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ORIGINAL PAPER

Taxonomy, affinities, and paleobiology of the tiny metatherian mammal *Minusculodelphis*, from the early Eocene of South America

Édison Vicente Oliveira[1,2] · **Natalia Zimicz**[3,4] · **Francisco J. Goin**[4,5]

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Abstract With less than 3 g of estimated body mass, the early Eocene *Minusculodelphis minimus* Paula Couto (Mammalia, Metatheria, Jaskhadelphyidae) is one of the smallest mammals, living or extinct. It has alternatively been regarded as a didelphid or a derorhynchid "ameridelphian," or even as an eometatherian marsupial. Here, we describe a new species of *Minusculodelphis* coming from the same locality (Itaboraí Quarry, Brazil) and age (Itaboraian age) of the type species of the genus. It differs from *M. minimus* in its larger size and several dental characters. The new species offers data on the upper dentition and femur, which are unknown in the type species. Compared to other Paleogene metatherians, *Minusculodelphis* shows closer relationships with *Jaskhadelphys*, from the early Paleocene of Tiupampa, Bolivia, as well as with *Kiruwamaq*, from the late Eocene-early Oligocene of Perú. A cladistic analysis places all three genera within the family Jaskhadelphyidae (Metatheria, Order indet.), which includes small to tiny, insectivorous-like metatherians. We argue that insectivory (soft insects) is the best-supported diet for both species of *Minusculodelphis*, and that the most probable microhabitat for them was the understorey or leaf litter of tropical, rain forested environments.

Keywords Metatheria · Systematics · Jaskhadelphyidae · Paleogene · Itaboraí · Brazil

Abbreviations

DNPM	Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil
MCT (ex DGM)	Museu de Ciências da Terra, Rio de Janeiro, Brazil
MCN-PV	Setor de Paleontologia, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, RS, Brazil
MN	Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil
SALMA	South American Land Mammal Age
p1, p2, p3	Lower premolars
M1/m1	M2/m2, M3/m3, M4/m4, upper and lower molars
St	StA, StB, StC, StD, stylar cusps A, B, C, and D, respectively
Ac	Anterior cingulum
Me	Metacone
Mec	Metaconule
Pa	Paracone

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✉ Édison Vicente Oliveira
vicenteedi@gmail.com

[1] Departamento de Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, UFPE, Av. Acadêmico Hélio Ramos s/n, CEP 50740-530 Recife, PE, Brazil

[2] CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico), Brasilia, Brazil

[3] IBIGEO (Instituto de Bio y Geociencias del Noroeste), Facultad de Ciencias Naturales, Universidad Nacional de Salta, 9 de Julio 14, Rosario de Lerma 4405, Salta, Argentina

[4] División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina

[5] CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Buenos Aires, Argentina

pome	Postmetacrista
Pr	Protocone
prepc	Preprotocrista
prpa	Preparacrista
co	Cristid obliqua
ec	Entocristid
en	Entoconid
hld	Hypoconulid
hyp	Hypoconid
me	Metaconid
pa	Paraconid
pc	Postcingulid
pohc	Posthypocristid
popc	Postprotocristid
pr	Protoconid
prec	Precingulid

Introduction

The diversity of metatherians from the early Eocene Itaboraí fauna of southeastern Brazil ranges from *Didelphis*-sized taxa, as the protodidelphids, to very small-sized forms, as is the case of *Minusculodelphis minimus* Paula Couto, 1962. In his original description of this species, as well as in a later study, Paula Couto (1962) assigned *Minusculodelphis* to the Didelphidae (Order Didelphimorphia). Later, Marshall (1987) compared it with *Derorhynchus* and included both genera also in the Didelphidae, subfamily Derorhynchinae. Later studies (de Muizon 1992; de Muizon and Brito 1993; Oliveira ÉV 1998) suggested the affinities between *Minusculodelphis* and *Jaskhadelphys* from the early Paleocene of Tiupampa, Bolivia. More recently, Ladevèze and de Muizon (2010) suggested a sister-group relationship of *Minusculodelphis* and *Monodelphopsis* plus dasyurids, as representatives of the Australasian Eometatheria. Besides the Itaboraí fauna, the genus *Minusculodelphis* has also been recorded in the Itaboraian-aged locality of Las Flores, in central Patagonia, Argentina (Bond et al. 1995; Goin et al. 1997; Woodburne et al. 2014).

Here, we describe a new species of *Minusculodelphis* and discuss its affinities, dental morphology, and paleobiological features; among the latter, aspects of its inferred diet and body size are considered. This study is mainly based on fossil collections housed in DNPM and includes two dentaries and a minute femur, which are here described and assigned to *Minusculodelphis*. All these materials were recovered from fissure fillings in the travertine limestones of the Itaboraí Basin, located at São José district, Itaboraí, State of Rio de Janeiro, Brazil (Fig. 1). The Itaboraí fauna was basal for the recognition of the Itaboraian SALMA, first thought to be early to mid Paleocene in age, until a recent dating suggested as more probable at an early Eocene age (53–50 Ma; Woodburne et al. 2014).

Fig. 1 Location map showing the region of the Itaboraí Basin (SE Brazil)

Material and methods

For molar cusps and cristae nomenclature and terminology, see Fig. 3e. In dental measurements, *L* is length and *W* is width. All measurements are in millimeters. In the estimation of the body mass of *Minusculodelphis*, we used the database of Gordon (2003) to construct several regression equations. This database contains molar measurements of 21 species of living didelphids and dasyurids. The regressions have the form $\ln Y = a + b(\ln X)$, where Y is the natural logarithm of body mass; a is the intercept; b is the slope, and X is the natural logarithm of the molar measurement (length or area). Because the specimens of *Minuculodelphis* are minute, we incorporated to the database four of the smallest placental mammals in the world (i.e., *Suncus etruscus* (2 g), *Sorex hoyi* (3 g), *Sorex minutus* (2.5 g), and *Crocidura leucodon* (10.8 g)) and the smallest living marsupial (*Planigale ingrami* (4.2 g)). In this way, we avoid the possibility that our fossil constitutes outliers in the regressions. Ten least square regressions (Sokal and Rohlf 1995) were generated to infer the body mass from each molar locus available in the fossil specimens (Table 1). The equations derived from M4/m4 measurements were excluded because they were weak predictors of body mass (Gordon 2003). To avoid the biases due to the re-

Table 1 Measurements of upper and lower molars of *Minusculodelphis*

	MN 2342-V M. minimus (holotype)	DGM 921a-M M. modicum sp. nov. (holotype)	DMG 921b-M M. modicum sp. nov.	MCN 1792 M. modicum sp.nov.	MCT 2815 M. modicum sp.nov.	MN 2479-V M. modicum sp.nov.
Lp1/Wp1	0.50/0.20	0.5/0.10				
Lp2/Wp2	0.60/0.20	0.5/0.20				
Lp3/Wp3 (MN 2503-V)	–	0.5/020				
Lm1/Wm1	0.7[a]/0.4[a]	0.94/0.60				
Lm2/Wm2	0.84/0.50	1.02/0.72				
Lm3/Wm3	0.88/0.55	1.08/0.70	1.04/0.66			
Lm4/Wm4	0.80/0.50	1.00/0.65				
Lm1–4	~3.22	4.04				
Lm2–m4	2.54	3.01				
LM2/WM2						1.37/1.79
LM3/WM3				1.10/1.70	1.10/1.70	1.40/1.7[a]

[a] From Marshall (1987)

transformation, we applied a correction factor (smearing estimate; Smith 1993) to the logarithmized result of body mass. We selected the best prediction based on the highest R^2 and lowest values of PE (prediction error) and SEE (standard error of the estimate) (Table 2).

The relief between trigonid and talonid and the relative crest length were measured on the m2. The former was calculated as the difference in height between the highest cusp of the trigonid and talonid. The second is the sum of the length of all the crests of the tooth divided by the m2 length.

For assigning femur to dental remains, a regression equation was generated from didelphids (see Electronic Supplementary Material; Appendix 1). The allometric equation resulting from the didelphid database is given in Table 3. The data was transformed into a linear equation, $\ln Y = b \ln x + \ln a$. Data were analyzed using the PAST program (version 2.0; Hammer et al. 2001). All data were transformed using the natural (base e) logarithm.

In order to test the phylogenetic affinities of *Minusculodelphis*, we performed a parsimony analysis based on the morphological data matrix of Oliveira and Goin (2011). An issue to be tested is the relationships between *Minusculodelphis* and the Tiupampaian *Jaskhadelphys* (de Muizon 1992; de Muizon and Brito 1993). Few changes of characters and scoring in the matrix of Oliveira and Goin (2011) were made according to the inclusion of *Kiruwamaq* and to the reanalyses of the remaining taxa analyzed. A revised list and coding of characters are in the Electronic Supplementary Material (Appendix 2). The phylogenetic analysis was carried out using the heuristic search algorithm of PAUP* 4.0b 10 (Swofford 2002) with an initial search of 2000 replications. The analysis included 31 taxa and 70 characters. Twenty-two

Table 2 Coefficients and statistic parameters of the regression equations used for the prediction of body mass in *Minusculodelphis*

	a	B	R^2	SE	%PE	%SEE	BM *M. minimus* (g)	BM *M. modicum* sp. nov. (g)
LM2	1.69	3.28	0.94	1.15	9.67	49.16		17.589
AM2	1.40	1.69	0.93	1.22	11.32	55.10		22.357
LM3	2.69	2.51	0.93	1.12	8.84	43.82		20.970
AM3	2.00	1.46	0.95	1.22	12.00	55.71		22.601
Lm1	1.45	3.68	0.91	1.05	4.83	31.05	1.205	3.565
Am1	2.43	1.81	0.88	1.06	5.08	32.30	1.210	4.284
Lm2	1.31	3.58	0.94	1.07	7.06	37.60	2.120	4.244
Am2	2.12	1.82	0.93	1.07	6.58	36.54	1.836	5.067
Lm3	1.86	3.09	0.93	1.14	9.47	47.47	4.912	8.721
Am3	2.47	1.63	0.94	0.99	9.35	47.55	3.598	28.850
						Average	2.48	13.82

a, intercept; *b*, slope; R^2, determination coefficient

SE smearing estimate, *PE* prediction error, *SEE* standard error of the estimation, *BM* corrected body mass

Table 3 Bivariate regression equation and prediction of femoral length in *Minusculodelphis minimus* and *M. modicum* sp. n

Anatomical dimensions	N	r	r^2	Equation ln	Predicted femur length	
					M. minimus	*M. modicum* sp. nov. DGM 921c-M
m2 area × femur L	28	0.9666	0.93431	ln femur L (y) = 0.64283 (ln x) + 2.6356	7.98	11.4

characters were regarded as ordered. Bremer support, consistency index, and retention index were calculated.

Results

Systematic paleontology

Class Mammalia Linnaeus, 1758

Infraclass Metatheria Huxley, 1880

Order indet.

Family Jaskhadelphyidae de Muizon 1992
Jaskhadelphyidae de Muizon 1992:578 [lapsus calami]

Type genus *Jaskhadelphys* Marshall and de Muizon 1988

Included genera The type genus, *Minusculodelphis* Paula Couto, 1962, and *Kiruwamaq* Goin and Candela 2004.

Distribution Early Paleocene (Tiupampaian SALMA) to latest Eocene-Early Oligocene (?Tinguiririan SALMA), South America.

Diagnosis Very small to tiny metatherians from the early Paleogene of South America. Upper molars with low, small, anteroposteriorly compressed protocones, slightly V-shaped centrocrista, small and centrally placed StC, large StA, and with the lingual face of metacone only slightly most lingually placed than that of paracone.

Minusculodelphis de Paula Couto 1962

Type species *Minusculodelphis minimus* Paula Couto, 1962.

Included species *M. minimus* and *M. modicum* sp. nov.

Distribution Early Eocene of South America.

Locality and age Itaboraí Basin and Formation, Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist et al. 2009); early Eocene, Itaboraian SALMA (ca 53–50 Ma; Woodburne et al. 2014).

Diagnosis Very small metatherians with elongated lower premolars bearing low cusps. Lower molars with reduced paraconid, which is clearly lower than the metaconid. Very short talonids relative to the trigonid, with poorly developed cusps, being the entoconid almost indistinguishable. The hypoconulid is minute and located at the posterolingual corner of tooth; the posthypocristid is transversal to the dental axis. Femur presents a robust third trochanter that is distally located in relation to the level of the lesser trochanter ends. Upper teeth differs from *Jaskhadelphys* in having deeper ectoflexus in M2-3, metacone much higher than paracone, less compressed and not posteriorly displaced protocone, and paraconule is absent. It differs from *Kiruwamaq* in its unreduced paracone, shorter postmetacrista, and narrower anterior cingulum.

Remarks Paula Couto (1962, p. 162, fig. 13) described the type and referred MN 2503-V to the hypodigm; later, he (de Paula Couto 1970) added the specimen MN 2901-V. Marshall (1987) reviewed the type of materials and stated that the holotype was damaged after the Paula Couto's studies, being lost a large portion of the m1.

Minusculodelphis modicum sp. nov.

Etymology From the Latin *modicus*, "moderate", in allusion to its larger size in relation to the type species.

Holotype DGM 921a-M, an incomplete right dentary with complete m1–4.

Hypodigm The holotype, MCT 2815-M, a complete right M3; MCN-PV 1792, a complete right M3; MN 2479-V, an incomplete right maxilla with complete M2 and incomplete M3; DGM 921b-M, an incomplete right dentary with roots of m1, m2, portion of m4, and with complete m3; DGM 921c-M, a complete left femur.

Locality and age São José de Itaboraí Basin and Formation, Itaboraí, State of Rio de Janeiro, Brazil (Bergqvist et al. 2009); early Eocene, Itaboraian SALMA (ca 53–50 Ma; Woodburne et al. 2014).

Diagnosis Differs from *Minusculodelphis minimus* in its larger size, m2 with a more anteroposteriorly compressed trigonid, less lingually placed paraconid, hypoconulid comparatively more developed, and hypoconid slightly less labially salient; m1-3 with more developed anterior and posterior cingulids; m3 with metaconid less lingually projected and with the talonid comparatively less developed transversely; m4 with the paraconid anteriorly compressed.

Description

Dentary and dentition The dentary is represented by two specimens (Fig. 2) lacking the coronoid process and the remaining portions of the posterior and anterior regions. The mandibular symphysis is not preserved. Total length for m1-4 is 4.04 mm (~3.22 mm in *M. minimus*; see Table 1). There is a relatively long retromolar space between the last molar and the anterior edge of the coronoid process. The greatest depth of ramus is below the anterior root of m4 and is nearly one to one-half the height of m3. The posterior mental foramen is large and is placed below the anterior edge of m2. Judging from the distal edge of its posterior alveolus, the p3 was not reduced. As seen in m2-4 (Fig. 2a–b), the trigonid is anteroposteriorly elongated and much higher than the talonid. The paraconid is not reduced and is slightly anterolabial to the metaconid. The metaconid is robust, distinctly more voluminous than the paraconid, and its distal edge is slightly distal to that of the protoconid (Fig. 2e, f). The talonid is shorter than the trigonid. The cristid obliqua contacts the trigonid labial to the postprotocristid notch. The hypoconulid is small and located on the posterolingual corner of the tooth. The entoconid is very reduced. The posthypocristid is gently curved and runs parallel to the transverse dental axis. The precingulid and the postcingulid are short and very narrow. The m2 is slightly larger than the m1 (Fig. 2e). Although very worn on the holotype, the paraconid is not reduced. The trigonid is much higher and wider than the talonid. The metaconid and the protoconid are transversely aligned. The hypoconid and the cristid obliqua are poorly developed. The m3 differs from the m2 only in its larger size (Figs. 2e–f and 3a, b). In DGM 921b-M, the protoconid is tall, and its labial wall is gently convex from the basis to the tip. The postprotocristid is shorter than the preprotocristid and runs slightly oblique to the transversal dental axis (Fig. 3a). The base of the entoconid is oval and very small in size. On m4, all the trigonid cusps are well-preserved (Fig. 2e). The metaconid and the protoconid are very tall in relation to the talonid cusps. The paraconid is smaller and very low relative to the metaconid. The talonid is narrower than on anterior molars with a very reduced basin. The hypoconulid is slightly more robust than in m1–3 and is more labially placed.

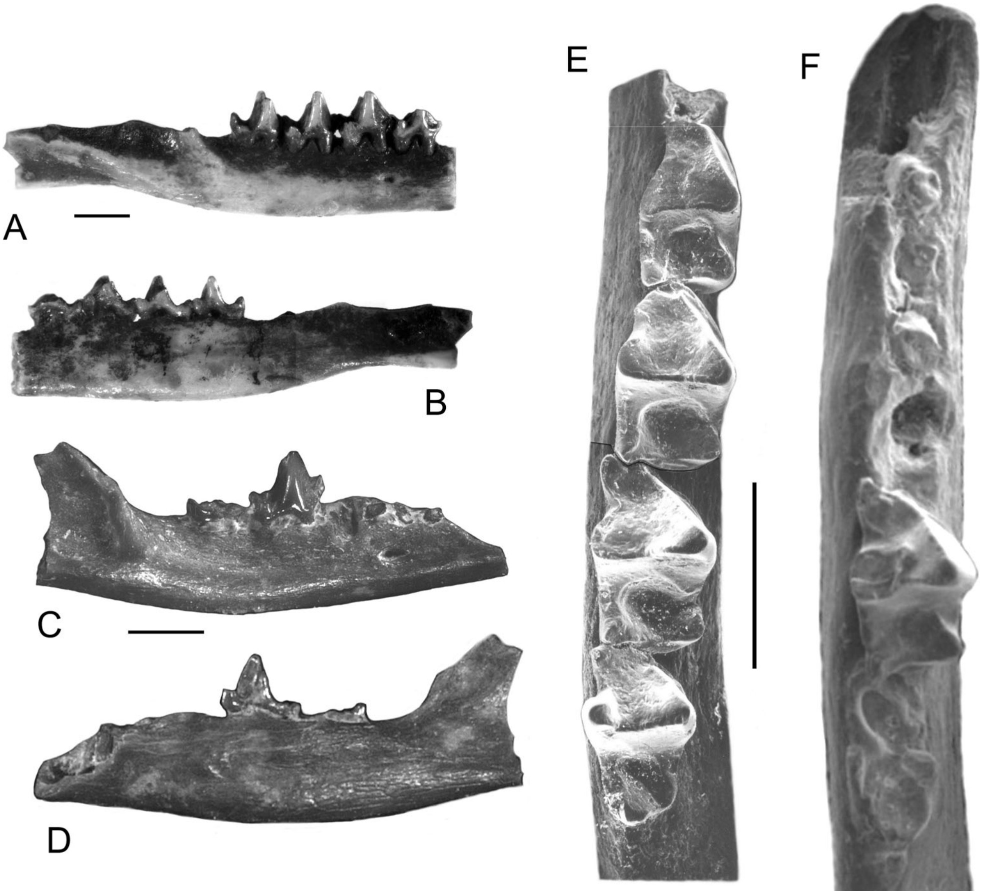

Fig. 2 Dentaries of *Minusculodelphis modicum* sp. nov. **a** DGM 921a-M (holotype) dentary in labial view. **b** BDGM 921a-M (holotype) dentary in lingual view. **c** DGM 921-Ma (holotype) m1–m4 in labial view. **d** DGM 921b-M dentary in lingual view. **e** DGM 921a-M dentary in occlusal view. **f** DGM 921b-M dentary in occlusal view. *Scale* indicates 1 mm

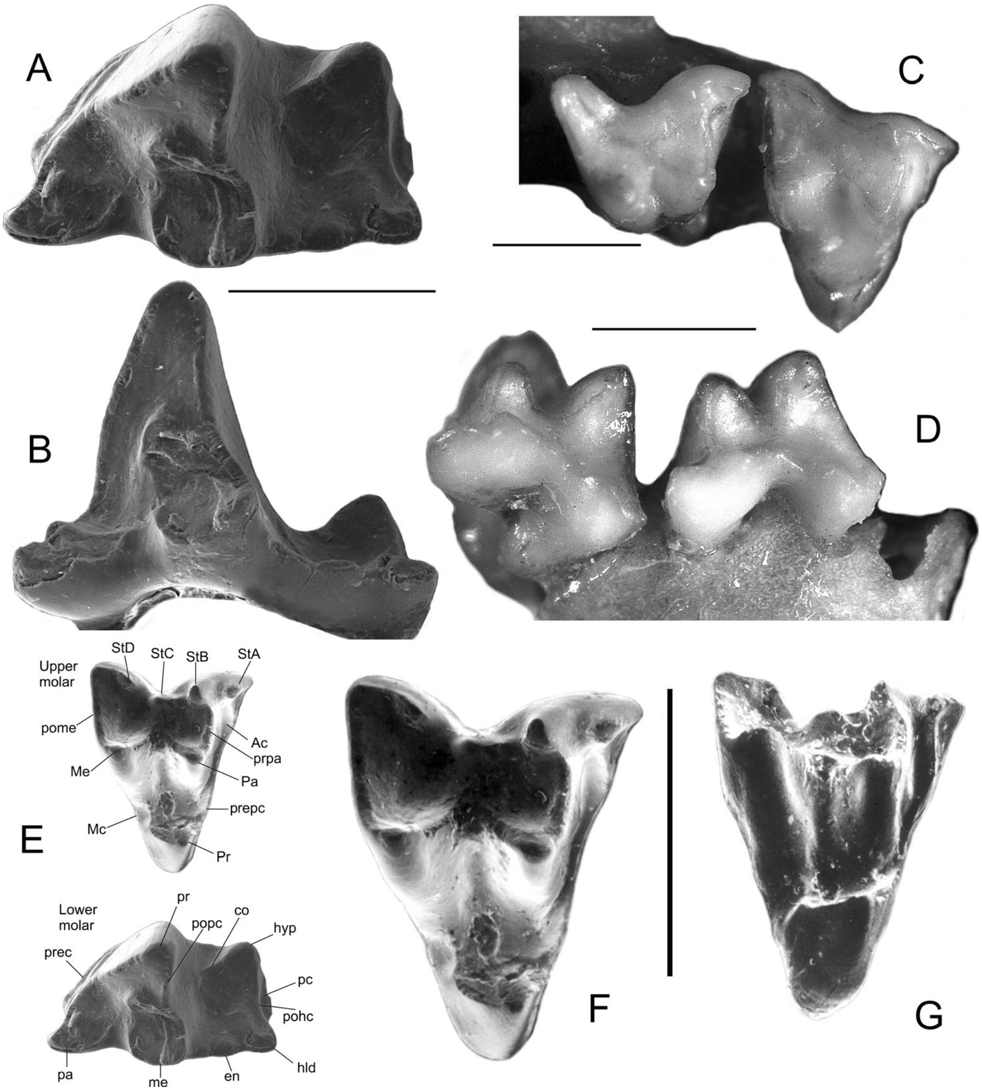

Fig. 3 Lower and upper molars of *Minusculodelphis modicum* sp. nov. (**a**) DGM 921b-M in occlusal view, (**b**) lingual view. *Scale* indicates 500 μm. (**c**) MN 2479-V M2–M3 in occlusal view, (**d**) MN 2479-V in labial view. *Scale* indicates 1 mm. (**e**) Upper and lower molar anatomical nomenclature, (**f**) MCT 2815-M, M3 in occlusal view, and (**g**) MCT 2815-M M3 in lingual-occlusal view. *Scale* indicates 1 mm

A partial right maxilla (MN 2479-V) bearing a complete M2 and the labial half of M3 (Fig. 3c, d) has been referred to *M. modicum*. The M2 is slightly longer than the M3. The ectoflexus of M2 is shallow and is restricted to the labial face of StC. The stylar shelf is wide, mainly in its posterior half. StB is the largest stylar cusp while StE is minute and located on the posterolabial corner of tooth. In comparison, StB > StD > StA > StC > StE. The anterior cingulum descends steeply from the crest between StB and StA and continues lingually below the paracone, meeting with the preprotocrista. The preparacrista is curved posteriorly along its labial portion and ends labially to the apex of StB. The metacone is higher and more voluminous than the paracone, but its lingual face is only slightly more lingual than that of the paracone. There are no traces of paraconule; the metaconule is poorly developed. The M3 of MN 2479-V (Fig. 3c, d) is lacking the protocone and conules, but an isolated complete M3 (MCT 2815-M) has also been referred to the new species (Fig. 3f, g). The M3 of *M. modicum* is characterized by a greater transversal development of the stylar shelf and by a smaller size of the protocone. The stylar shelf is wide anteriorly and posteriorly. The ectoflexus is deeper than in M2 and reaches its most lingual point just at StC. The StA is strong and anterolabially projected, so that the anterolingual corner of the tooth is very salient; StB is the largest and highest stylar cusp; both StB and StA are lingually bent; StC is subequal in size to StD and is connected to StB by a crest; StD is larger than StC and bladed. The preparacrista is slightly shorter than the postmetacrista and is subparallel to the postmetacrista. The metastylar corner of tooth is labially expanded, because of the almost transversal orientation of the postmetacrista. As in the M2, the centrocrista is slightly V-shaped and not labially invasive. The metacone is taller than the paracone; both cusps are anteroposteriorly compressed. The anterior cingulum is narrow and connected to the preprotocrista. The protocone is very compressed anteroposteriorly and is deflected anteriorly so that it is transversely aligned with the paracone and the StB. The metaconule is present, and the paraconule is absent.

Remarks This species is based on undescribed material from MCN and MCT, and in the MN 2479-V, previously referred to *Marmosopsis juradoi* (Marshall 1987).

Femur The femur is 8.90 mm in length, 1.85 mm wide at the proximal epiphyses, and ~1.42 mm at the distal epiphyses (Fig. 4a, d). It is ~30 % smaller when compared with a femur of *Gracilinanus agilis*, one of the smallest living Didelphidae. The specimen exhibits signals of abrasion in the epiphyses. The epiphyses are fused with the diaphysis. Adult (or subadult) characters of the specimen are the well-developed trochanteric fossa and lesser trochanter (see Szalay and Sargis 2001). The femur is relatively strong and presents a straight shaft. The femural neck is short and thick. Judging from the proximal end of the trochanteric fossa, the height of greater trochanter was probably not higher than the head, although abrasion in this area makes this assessment uncertain. The trochanteric fossa is delimited by a straight paratrochanteric crest that extends distally to the proximal area of the lesser trochanter. A well-developed nutrient foramen is observable in medial view. The lesser trochanter is large and resembles that of *Rhyncholestes* and *Dromiciops* (Abello and Candela 2010); it is placed well above the third trochanter. The third trochanter is robust (Fig. 4a, b) as in *Rhyncholestes* and *Herpetotherium* (Sánchez-Villagra et al. 2007), but it is distally located relative to the level of the lesser trochanter ends on the other side of the diaphysis. The sulcus above the distal epiphysis for the tendon of the quadriceps femoris is well-emphasized. Despite abrasion in distal view, the femorotibial articular condyles are nearly symmetrical (Fig. 4d).

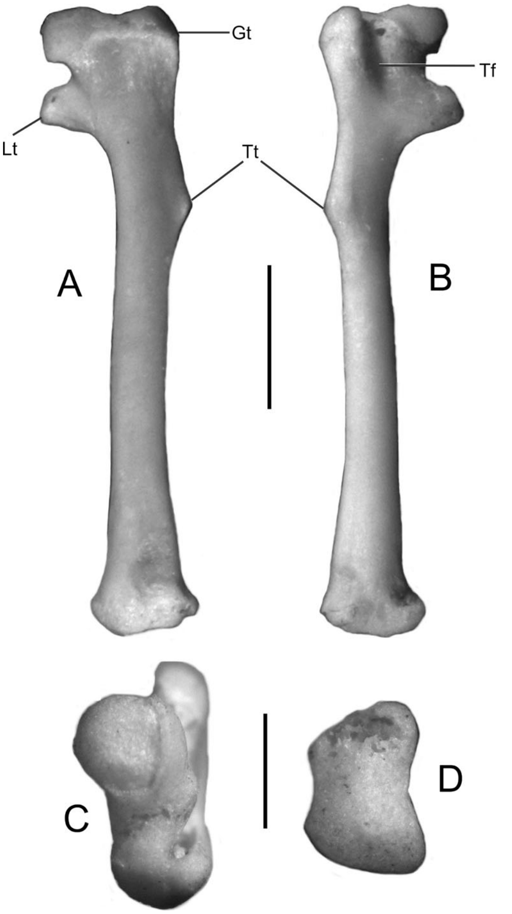

Fig. 4 Femur of *Minusculodelphis*, DGM 921c-M. **a** Anterior view. **b** Posterior view. **c** Proximal view. **d** Distal view. **a**, **b** *Scale* indicates 2 mm. **c**, **d** *Scale* indicates 1 mm. *Gt* great trochanter, *Lt* lesser trochanter, *Tf* trochanteric fossa, *Tt* third trochanter

Discussion

Phylogeny

The parsimony analysis resulted in four equally parsimonious trees of 277 steps, consistency index of 0.4332, and retention index of 0.6873. A strict consensus tree is given in Fig. 5. The Tiupampaian *Khasia* and the Itaboraian *Mirandatherium* were recovered as successive sister-taxa to the remaining taxa analyzed. Polydolopimorphians such as *Epidolops*, *Gashternia*, *Bobbschaefferia*, and *Roberthoffstetteria* plus the microbiothere *Microbiotherium* compose a groupment that is the sistergroup of a large clade including protodidelphids and didelphids plus several Tiupampaian and Itaboraian taxa. Inside this latter large clade is the recovered Jaskhadelphyidae, which is supported in the first two trees (topology A) by 12 synapomorphies (including two unambiguous) and in two trees (topology B) by three synapomorphies (with only one unambiguous synapomorphy). In the first topology, the two unambiguous synapomorphies include a very smaller protocone in relation to stylar shelf (28; 1) and a perpendicular posthypocristid to the dental axis (70; 1). The other ten additional synapomorphies include a very smaller StD relative to metacone (13/0; CI 0.33), centrocrista moderately developed (17/1; CI 0.4), moderately higher stylar shelf relative to trigon basin (19/1; CI 0.5), paracone placed set apart in relation to StB on M1-2 (23/0; CI 0.5), anteroposteriorly very narrow protocone (29/2; CI 0.5), eccentric protocone on M1 or M2 (30/1; CI 0.33), shallow trigon basin (31/1; CI 0.25), preparacrista proportionally longer than half of postmetacrista (35/0; CI 0.33), very reduced hypoconulid, posthypocristid extended farther lingually (64/1; CI 0.25), and minute sized (69/2; CI 0.33). In topology B, the unambiguous synapomorphy defining Jaskhadelphyidae includes character 70 (state 1) plus characters 64 and 69 as described above for topology A.

The molar morphology of *Minusculodelphis* is significantly distinct from that of the other South American Paleogene metatherians. Because the short lower molars of *Minusculodelphis* are concomitent with the same condition on the upper molars, the very short talonid of *Minusculodelphis* suggests a similar anteroposterior compression of the

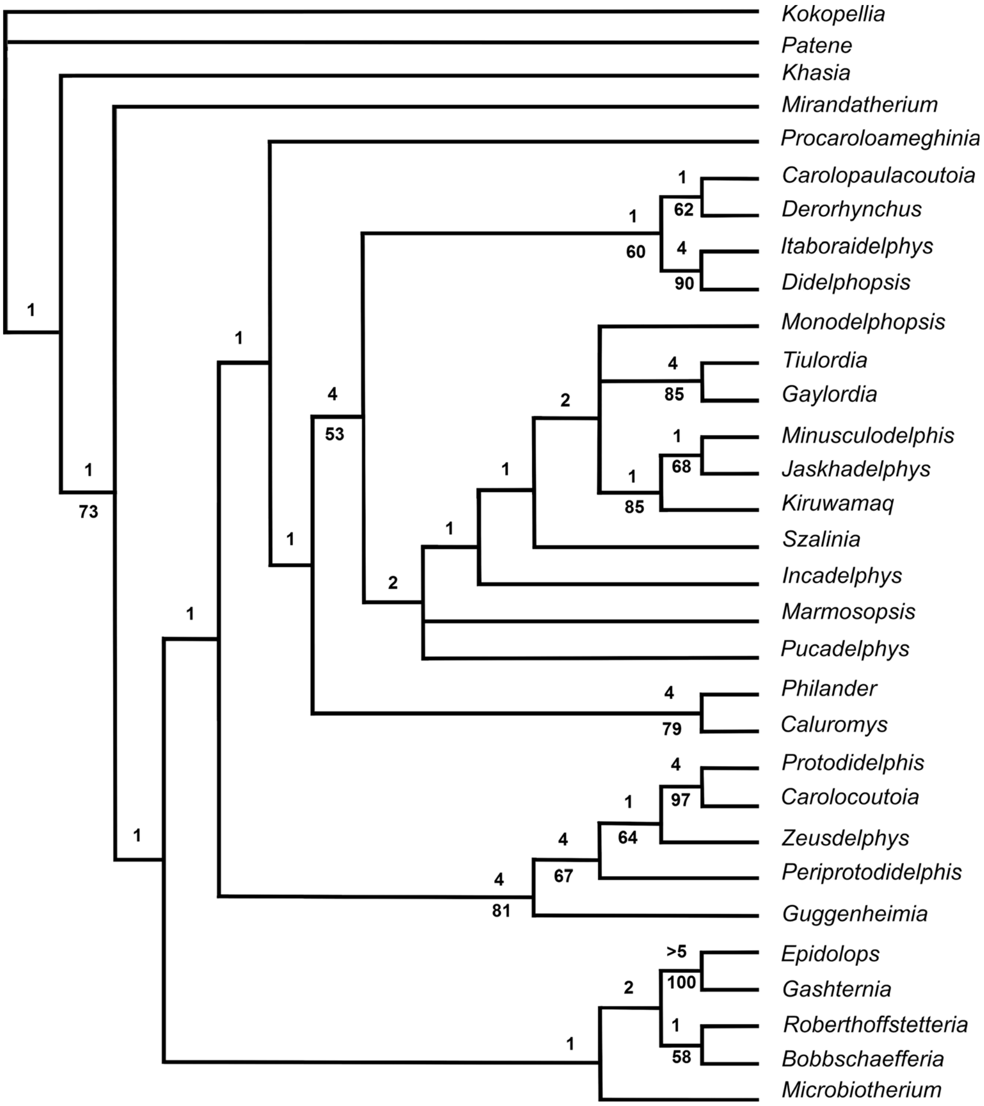

Fig. 5 Strict consensus cladogram of four most parsimonious trees (tree length = 277; consistency index excluding uninformative characters = 0.4291; retention index = 0.6873; rescaled consistency index = 0.2977). *Numbers to the upper left* correspond to Bremer supports, and *numbers to the lower left* represent bootstrap values (bootstrap values below 50 not shown)

protocone. Furthermore, the great difference in height between the trigonid and the talonid suggests an occlusion with a very low protocone in relation to stylar shelf. This condition is in part associated with the transverse orientation of the postmetacrista in relation to the tooth axis, as well as to the very deep ectoflexus. Therefore, the morphology of upper molars referred to *Minusculodelphis modicum* is consistent with that of the lower molars of this new species.

Minusculodelphis is of interest in its apparently plesiomorphic condition, relative to other South American "didelphimorphian" metatherians. Unlike most of the other Paleogene "didelphimorphians," *Minusculodelphis* exhibits (1) a deep ectoflexus in M2 and M3; (2) a stylar shelf, which is almost as wide anteriorly as posteriorly; (3) a large and anterolabially projected StA in M3; (4) a small StC, which is located apart from StD or StB, and (5) the lingual basis of the metacone, which is only slightly expanded lingually in relation to that of the paracone. Comparatively, all these characters are also observed in North American peradectids (see Rose 2010). However, in the lower dentition, *Minusculodelphis* is derived relative to most Paleogene metatherians: the distal faces of the metaconid and protoconid are aligned transversely, the talonid is shortened relative to trigonid, the entoconid is virtually absent, and the hypoconulid is located on the posterolingual corner of tooth.

Comparisons of *Minusculodelphis* with other metatherians show some similarities with *Derorhynchus singularis*. Specimen MN 2506-V consists in a maxillary fragment with M1-3 (see Goin et al. 2009); it exhibits a deep ectoflexus on M2-3, a slightly V-shaped centrocrista, and similarly sized metacone and paracone. However, the lower molars of *Minusculodelphis* differ from those of derorhynchids in having a less developed hypoconid and a small entoconid, which is well-developed and conical in *Derorhynchus*.

Minusculodelphis also shows some resemblances to the African herpetotheriid *Peratherium africanum*, in having deep ectoflexus in M2-3, transversely elongated molars, small StC, slightly V-shaped centrocrista, small protocone relative to stylar shelf, short talonid, hypoconulid located on the posterolingual corner of tooth, and relatively elongated premolars. *Peratherium africanum* has been regarded as a member of Herpetotheriidae, closely related to European taxa (Hooker et al. 2008).

The upper teeth of *Minusculodelphis* herein described show clear resemblances to those of *Jaskhadelphys* from the early Paleocene of Tiupampa, Bolivia (Marshall and de Muizon 1988, de Muizon 1992) and *Kiruwamaq* from the late Eocene-early Oligocene of Perú (Goin and Candela 2004; Ciancio et al. 2013). These resemblances include the following: anteroposteriorly compressed upper molars, small protocones, which are also anteroposteriorly compressed and low compared to the paracone-metacone, long preparacrista and postmetacrista, whereas the premetacrista and the postparacrista are noticeably shorter, and barely V-shaped centrocristae (actually, they look almost straight at first sight). However, important differences between the upper molars of *M. modicum* and *Jaskhadelphys minutus* (approximately equal in size) include the posteriorly displaced protocone in *Jaskhadelphys*, the deeper ectoflexus in *Minusculodelphis*, and the better developed paraconule than metaconule in *Jaskhadelphys*. In relation to *Kiruwamaq*, *Minusculodelphis* is more plesiomorphic in the presence of an unreduced paracone and in the smaller stylar shelf and postmetacrista.

Minusculodelphis has alternatively been regarded as a "didelphid" derorhynchine (Marshall et al. 1990), or an eometatherian (Ladevèze and de Muizon 2010). One of the most recent phylogenetic proposals refers *M. minimus* to the Type VIII petrosal, which places it as a stem metatherian whereas two synapomorphic dental characters (p2 and p3 subequal in size and oblique protocristid) suggest a sister-group relationship with *Monodelphopsis* plus the Australian dasyurids. For the reasons stated above, we refer *Minusculodelphis* to the Jaskhadelphyidae (see also Oliveira and Goin 2006) and consider that this family cannot be confidently assigned to the Didelphimorphia or to any other order of South American metatherians.

Paleobiology

Despite its tiny size, the new species *Minusculodephis modicum* is about 27 % larger than the type species. The best prediction for *M. minimus* resulted in a body mass estimation of 1.83 g using the area of m2, while the average of all estimations resulted in 2.48 g (Table 2). The best prediction for *M. modicum* was 5.06 g based on the area of m2 while the average of all estimations was 13.82 g (Table 2). *M. minimus* is the smallest known metatherian, living or extinct, with a size comparable to that of the living white-toothed pigmy shrew. A comparison with body mass values estimated for Cretaceous metatherians shows that *Minusculodelphis* occupied the lowermost range of body masses, as it happens with Paleogene insectivores (Bloch et al. 1998).

The small body masses inferred for the species of *Minusculodelphis* suggest a diet rich in highly caloric items such as nectar, exudates, or invertebrates (see McNab 2008) that allowed them to sustain the high metabolic rates imposed by its minute size. Among mammals, nectarivory is a feeding adaptation, which mostly occurs in bats, but also in some marsupials, such as the honey possum (*Tarsipes rostratus*: Bradshaw and Bradshaw 2002). Insectivory (invertebrates) is a dietary category shared by many mammalian lineages (see Eisenberg 1981) including marsupials. Several small dasyurids are insectivores (Hume 1999) as the long-tailed *Planigale* (*Planigale ingrami*), the smallest living marsupial. Despite its tiny size, *P. ingrami* is a ferocious nocturnal predator that preys on virtually all tiny items present in the substrate (centipedes, spiders, grasshoppers, other insects and their larvae) even small lizards and young mammals (Wilson and Mittermeier 2015).

The most reliable way to distinguish between a nectivore and an insectivore mammal is through the inspection of cranial morphology. Nectar feeders have longer skulls, dentaries, and lower coronoid processes than insect, fruit, or exudate feeders (Freeman 1995; Dumont 1997). The teeth diminish their role in food processing because the tongue is the functional element to gather the nectar (Freeman 1995); consequently, a strong reduction in the number of teeth characterizes the nectivore masticatory apparatus. In the honey possum, as in bats, the dentary is reduced to a thin, flexible rod, bearing a single elongated incisor and two to three tiny, peg-like postcanines, being the lower canine absent (Rosenberg and Richardson 1995). Upper dentition of *T. rostratus* is also reduced in teeth number and size, and the maxillary teeth are flattened with rounded tips (Rosenberg and Richardson 1995). Additional features that distinguish nectivores from insectivores are a proportionally longer distance between the condyle and the last lower molar, a reduced total tooth area with respect to palatal space, and reduced stylar shelves on the upper molars (Freeman 1995; Dumont 1997). Unfortunately, there are no complete cranial remains of *Minusculodelphis*, and the dentary is only partially preserved in specimens DGM 921a, b-M, thus obscuring the identification of key features. Although the slenderness of the dentary and a long retromolar space are features consistent with nectarivory, the lower dentition of *Minusculodelphis* is not reduced in tooth number and size in the degree of the honey possum. Lower molars of *Minusculodelpis* have sharp cusps and high relief (talonid/trigonid height difference) compared with the flattened, rounded molars of *T. rostratum* (Rosenberg and Richardson 1995). Insectivore dentition varies as a function of the hardness of insect exoskeleton that the animal consumes. Freeman (1981) determined that insectivores preying on soft insects have longer crests and higher reliefs compared with those preying on hard invertebrates (Freeman 1981: Table 8). We calculate the relief and crest length on the m2 of *M. minimus* and compared the result with table values on Zimicz (2012). *M. minimus* has a relief of 0.411 and a relative crest length of 1.84; both values fall within the spectrum of soft insect eaters. Based on this and in the absence of additional elements, we postulate that insectivory on soft insects is the best supported diet for *Minusculodelphis* species. Soft categories I and II of Freeman (1981) involve the following orders of invertebrates: Ephemeroptera, Isoptera, Trichoptera, Plecoptera, Neuroptera, Mecoptera, Diptera, Odonata, Homoptera, Lepidoptera, and Arachnida. In turn, categories IV and V include the hardest invertebrates of the orders Hemiptera, Hymenoptera, Chilopoda, Diplopoda, and Coleoptera. The Orthoptera and Scorpionida occupy an intermediate position in the spectrum of hardness (Freeman 1981, p. 167).

Odonata, Homoptera, and Orthoptera have been recorded in the Paleocene-Eocene of northwestern Argentina (Petrulevicius and Martins-Neto 2000; Petrulevicius and Popov 2014). This region corresponds to the Transition Zone between the Neotropical and Andean biogeographic regions of Morrone (2006). The Brazilian records of Paleogene invertebrates, mainly insects, include several taxa described by the Fonseca Formation, which is late Eocene in age as suggested by palynomorphs (Lima and Salard-Cheboldaeff 1981; Mendes in press). This record is represented by soft-bodied invertebrates such as Isoptera, Blattoidea, and hardest elements as Hymenoptera and Coleoptera (Mendes and Pinto 2001; Martins-Neto and Mendes 2002).

Tropical rain forests were already well established in South America by the Eocene and probably since the Late Paleocene (Burnham and Johnson 2004; Wing et al. 2010). Then, the habitat of *Minusculodelphis* was probably a multistory forest similar to the present Amazonian rainforest. The invertebrate fauna of present tropical forests can be divided into two main vertical strata: floor and canopy (Moore 2008). Although such division is a simplification of the highly complex structure of forest architecture and biology (see Basset et al. 2003), in the context of this contribution, it allows an adequate characterization. The floor assemblage is mostly composed of Arachnida (mites and spiders), Collembola (springtails), Diplopoda (millipedes), Gasteropoda (snails and slugs), Onychophora (velvet worms), Annelida (annelid worms), Isoptera (termites), Hymenoptera (ants), Orthoptera (crickets), and Coleoptera (beetles) (Moore 2008). Canopy assemblages are dominated by Lepidoptera (butterflies, moths and their caterpillars), Hymenoptera (wasps, bees and leaf cutter ants) and Mantodea (mantids) (Moore 2008). When analyzing the hardness scale for invertebrates of each forest stratum, the greatest abundance of soft-bodied invertebrates occurs in the understorey. Based on this statement, the most probable microhabitat for the species of *Minusculodelphis* was the understorey or leaf litter of rain forests. Similar habits have been reported for the pygmy shrew (*Sorex hoyi*), also a very small-sized mammal that inhabits the temperate forests of the Rocky Mountains in North America (Baker 1983).

In addition to dental evidence for dietary preferences of *Minusculodelphis*, morphology of femur reveals the presence of a well-developed third trochanter, which supports a most probable terrestrial (understorey) than arboreal habitat preference. The presence of a third trochanter has been listed by Szalay and Sargis (2001) as a consistent morphological difference in femurs of arboreal and terrestrial marsupials. In addition, these authors also observed that the femur head of terrestrial forms has little extension of articular surface laterally and posteriorly, and that the distal end of the femora is invariably greater than in arboreal forms; the femur here referred to *Minusculodelphis* agrees with most of these terrestrial features observed in living marsupials.

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References

Abello MA, Candela AM (2010) Postcranial skeleton of the Miocene marsupial *Palaeothentes* (Paucituberculata, Palaeothentidae): paleobiology and phylogeny. J Vertebr Paleontol 30:1515–1527

Baker R (1983) Michigan mammals. Michigan State University Press, Detroit

Basset Y, Hammond PM, Barrios H, Holloway JD, Miller SD (2003) Vertical stratification of arthropod assemblages. In: Basset Y, Novotny V, Miller SE, Kitching RL (eds) Arthropods of tropical forests. Cambridge University, London, pp 1–474

Bergqvist LP, Mansur K, Rodrigues MA et al. (2009) Bacia de São José de Itaboraí, RJ – berço dos mamíferos no Brasil. In: Winge M, Schobbenhaus C, Souza CRG, Fernandes ACS, Berbert-Born M, Queiroz ET (eds) Sítios Geológicos e Paleontológicos do Brasil, CPRM 2:413-432

Bloch JI, Rose KD, Gingerich PD (1998) New species of *Batodonoides* (Lipotyphla, Geolabididae) from the Early Eocene of Wyoming: smallest known mammal? J Mammal 79:804–827

Bond M, Carlini AA, Goin FJ, Legaretta L, Ortiz- Jaureguizar E, Pascual R, Uliana MA (1995) Episodes in South American land mammal evolution and sedimentation: testing their apparent concurrence in a Paleocene succession from central Patagonia. VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, Argentina, Actas, pp 47-58

Bradshaw SD, Bradshaw FJ (2002) Short-term movements and habitat utilisation of the marsupial honey possum, *Tarsipes rostratus*. J Zool 258:343–348

Burnham RJ, Johnson KR (2004) South American palaeobotany and the origins of neotropical rainforests. Philos TranS Royal Soc London B 359:1595–1610

Ciancio MR, Carlini AA, Campbell KE, Scillato-Yané SJ (2013) New Palaeogene cingulates (Mammalia, Xenarthra) from Santa Rosa, Perú and their importance in the context of South American faunas. J Syst Palaeontol 11(6):727–741

de Muizon C (1992) La fauna de mamíferos de Tiupampa (Paleoceno Inferior, Formación Santa Lucia), Bolivia. In: Suarez-Soruco R (ed) Fósiles y Facies de Bolivia. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz-Bolivia, pp 575–624

de Muizon C, Brito IM (1993) Le bassincalcaire de São José de Itaboraí (Rio de Janeiro, Brésil): ses relations fauniques avec le site de Tiupampa (Cochabamba, Bolivie). Annales de Paléontologie 79:233–269

de Paula Couto C (1962) Didelfídeos fósiles del Paleoceno de Brasil. Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Ciencias Zoologicas 112:135–166

de Paula Couto C (1970) News on the fossil marsupials from the Riochican of Brazil. An Acad Bras Cienc 42:19–34

Dumont E (1997) Cranial shape in fruit, nectar, and exudate feeders: implications for interpreting the fossil record. Am J Phys Anthropol 102:187–202

Eisenberg JF (1981) The mammalian radiation: an analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago

Freeman PW (1981) Correspondence of food habits and morphology in insectivorous bats. J Mammal 62:166–173

Freeman PW (1995) Nectarivorous feeding mechanism in bats. Biol J Linn Soc 56:439–463

Goin FJ, Candela AM (2004) New paleogene marsupials from the Amazon Basin of eastern Peru. In: Campbell KE (ed) The Paleogene mammalian fauna of Santa Rosa, Amazonian Peru. Science Series, Natural History Museum of Los Angeles, pp 15-60

Goin FJ, Candela AM, Forasiepi A et al. (1997) New, middle Paleocene marsupials from central Patagonia. Annual meeting ofthe Society of vertebrate paleontology, New York, Abstracts: 49A

Goin FJ, Candela AM, Abello MA, Oliveira ÉV (2009) Earliest South American paucituberculatans and their significance in the understanding of ‘pseudodiprotodont’marsupial radiations. Zool J Linnean Soc 155:867–884

Gordon CL (2003) A first look at estimating body size in dentally conservative marsupials. J Mamm Evol 10:1–21

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1–9

Hooker JJ, Sánchez-Villagra M, Goin FJ, Simons EL, Attia Y, Seiffert ER (2008) The origin of Afro-Arabian “didelphimorph” marsupials. Palaeontology 51:635–648

Hume ID (1999) Marsupial nutrition. Cambridge University Press, Cambridge, 389 pp

Ladevèze S, de Muizon C (2010) Evidence of early evolution of Australidelphia (Metatheria, Mammalia) in South America: phylogenetic relationships of the metatherians from the Late Palaeocene of Itaboraí (Brazil) based on teeth and petrosal bones. Zool J Linnean Soc 159:746–784

Lima MR, Salard-Cheboldaeff M (1981) Palynologie des Bassins de Gandarela et Fonseca (Eoceno de l’État de Minas Gerais). Boletim do Instituto de Geociências USP12: 33–54

Marshall LG (1987) Systematics of Itaboraian (middle Paleocene) age “opossum-like” marsupials from the limestone quarry at São José de Itaboraí, Brazil. In: Archer M (ed) Possums and opossums: studies in evolution. Surrey Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney, pp 91–60

Marshall LG, de Muizon C (1988) The dawn of the age of mammals in South America. Natl Geogr Res 5:268–661

Marshall LG, Case J, Woodburne MO (1990) Phylogenetic relationships of the families of marsupials. In: Genoways HH (ed) Current mammalogy. Plenum Press, New York, pp 433–505

Martins-Neto RG, Mendes M (2002) The Fonseca Formation paleoentomofauna (Fonseca Basin, Oligocene of Minas Gerais, Brazil), with description of new taxa. Acta Geol Leopold 55:27–33

McNab BK (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. ComparaT Biochem Physiol, Part A 151:5–28

Mendes MT (in press) Um novo gênero e duas novas espécies de Pergidae (Insecta, Hymenoptera) na Formação Fonseca (Bacia de Fonseca, Paleógeno), Minas Gerais, Brasil. Revista Geologia do Ceará

Mendes MT, Pinto ID (2001) The first findings of Blattea (Insecta, Blattidae) from the Fonseca Formation, Oligocene period, Minas Gerais, in the South East Brazil. Acta Geol Leopold 24:283–290

Moore P (2008) Tropical forests. Facts On File Inc. Infobase Publishing, New York

Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu Rev Entomol 51: 467–494

Oliveira ÉV (1998) Taxonomia, filogenia e paleobiogeografia de marsupiais “poliprotodontes” do Mesopaleoceno da Bacia de Itaboraí, Rio de Janeiro, Brasil. Unpublished thesis, Universidade Federal do Rio Grande do Sul, Programa de pós-graduação em Geociências, Porto Alegre

Oliveira ÉV, Goin FJ (2006) Marsupiais do início do Terciário do Brasil: origem, irradiação e história biogeográfica. In: Cáceres NC, Monteiro-Filho ELA (eds) Os Marsupiais do Brasil: biologia, ecologia e evolução. Editora UFMS, Campo Grande, pp 608–649

Oliveira EV, Goin FJ (2011) A reassessment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): systematics and age of the Itaboraian SALMA. Revista Brasileira de Paleontologia 14:105–136

Petrulevicius JF, Martins-Neto RG (2000) Checklist of South American Cenozoic insects. Acta Geol Hisp 35:135–147

Petrulevicius JF, Popov YA (2014) First fossil record of Discocephalinae (Insecta, Pentatomidae): a new genus from the middle Eocene of Río Pichileufú, Patagonia, Argentina. ZooKeys 422:23–33

Rose KD (2010) New marsupial from the early Eocene of Virginia. J Paleontol 84:561–565

Rosenberg HI, Richardson KC (1995) Cephalic morphology of the honey possum, *Tarsipes rostratus* (Marsupialia: Tarsipedidae), an obligate nectarivore. J Morphol 2233:303–323

Sánchez-Villagra M, Ladevèze S, Horovitz I, Macrini TE, Martin JE, Moore-Fay S, Muizon C, Schmelzle T, Asher RJ (2007) Exceptionally preserved North American Paleogene metatherians: adaptations and discovery of a major gap in the opossum fossil record. Biol Lett 3:318–322

Smith RJ (1993) Logarithmic transformation bias in allometry. Am J Phys Anthropol 90:215–228

Sokal RR, Rohlf FJ (1995) Biometry, 3^{a}th edn. Freeman, New York

Swofford DL (2002) PAUP* phylogenetic analysis using parsimony (*and other methods). Sinauer Associates, Inc., Sunderland

Szalay FS, Sargis EJ (2001) Model-based analysis of postcranial osteology of marsupials from the Palaeocene of Itaboraí (Brazil) and the phylogenetics and biogeography of Metatheria. Geodiversitas 23:139–302

Wilson DE, Mittermeier RA (2015) Handbook of the mammals of the world. Vol. 5. Monotremes and marsupials. Lynx Edicions, Barcelona, 799 pp

Wing SL, Herrera F, Jaramillo CA, Gómez-Navarro C, Wilf P, Labandeira CC (2010) Late Paleocene fossils from the Cerrejón Formation, Colombia, are the earliest record of Neotropical rainforest. Proc Natl Acad Sci U S A 106:18627–18632

Woodburne M, Goin FJ, Raigemborn MS, Heizler M, Gelfo JN, Oliveira ÉV (2014) Revised timing of the South American early Paleogene land mammal ages. J South Am EarthSci 54:109–119

Zimicz AN (2012) Ecomorfología de los marsupiales paleógenos de América del Sur. Unpublished thesis. Universidad Nacional de La Plata