculatan and, based on its

lower antemolar formula (i2, c1, p2), among other characters, a species closely related to palaeothentids and abderitids (Goin & Candela, 2004). In agreement with the assessments of Goin & Candela (2004), *Sasawatsu* was recovered here as closely related to palaeothentids and abderitids. In this analysis, two synapomorphies group *Sasawatsu* with the *Pilchenia* + (Abderitidae + Palaeothentidae) clade: molar crowns basally wide (31<sup>1</sup>) and lower molars with vestigial anterobasal cingulum (32<sup>4</sup>). Even though any inference of the lower antemolar formula of paucituberculatans is highly speculative (see Dental Homologies), the presence of five or possibly six antemolar teeth (see Goin & Candela, 2004: 39) additionally relates *Sasawatsu* to abderitids and palaeothentids.

The *Pilchenia* clade (Fig. 7A) was the sister-group to the Palaeothentidae + Abderitidae, and grouped the type species *P. lucina*, the two recently described species, *P. intermedia* and *P. antiqua* (Goin *et al.*, 2010), and *Palaeothentes boliviensis*. Among the most important implications of the topology obtained is that *P. boliviensis* is not a species of *Palaeothentes*, and that *P. boliviensis* and *P. lucina* are not members of Palaeothentidae, as previously considered (Patterson & Marshall, 1978; Marshall, 1980; Bown & Fleagle, 1993), but that these species are actually basal to palaeothentids, and members of a new paucituberculatan clade. As an additional result, the membership of *P. intermedia* and *P. antiqua* in the genus *Pilchenia* (Goin *et al.*, 2010) was corroborated. In the three analyses *Pilchenia* species were resolved as monophyletic, with *P. boliviensis* as sister to the *P. lucina* (*P. intermedia* + *P. antiqua*) clade.

*Abderitidae*: Six unambiguous synapomorphies (13<sup>5</sup>, 27<sup>1</sup>, 28<sup>1</sup>, 50<sup>1</sup>, 53<sup>1</sup>, 68<sup>1</sup>) and high absolute frequency and GC values (91/91) support the Abderitidae clade, which includes the traditionally recognized abderitid genera *Parabderites*, *Abderites*, and *Pitheculites* (Marshall, 1976, 1980; Ortiz Jaureguizar, 2003; Abello, 2007).

In agreement with the inferences of Marshall (1980: 130–131), molar lophodonty (68<sup>1</sup>; Fig. 4C, L) and the sectorial morphology of the m1 trigonid (Fig. 4A, E) are considered derived characters of abderitids. In the Abderitidae, the main trigonid cusps of the m1 are aligned (13<sup>5</sup>; Fig. 4A, F) and laterally compressed, forming a large blade-like structure. It is worth mentioning that the sectorial m1 trigonid is part of the plagiaulacoid dentition that characterizes this group (see Introduction); this type of dentition, involving different teeth, has evolved differently in the two main abderitid lineages (*Parabderites* and *Abderites* + *Pitheculites* clade, see below). In *Parabderites* the cutting structure of the



m1 trigonid is also accompanied by the cutting morphology of the p3 (Fig. 4F, I). In the species of this genus, the p3 is a high tooth with the crown labiolingually compressed at the occlusal margin; thus, a continuous cutting edge exists from the trigonid of m1 and the p3. In contrast, in *Abderites* and *Pitheculites* the whole cutting structure of the lower dentition is linked to the modification of the m1 trigonid (Fig. 4A, E), which is much more developed than in *Parabderites*. The p3 in the species of *Abderites* and *Pitheculites*, unlike the condition in *Parabderites*, is strongly reduced (5<sup>1</sup>; Fig. 5E) and does not participate in occlusion, other than by forming a sort of support for the anterior portion of the m1 trigonid (Abello & Rubilar-Rogers, 2012). In the upper dentition, the occlusal antagonist of the p3–m1 of *P. bicrispatus*, and of the m1 trigonid of *Abderites* and *Pitheculites*, is the P3 (Abello, 2007).

Several previous hypotheses about abderitid ingroup relationships were confirmed. Among them are the relationships between *Parabderites*, *Abderites*, and *Pitheculites* proposed by Marshall (1976, 1980), Ortiz Jaureguizar (2003), and Abello (2007). Originally Marshall (1976, 1980) proposed that *Abderites* and *Pitheculites* are more closely related to each other than either is to *Parabderites*. These ideas were further supported by the phylogenetic analyses of Ortiz Jaureguizar (2003) and Abello (2007); in these analyses, as well as in the present study, *Abderites* and *Pitheculites* were strongly monophyletic. Eight synapomorphies support the *Abderites* + *Pitheculites* clade; two of these, small p3 (5<sup>1</sup>) and the presence of a parastylar cusp on M2 (69<sup>0</sup>; Fig. 4J, K), were previously considered by Marshall (1980).

The traditionally recognized species of *Parabderites* and *Pitheculites* (Marshall, 1976, 1980; Ortiz Jaureguizar, 2003; Abello, 2007) were recovered as monophyletic groups. Two species, *P. minusculus* and *P. bicrispatus*, were grouped in *Parabderites*, but their sister-group relationship, recovered in analyses I and III, was poorly supported (one synapomophy 9<sup>1</sup>). Three species were clustered in *Pitheculithes*, *P. minimus*, *P. rothi*, and *P. chenche*, but the relationships between them remain unresolved, thus forming a trichotomy. Terminal polytomies can be interpreted as a result of lack of resolution or as a statement about multiple speciation (Maddison, 1989; Wilkinson, 1994); if the first interpretation is assumed to be more likely, then this result is consistent with the previous hypotheses of the closest relationships between *P. minimus* and *P. chenche* (Dumont & Bown, 1997; Ortiz Jaureguizar, 2003), or alternatively, the derived condition of *P. rothi* with respect to *P. minimus* (Marshall, 1990) if *P. rothi* and *P. chenche* constitute sister-taxa.

The *Abderites* clade, formed by *A. meridionalis*, *A. crispus*, and *A. aisenense*, was fully resolved and was relatively well supported in terms of GC values (GC = 46). The taxonomic composition of this clade differs from that of Marshall (1976, 1980) and Ortiz Jaureguizar (2003) in the exclusion of *A. pristinus*, and the inclusion of the recently described species *A. aisenense* (for a taxonomic review of *Abderites* see Abello & Rubilar-Rogers, 2012).

*Palaeothentidae*: The Palaeothentidae, as recognized here, constitute a clade supported by one unambiguous synapomorphy (26<sup>2</sup>, anterolabial-posterolingually oblique postparacristida; Fig. 3H, I), and well supported by absolute frequency and GC values (58/54). Three additional characters (23<sup>1</sup>, 65<sup>1</sup>, and 73<sup>1</sup>) are palaeothentid synapomorphies under ACCTRAN. Comparing with the remaining traditional paucituberculatan groupings (e.g. Pichipilidae and Abderitidae), Palaeothentidae was the clade that presented the greatest differences in taxonomic composition and ingroup relationships with respect to previous phylogenetic hypotheses (Marshall, 1980; Marshall *et al.*, 1990; Bown & Fleagle, 1993). As mentioned above, *P. lucina* and *P. boliviensis* are not Palaeothentes species, nor even palaeothentids, as was previously suggested (Marshall, 1980; Bown & Fleagle, 1993), but are part of the *Pilchenia* clade. In the most recent revision of the Palaeothentidae, Bown & Fleagle (1993) recognized three main palaeothentid clades: *Hondathentes cazador*, Palaeothentinae, and Acestorinae. As in the phylogenetic hypothesis of Bown & Fleagle (1993), Palaeothentinae and Acestorinae were recovered as two of the three major palaeothentid lineages. The position of *H. cazador* could not be evaluated because this species was not included in the phylogenetic analysis (see Taxon sampling). However, by contrasting the characters that could be distinguished in the figures reported by Bown & Fleagle (1993), and the diagnostic characters of the palaeothentines that emerge from this study (15<sup>0</sup> and 31<sup>0</sup>, see Appendix S1), *H. cazador* is most likely a member of Palaeothentinae.

In accordance with the results of Bown & Fleagle (1993), Palaeothentinae and Acestorinae were recovered as sister-groups. On the other hand, and in contrast to the inferences of these authors, *Carlothentes chubutensis* was not nested within the Palaeothentinae but was resolved as sister to the Palaeothentinae + Acestorinae clade.

*Palaeothentinae*: In the present phylogeny most of the previously recognized palaeothentines (*sensu* Bown & Fleagle, 1993) were recovered as a monophyletic group. Within the Palaeothentinae, as here recognized, *P. primus* was resolved as the sister-group of

the rest of *Palaeothentes* species. Phylogenetic relationships among most *Palaeothentes* species remain unresolved, forming a large polytomy that includes *P. minutus*, *P. marshalli*, *P. migueli*, *P. intermedius*, *P. lemoinei*, and *P. aratae*. Even though *Palaeothentes pascuali*, a taxonomic equivalent to *P. intermedius* and *P. migueli*, was not included in analysis III, it may be considered part of the *Palaeothentes* clade (see Fig. 2B, C).

Even though *Palaeothentes* species, being represented by mostly complete upper and lower dentition, are well known in the context of this analysis, phylogenetic resolution within *Palaeothentes* could not be reached; it is probable that other data sets that are currently unknown, such as cranial and postcranial characters, will be necessary to further enhance the resolution of their interrelationships and to gain insight about the evolution of *Palaeothentes*.

Marshall (1980) considered that *Palaeothentes* and *Acdestis* were the only two main Palaeothentidae clades, and *Palaeothentes* as the most generalized of both taxa. According to current knowledge of palaeothentid systematics, the concept of *Palaeothentes sensu* Marshall (1980) actually includes diverse palaeothentid species, and more basal taxa, such as *P. boliviensis* and *P. lucina*. Among the systematic implications of the *Palaeothentes* (= Palaeothentinae of this work) phylogenetic tree of Marshall (1980, fig. 35) are the basal phylogenetic position of *P. minutus* and the closest relationships of the following species pairs: *P. lucina*–*P. lemoinei*, *P. boliviensis*–*P. chubutensis* (= *C. chubutensis* of Bown & Fleagle, 1993), and *P. primus*–*P. intermedius*. None of these statements was supported in this study. As was discussed above, neither *P. lucina* nor *P. boliviensis* are palaeothentids closely related to *Palaeothentes* or *Carlothentes*. *Palaeothentes primus* and *P. intermedius* are not a lineage; instead, *P. intermedius* is a member of the *Palaeothentes* polytomy and *P. primus* is sister to this polytomy. Finally, in the context of the Palaeothentinae, *P. minutus* is not a basal taxon, but a more derived species, nested within *Palaeothentes*.

In the phylogeny presented by Bown & Fleagle (1993, fig. 42) the Palaeothentinae encompass four main clades: *Propalaeothentes* (= *Palaeothentes*, see Taxon sampling), *C. chubutensis*, *P. lucina*, and *Palaeothentes*. However, results of the present study contradict these proposals because *C. chubutensis* is a palaeothentid basal to the Palaeothentinae, and *P. lucina* is a yet more basal taxon (see above).

In the phylogeny of Bown & Fleagle (1993) the synapomorphy that supported the Palaeothentinae monophyly was the ‘vespiform constriction’ at the cristid obliqua and entoconid notch on m2–3. This molar morphology was considered here otherwise, as the combination of two different characters: entocris-

tid shape (character 37) and cristid obliqua orientation (character 42). In this view, ‘vespiform’ molars are those with labially concave entocristid and cristid oblique anterior end lingually oriented (Fig. 3H; character states 37<sup>1</sup> and 42<sup>0</sup>, respectively; see additional discussion in Appendix S1). Since 37<sup>1</sup> and 42<sup>0</sup> were both derived character states shared by *Palaeothentes* species, then ‘vespiform’ molars can be considered diagnostic for *Palaeothentes*, and not for the Palaeothentinae as suggested by Bown & Fleagle (1993). The cladistics of *Palaeothentes sensu* Bown & Fleagle (1993, fig. 35) can be expressed in the following hypotheses of phylogenetic relationships: (a) *P. boliviensis* (*P. primus* + *P. aratae*); (b) *P. intermedius* (*P. marshalli* + *P. migueli*); (c) *P. lemoinei* (*P. minutus* + *P. pascuali*); (d) b and c clades are monophyletic. In relation to the present results, except for the first hypothesis (see the earlier discussion of phylogenetic position of *C. boliviensis*), the remaining are consistent with the phylogeny obtained here because b, c, and d are all possible resolutions of the *Palaeothentes* polytomy.

*Acdestinae*: In all analyses, acdestines emerge as a well-supported clade (90/54 absolute and GC frequencies). In analysis III the Acdestinae clade, including *Titanothentes* sp., *T. simpsoni*, *A. lemairei*, *A. owenii*, and *T. rothi*, was supported by six unambiguous synapomorphies and high absolute frequency and GC values. *Acdestodon bonapartei* and *A. maddeni* were taxonomic equivalents that, following the deleting rules and node of origin of equivalent pruned taxa proposed by Wilkinson (1995), should be also considered as members of Acdestinae (see also Fig. 7B). Of the acdestinae synapomorphies proposed here, reduced p3 (5<sup>1</sup>), absence of p3 anterobasal cusp (7<sup>0</sup>), metaconid of m1 very posterior with respect to the protoconid, and widely separated para- and metaconid (13<sup>4</sup>) were previously suggested by Bown & Fleagle (1993).

Marshall (1980) recognized only two Acdestinae species, *Acdestis owenii* and *Acdestis praecursor* (= *Acdestoides praecursor* of Bown & Fleagle, 1993), and Bown & Fleagle (1993) added three new species: *Acdestis lemairei*, *Acdestodon bonapartei*, and *T. rothi*. In the present analysis, the taxonomic content of the Acdestinae *sensu* Bown & Fleagle (1993) was corroborated, but excluding *A. praecursor*. Besides the mentioned acdestines, three further species were grouped here: *A. maddeni*, *T. simpsoni*, and *Titanothentes* sp. The memberships of *A. maddeni* and *Titanothentes* sp. in the Acdestinae were suggested in their original descriptions (Goin *et al.*, 2003; Kramarz *et al.*, 2010), but this is not the case for *T. simpsoni*, which was originally considered as a palaeothentine closely related to *P. aratae* and

*P. primus* (Rae *et al.*, 1996: 7). However, the increased knowledge of the dentition of *T. simpsoni* (Abello, 2007), and the scoring of previously undescribed dental characters, allowed us to test its phylogenetic position using a wider set of characters. As a result, *T. simpsoni* was nested within Acdestinae with high support. *Titanothentes* sp. was assigned to *Titanothentes* (Kramarz *et al.*, 2010), but no synapomorphies were found that provide support for this grouping.

Regarding Acdestinae ingroup relationships, and in agreement with the phylogeny inferred by Bown & Fleagle (1993), *A. lemairei* and *A. owenii* formed a terminal clade. On the other hand, and in contrast to the results of Bown & Fleagle (1993), *T. rothi* was positioned as sister to the *Acdestis* clade, and not as sister to all other acdestines.

## CONCLUSIONS

### DENTAL HOMOLOGIES AND PHYLOGENETIC ANALYSIS

Based on morphological grounds, the two most anterior lower incisors of paucituberculatans are considered to be homologous to i2–3. In species with complete lower antemolar series (i.e. eight teeth), the homologies proposed are: i2, i3, i4, i5, c, p1, p2, and p3. However, given our present knowledge, the homologies of the antemolar series between i3 and p3 are still uncertain for most paucituberculatans. In cases of number reduction, as in the antemolars of palaeothentids and abderitids, it is not possible to establish which is/are the lost tooth/teeth; thus, characters corresponding to ‘i4’ to ‘p2’ teeth, as well as dental formulas, should not be used in systematic studies. Taxon sampling and reinterpretations of molar cusp and crest homologies have played an important role in this analysis in the generation of new phylogenetic hypotheses, particularly among palaeothentids. Examples of these are the exclusions of *Palaeothentes boliviensis* and *Pilchenia lucina* from the Palaeothentidae, and the resulting *Pilchenia* clade.

This phylogenetic analysis provides a comprehensive update of the phylogenetic relationships among paucituberculatan species. The Caenolestidae and Pichipilidae, including two and three new unnamed species, respectively, are more diverse than previously recognized, and the cladistics of species referred to Palaeothentidae differs from previous proposals (Marshall, 1980; Bown & Fleagle, 1993). The most notable differences refer to the closest phylogenetic relationships of *P. lucina* and *P. boliviensis*; as noted above, both these species, as well as the recently described *Pilchenia antiqua* and *Pilchenia intermedia* (Goin *et al.*, 2010), are not members of Palaeo-

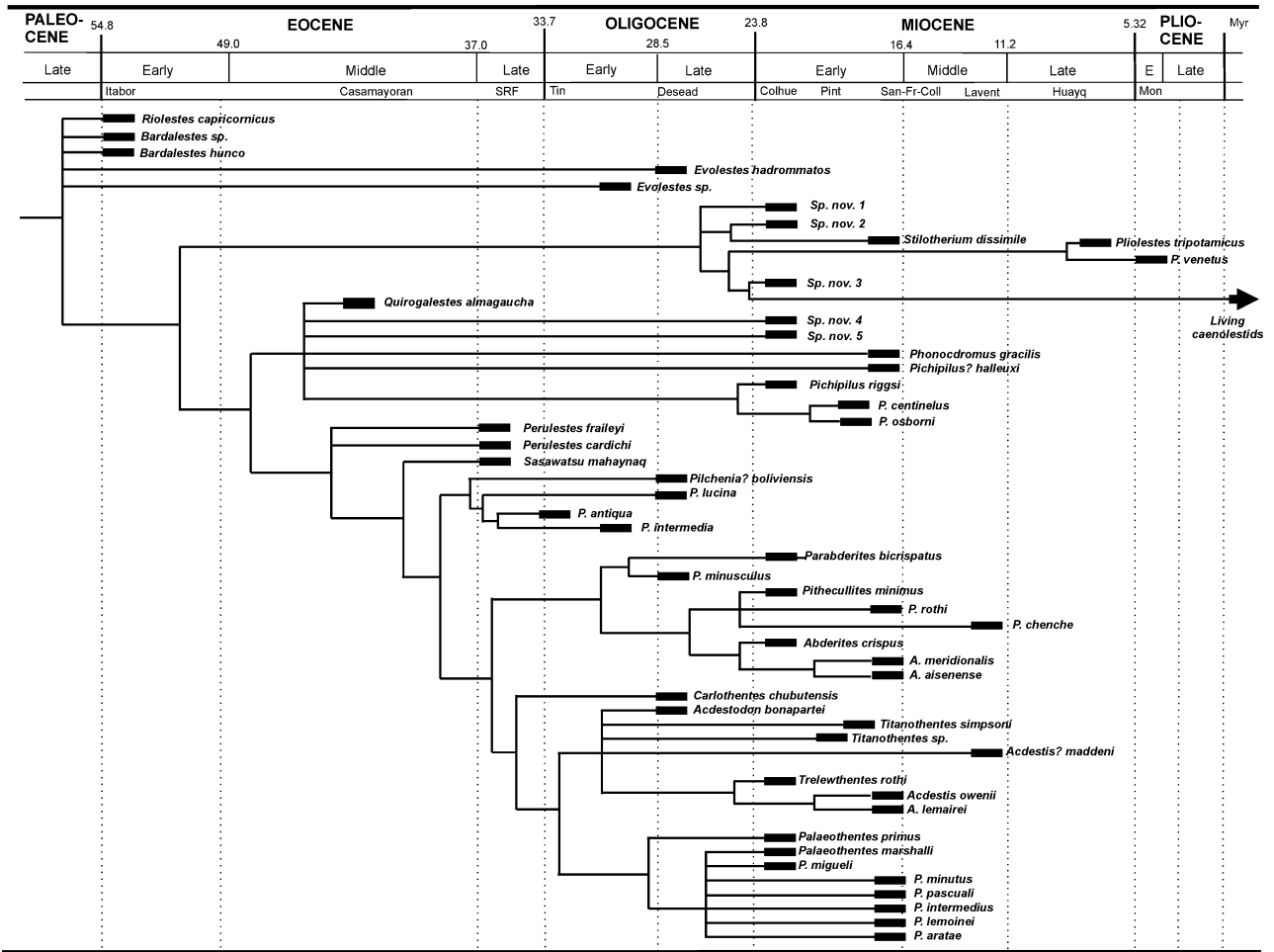
thentinae, but form a clade that is sister to Palaeothentidae + Abderitidae. The Acdestinae currently includes two new species, *Titanothentes* sp. and *Titanothentes simpsoni*; the latter was previously considered a member of Palaeothentinae (Rae *et al.*, 1996).

The resultant consensus tree shows several poorly resolved clades, as part of the ambiguity due to missing data. However, the exclusion of species that are unstable due to missing entries revealed the closest relationships between certain others; the elimination of *Pichipilus? halleuxi* revealed the monophyly of *Pichipilus* species and the removal of *Acdestis maddeni* and *Acdestodon bonapartei* revealed the sister-group relationships between *Trelewthentes rothi* and the *Acdestis lemairei* + *A. owenii* clade.

The inclusion of poorly known taxa in phylogenetic analyses has been considered problematic, leading to poorly resolved consensus trees; therefore, some authors have proposed the deletion of incomplete taxa because of their supposed lack of informativeness (for a review see Wiens, 2003). However, this study showed that some highly incomplete species may yet have informative characters that are able to resolve their phylogenetic relationships unambiguously. This is the case of *Pichipilus osborni* with 67% of missing entries but a highly supported sister-group relationship with *Pichipilus centinelus*. In contrast, species such as *P. minutus*, *P. lemoinei*, and *P. aratae*, highly complete in the context of the present data set (7% of missing entries), have poorly resolved relationships, due to character incongruence rather than to missing data. The absence of resolution could be resolved in the future by including other sets of characters, such as cranial or postcranial features, which are unfortunately yet unknown.

### DIVERSITY AND EVOLUTION OF PAUCITUBERCULATA

The Caenolestidae, Palaeothentidae, and Abderitidae were the three main groups traditionally recognized among paucituberculatans. In the model of paucituberculatan evolution proposed by Simpson (1944) and Pascual & Herrera (1973), these groups were considered as successive evolutionary grades, from the caenolestids to the abderitids, each more specialized than the preceding one. Marshall (1976, 1980) also considered the Caenolestidae to be the most primitive group and the origin of the more specialized palaeothentids and abderitids. On the contrary, as a result of this study more clades were recognized and, corroborating the hypotheses of Goin *et al.* (2007) and Goin *et al.* (2009), the most primitive paucituberculatans are currently not the Caenolestidae, but *Riolestes capricornicus*, *Bardalestes hunco*, *Bardalestes* sp., *Evolestes* sp., and *Evolestes hadrommatos*.



**Figure 8.** Time-calibrated phylogeny of Paucituberculata based on relationships recovered in the strict consensus tree of 298 most parsimonious trees produced by the analysis of the reduced matrix under implied weights (taxonomic equivalents are included, see Clade Discussion). Heavy lines = known temporal ranges; thin lines = missing ranges. Geochronological units, mammal ages, and faunas based on Gelfo *et al.* (2009), Madden *et al.* (1997), and Madden *et al.* (2010). Itabor, Itaboraian; SRF, Santa Rosa Fauna; Tinguir, Tinguirirican; Desead, Deseadan; Colhue, Colhuehupian; Pint, Pinturan Fauna; Sant–Fr–Coll, Santacrucian, Friasian, and Colloncuran; Lavent, Laventan; Huay, Huayquerian; Mon, Monterrosean.

The upper molar morphology of *Bardalestes hunco* and *Evolestes hadrommatos*, with well-developed para- and metacone, StB and StC+D distant to para- and metacone, StB larger than StC+D, and poorly developed (not hypocone-like) metaconule could be seen as representing the plesiomorphic upper molar pattern of Paucituberculata (Fig. 2A).

From the records of the oldest paucituberculatans (Fig. 8), *Bardalestes* and *Riolestes*, the origin of the group could be traced back at least to the early Eocene. The oldest paucituberculatans occur jointly with several metatherian lineages such as microbiotheriids, sparassodonts, polydolopimorphians, and ‘didelphimorphs’ (Oliveira & Goin, 2006; Goin *et al.*, 2009) in fossil assemblages of the early Eocene (Itabo-

raian age, Gelfo *et al.*, 2009) that reflect the already well-diversified South American metatherians. The differentiation of the main paucituberculatan clades, Caenolestoidea and Palaeothentoidea, during the late early to middle Eocene, was the first prominent cladogenetic event in paucituberculatan evolution. A substantial ghost lineage is apparent at the base of Caenolestoidea, as the oldest members of the group are early Miocene in age. This missing lineage reveals a great gap of knowledge regarding the early history of the caenolestids. Taking into account that caenolestids have not been recovered from the rich and well-sampled fossiliferous levels of Eocene and Oligocene age of Patagonia (Tejedor *et al.*, 2009; Goin *et al.*, 2010) or Peru (Goin & Candela, 2004), it is

possible that the earliest stages of caenolestid evolution may have occurred in areas with yet under-sampled Paleogene levels. A new species from the early Miocene of Patagonia (Colhuehuapian age, Argentina) represents the closest extinct relative of modern caenolestids; thus, a long ghost lineage, approximately 20 Mya, is needed to link extant to extinct caenolestids.

Palaeothentoidea, which groups most of the currently known paucituberculatans, has an ancient phylogenetic split, probably middle Eocene in age, between Pichipilidae and its large sister group that clusters *Perulestes*, *Sasawatsu*, *Pilchenia*, abderitids, and palaeothentids. Relationships among pichipilids remain poorly resolved except for the monophyly of *Pichipilus* species. Despite the fact that Pichipilidae date back to the middle Eocene, the group becomes only well documented in the early Miocene (Colhuehuapian age), having reached its highest taxonomic diversity by this time.

A radiation occurred within the sister group of Pichipilidae near the Eocene–Oligocene boundary (EOB), with many lineages of abderitids and palaeothentids emerging at that time. In contrast, from the middle Miocene paucituberculatan diversity declines abruptly and most of the groups that had flourished during the early Neogene (Pichipilidae, Palaeothentidae, and Abderitidae) become extinct. As far as is known, the middle Miocene (Laventan age, Madden *et al.*, 1997) is when the last records of Abderitidae (*Pitheculites chenche*) and Palaeothentidae (*Hondathentes* and *Acestis maddenii*) occur (Dumont & Bown, 1997; Goin *et al.*, 2003). During the late Miocene to early Pliocene, only the Caenolestidae persist with a single genus, *Pliolestes*, and the lineage leading to modern caenolestids.

Paucituberculatan evolution has probably been shaped by the palaeoclimatic events that occurred during the Cenozoic of South America, which strongly affected the southern areas of the continent (Ortiz Jaureguizar & Cladera, 2006). The global cooling that took place at the EOB, probably as a consequence of the onset of Antarctic glaciation (Pearson & Palmer, 2000; Pagani *et al.*, 2005), has been recognized as the major climatic–environmental change affecting the evolution of South American metatherian fauna (Goin *et al.*, 2010). For the paucituberculatans, these extrinsic factors could set the stage for the mentioned radiation of palaeothentids and abderitids, as the climatic changes could have generated ecological opportunities promoting lineage diversification. On the other hand, the uplift of the Andes in southern South America progressively formed a major barrier to moisture-laden South Pacific winds, leading to the development of drier habitats from the west eastward, and from the south northward (Pascual, Ortiz

Jaureguizar & Prado, 1996). These changes and the global temperature drop were accentuated from the middle Miocene (Ortiz Jaureguizar & Cladera, 2006), appearing to be associated with the decreased diversity and extinction of palaeothentoids. By contrast, caenolestids were differently affected, as the cladogenetic events leading to modern caenolestid genera appear to be causally linked to the emergence of high-altitude arid environments in the Central Andes (Abello, Posadas & Ortiz Jaureguizar, 2010).

As yet, few studies about the palaeobiology of paucituberculatans have been approached taking into account phylogenetic information (Abello & Ortiz Jaureguizar, 2009; Abello *et al.*, 2010). The results of this study provide a global and updated phylogeny, which will allow the testing of previous palaeobiological hypothesis and performing comparative analyses of this group, thus placing the observed patterns (morphological, ecological, or biogeographical) in a historical context. In this way, future research will allow greater insight into the historical course of paucituberculatan evolution.

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**Appendix S1.** The appendix includes: a list of characters used in the phylogenetic analyses, the complete character-taxon matrix, the results of the STR application method (equivalent taxa and taxonomic equivalence), and a list of specimens referred to new species 1 to 5.