[Palaeontology, 2016, pp. 1–15]

ON THE EXISTENCE OF NON-MICROBIOTHERIAN AUSTRALIDELPHIAN MARSUPIALS (DIPROTODONTIA) IN THE EOCENE OF PATAGONIA

by MALENA LORENTE[1,2], LAURA CHORNOGUBSKY[1,3,4] *and* FRANCISCO J. GOIN[1,2]

[1]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina; mlorente@fcnym.unlp.edu.ar, fgoin@fcnym.unlp.edu.ar
[2]División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina
[3]Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, C1405DRJ, Buenos Aires, Argentina; lchorno@macn.gov.ar
[4]Departamento de Ciencias Básicas, Universidad Nacional de Luján,, Ruta Nacional 5 and Av. Constitución, 6700, Luján, Buenos Aires Province Argentina

Typescript received 21 September 2015; accepted in revised form 19 March 2016

Abstract: A diverse assemblage of extinct mammals of early–middle Eocene age (Ypresian–Lutetian boundary) come from the Patagonian localities of La Barda and Laguna Fría around Paso del Sapo in northwestern Chubut Province (Argentina). Metatherians are well represented, mostly by dental remains of 'Didelphimorphia', Paucituberculata, Sparassodonta, Microbiotheria, and Polydolopimorphia. Here we analyse three calcanea and one astragalus referable to the same, indeterminate taxon, from La Barda, showing the fusion of their ectal and sustentacular facets. This facet arrangement characterizes the Australidelphia, a marsupial clade represented by Microbiotheria from South America and Antarctica, plus all Australasian lineages. Other australidelphian features shown by these tarsals include: in the calcanea, a reduced peroneal process and a tripartite cuboid facet; in the astragalus, a round, very small astragalar head in relation to the body; a convex trochlea with a half for the tibia and half, in slightly lower position, for the fibula. Their size and other anatomical features suggest that the new tarsals cannot be referred to the Microbiotheria. Phylogenetic analysis suggests that the La Barda taxon lies within the Australidelphia, and that it is either closely related or belongs to, the Diprotodontia. The existence of advanced australidelphians in Patagonia adds further evidence of the close relationship between Patagonia, Antarctica, and Australia during the Late Cretaceous – early Palaeogene.

Key words: Australidelphia, South America, Paso del Sapo Fauna, Palaeogene, tarsal bones.

OUR knowledge of the radiations and affinities of South American metatherians has significantly improved since the seminal contributions on marsupial tarsal morphology by Szalay (1982*a*, *b*, 1994). Most noteworthy was his arguing in favour of a clade of marsupials that includes the South American (and the extinct Antarctic) Microbiotheria plus all the Australasian lineages. This monophyletic group was regarded as having derived characters in relation to the Didelphimorphia and the Paucituberculata. Tarsal bone morphology indicative of the more derived condition in the Australidelphia includes: in the calcanea, the reduction of the peroneal process (*Djarthia* being an exception; Beck 2008) and a 'tripartite' cuboid facet; in the astragalus, reduction of head and separation of navicular facet and trochlea; and, in both tarsals, the fusion of ectal and sustentacular facets in a 'continuous lower ankle joint pattern' (CLAJP) (see Szalay 1994; Beck 2012*a*).

Here we describe four australidelphian tarsal bones (one astragalus and three calcanea) with features that, together with their medium size, preclude their referral to any microbiotherian so far known from this locality. Moreover, these new specimens show several derived features not present in microbiotherians but seen in the Australasian Diprotodontia (e.g. small head, more sagittal navicular facet, presence of sustentacular accessory facet, lateral and medial orientation of cuboid facets in the calcanea, etc.). The existence of advanced australidelphians in Patagonia bears interesting biogeographical corollaries and provides additional evidence for the close relationship between Patagonia, Antarctica and Australia during the Late Cretaceous and early Palaeogene (Goin *et al.* 2012*a*; Reguero *et al.* 2013). The description of these specimens and the discussion of their possible affinities are the main purposes of this work.

© The Palaeontological Association
doi: 10.1111/pala.12241

Institutional abbreviations. FMNH, Field Museum of Natural History, Chicago, USA; LIEB-PV, Paleovertebrate Collection, Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de la Patagonia San Juan Bosco, Argentina; MACN Ma, Mammalogy Collection, Museo Argentino de Ciencias Naturales 'Bernadino Rivadavia', Buenos Aires, Argentina; MHNC, Museo de Historia Natural de Cochabamba, Bolivia; MLP, Museo de La Plata, Argentina; MNHN, Museum national d'Histoire naturelle, Paris, France; QMF, Queensland Museum Palaeontology collection.

MATERIAL AND METHOD

Material

Specimens here described include three calcanea (LIEB-PV 4094, 4148 and 4183) and one astragalus (LIEB-PV 4005), all of them referable to a single, still indeterminate, marsupial taxa from La Barda, Paso del Sapo (Fig. 1). Besides the metatherians from the Paso del Sapo localities, specimens of seven additional species were used for comparative purposes: *Dasyurus hallucatus* (MACN Ma 23572), *Didelphis albiventris* (MACN Ma 24192), *Dromiciops gliroides* (MACN Ma 23607), *Mayulestes ferox* (MHNC 8398), *Pucadelphys andinus* (MHNC 8266), *Dendrolagus bennettianus* (MNHN 1895-74) and *Echymipera* sp. (FMNH 121679).

Phylogenetic analysis

In order to test the relationships of the taxa represented by the tarsal remains we coded its characters into the matrix from Horovitz & Sánchez-Villagra (2003) with subsequent modifications by Horovitz *et al.* (2009) and Beck (2012*a*) downloaded from MorphoBank (Beck 2012*b*), (Lorente *et al.* 2016). We carried out a TBR analysis (1000 replications and 10 trees saved per replication) using the software Tree Analysis Using New Technology (TNT, v. 1.1).

Correlation models

Correspondence in size between the dentally defined marsupials and the tarsals from Paso del Sapo associations was analysed through living analogues and a generalized linear regression model. Living analogues analysis refers to direct size comparison with similar and better known but not necessary related species. The linear regression was calculated with the program R using a sample of seven living and fossil species with known postcrania in order to see if there is correspondence in size between the La Barda dentally defined marsupial species and the tarsals presented above. Upper molar and astragalar length were chosen as independent and dependent variables, respectively. Lower molars were not used in the correlation models because of their larger error. Natural logarithm transformation of the variables was performed. The normality of the residuals could not be properly tested, and the regression is considered approximate. A 'leave one out' cross validation method was used to control the weight of each taxon in the regression and to have a better understanding of the per cent prediction error (PE% = ((observed − predicted)/predicted) × 100). The least squares optimization method incorporated in the command *glm* for the program R-Gui Project was used. A general framework and discussion on the methodology here employed was recently detailed by Lorente (2015). Values for linear regression models for the superior molars are shown in Table 2.

Measurements

Tarsal bone and dental measurements (see Table 1) were taken in mm using digital calipers.

Anatomical abbreviations. Figure 2 shows the nomenclature of bones and facets used in this work. AFi, astragalofibular facet; ah, astragalar head; ampt, astragalar medial plantar tuberosity; an, astragalar neck; AN, astragalonavicular facet; at, anterior plantar tubercle; ATi, astragalotibial facet; ATim, medial astragalotibial facet; CaA, calcaneoastragalar or ectal facet; CaAd, auxiliary facet; CaCua, auxiliary cuboid facet; CaCul, lateral calcaneocuboid facet; CaCum, medial calcaneocuboid facet; CLAJP, continuous lower ankle joint pattern; gtpl, groove for tendon of the peroneus longus; pp, peroneal process; Su, sustentacular facet; SuAd, distal accesory sustentacular facet; tc, calcaneal tuber.

Other abbreviations. SALMA, South American Land-mammal Age; TBR, tree bisection and reconnection.

LOCALITY, FAUNA, GEOLOGY AND AGE

The specimens here described were recovered from early middle Eocene levels (Lutetian) at the locality of La Barda, Paso del Sapo, in northwestern Chubut Province, Argentina ('Paso del Sapo fauna', in Tejedor *et al.* 2009; Woodburne *et al.* 2014*a*). The Paso del Sapo fauna includes two fossil associations belonging to two close fossiliferous localities: Laguna Fría and La Barda (Fig. 1). The fossil associations found at these localities were almost contemporary, with Laguna Fría being approximately 2 m.y. older than La Barda, and no less

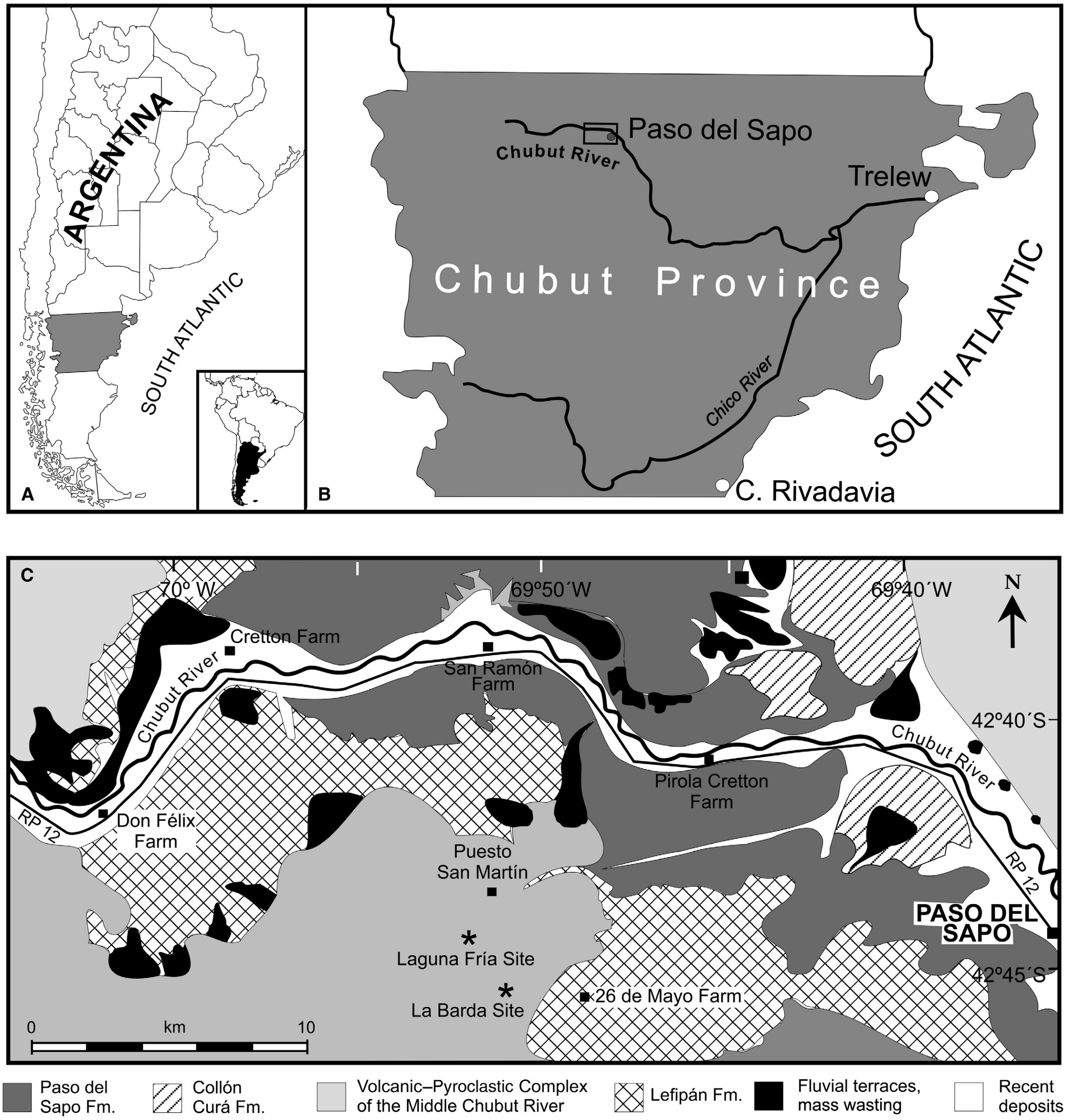

FIG. 1. Location map of the La Barda and Laguna Fría localities near Paso del Sapo. A, Argentina (Chubut Province in grey). B, Chubut province. C, geology of the Paso del Sapo area. Asterisks indicate the two Paso del Sapo fossil localities mentioned in this work.

than 10 species of metatherians are shared between them. Tejedor *et al.* (2009) provided an initial description of the overall mammalian diversity in both Paso del Sapo fossil localities and proposed a new biochronological unit (the 'Sapoan') for the Palaeogene South American SALMA scheme, The Sapoan interval is thus intermediate in time between the (older) Riochican SALMA and the (younger) Vacan Sub-SALMA (Casamayoran SALMA), as preliminarily discussed by Tejedor *et al.* (2009).

A preliminary study of both assemblages of the Paso del Sapo fauna led us to recognize no less than 29 metatherian species referable to 12 families and five orders (see Tejedor *et al.* 2009). The La Barda fossil locality bears by far the richer assemblage in terms of taxonomical diversity, with 21 species. However, no

TABLE 1. Measurements of metatherians used for the regression model.

Species	Collection	No.		m1		m2		m3		m4		M1		M2		M3		M4		AL
				tri	L	tri	L	tri	L	tri	L	W	L	W	L	W	L	W	L	
Dasyurus hallucatus	MACN	23 572	Right	–	–	–	–	–	–	–	–	3.31	4.48	4.21	5.1	4.39	5	4.72	1.28	6.95
Dasyurus hallucatus	MACN	23 572	Left	–	–	–	–	–	–	–	–	3.27	4.78	4	4.9	4.54	5.08	4.94	1.01	6.95
Didelphis albiventris	MACN	24 192	Right	2.54	4.77	2.84	5.19	2.84	5.58	2.94	5.35	4.06	4.91	4.08	4.96	5.33	4.77	3.2	5.33	7.18
Didelphis albiventris	MACN	24 192	Left	2.43	4.03	2.69	5.04	3.07	5.1	2.94	5.13	4.25	5.37	4.64	4.74	5.15	5.13	5.43	3.5	–
Dromiciops gliroides	MACN	23 607	Right	0.91	1.47	1.04	1.95	0.93	0.66	0.62	1.43	1.42	1.77	1.72	1.43	1.67	1.49	1.13	0.44	2.18
Dromiciops gliroides	MACN	23 607	Left	0.83	1.49	0.96	1.48	1.01	1.81	0.63	1.27	1.49	1.54	1.75	1.44	1.7	1.4	0.93	0.55	1.8
Mayulestes ferox	MHNC	8398	Right	2.87	3.09	3.74	3.6	1.45	1.45	1.82	1.75	2.97	3.04	2.88	1.3	2.77	3.34	3.92	3.69	3.38
Mayulestes ferox	MHNC	8398	Left	2.86	3.49	roto	3.82	1.34	1.74	roto	2.07	2.95	2.99	2.77	1.28	2.76	3.31	4	3.75	–
Pucadelphys andinus	MHNC	8266		0.92	2.13	1.11	2.3	1.13	2.72	1.09	2.46	1.61	1.57	1.91	1.81	2.2	1.69	2.09	1.53	3.26
Dendrolagus bennettianus	MNHN	1895–74	Right	5.19	5.65	5.91	6.05	3.49	4.47	4.45	5.03	5.35	6.31	6.51	5.87	5.55	5.74	5.92	5.22	17.09
Echymipera sp.	FMNH	121 679	Right	1.6	3	1.8	3.15	2	3.35	1.9	3.8	2.35	3.2	2.7	3.35	3.15	3.55	3.9	2.1	5.9
Australidelphia indet.	LIEB-PV	4005	Left	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.47

AL, astragalar length; L, length; m, inferior molar; M, superior molar; tri, trigonid width; W, width.

microbiotherians have yet been recovered from La Barda; all specimens referable to this order were found at the Laguna Fría fossil locality (see Discussion below). The two localities have provided 247 specimens, mostly isolated teeth.

The fossil locality of La Barda, which belongs to the designated Paso del Sapo Fauna, is placed in Estancia (farm) '26 de Mayo', 195 km northeast of Esquel and 28 km southwest of Paso del Sapo (Goin *et al.* 2012*b*; Fig. 1). Mammal-bearing levels at the La Barda locality occur within the Andesitas Huancanche interbedded tuffs. The Andesitas Huancanche are part of the so-called Middle Chubut River Volcanic–Pyroclastic Complex, the geology and stratigraphy of which was reviewed by Aragón & Mazzoni (1997). Additional information on the regional geology, stratigraphy, geochemistry, petrogenesis and palaeobotany of this complex has been provided by Petersen (1946), Archangelsky (1974), Volkheimer & Lage (1981), Lage (1982), Rapela *et al.* (1984), Aragón & Romero (1984), Aragón *et al.* (1987), Mazzoni & Aragón (1985) and Mazzoni *et al.* (1989). The Andesitas Huancache Upper Member comprises alkali basalts dated between 47.89 ± 1.21and 43 Ma. A time of deposition of these levels between 45 and 47 Ma was proposed by Tejedor *et al.* (2009).

TARSAL MORPHOLOGY

Because of size and morphology, all specimens are referred to the same, still indeterminate taxon of australidelphian marsupial (see below; Figs 2–3). The astragalus fits well in size and facet morphology with that of the calcanea studied here. The three calcanea are broken at different points (see Figs 2–3); and the tc is lacking in the three specimens. Among their most distinctive features, they show a tripartite kind of cuboid facet and a CLAJP (Figs 2–3) which are both characteristic of australidelphian marsupials. The large peroneal process characteristic of 'ameridelphians' is absent (see below).

LIEB-PV 4005 (Fig. 3A) is a left astragalus with a CLAJP; the AFi, the ATi and the ATim are almost in the same dorsal orientation, with the ATil slightly more dorsal. The AFi is separated from the ATi by a low ridge. The AFi is triangular and slightly smaller than the ATil. The ATim is reduced in comparison with the other trochlear facets. This configuration of the trochlea is similar to the one in *Thylacinus* (Szalay 1994, fig. 7.39F) or *Pseudocheirus* (Szalay 1994, fig. 7.57F). There is no astragalar foramen. Although the medial border is broken, the AN does not appear to be expanded to the medial side until the trochlea. There is a distinct and narrow an when compared to the trochlea and the AN is dorsoplantary-oriented, which could indicate a more terrestrial mode of

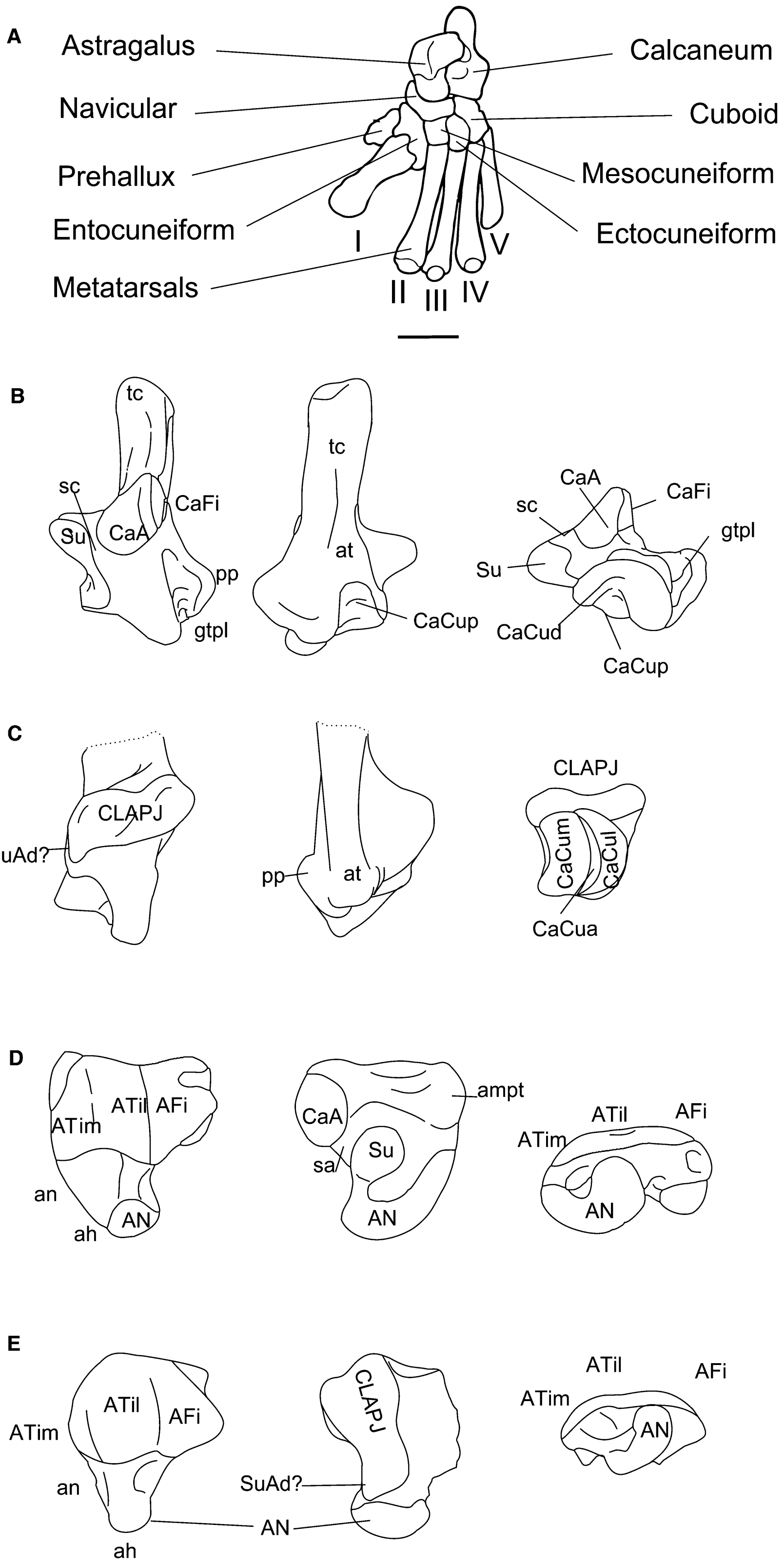

FIG. 2. A, metatherian pes bones. B, 'ameridelphian' left calcaneum. C, australidelphian left calcaneum (reconstructed from the three La Barda calcanea). D, 'ameridelphian' left astragalus. E, australidelphian left astragalus (LIEB-PV 4005). Dorsal, plantar and distal views. *Abbreviations*: AFi, astragalofibular facet; ah, astragalar head; ampt, astragalar medial plantar tuberosity; an, astragalar neck; AN, astragalonavicular facet; at, anterior plantar tubercle; ATil, lateral astragalotibial facet; ATim, medial astragalotibial facet; CaA, calcaneoastragalar or ectal facet; CaCua, accessory calcaneocuboid facet; CaCud, distal calcaneocuboid facet; CaCul, lateral calcaneocuboid facet; CaCum, medial calcaneocuboid facet; CaCup, proximal calcaneocuboid facet; CaFi, calcaneofibular facet; CLAJP, continuous lower ankle joint pattern; gtpl, groove for tendon of the Peroneus longus; pp, peroneal process; sa, sulcus astragali; sc, sulcus calcanea; Su: sustentacular facet. SuAd, accesory facet; tc, calcaneal tuber. Modified from Szalay (1994, p. 190).

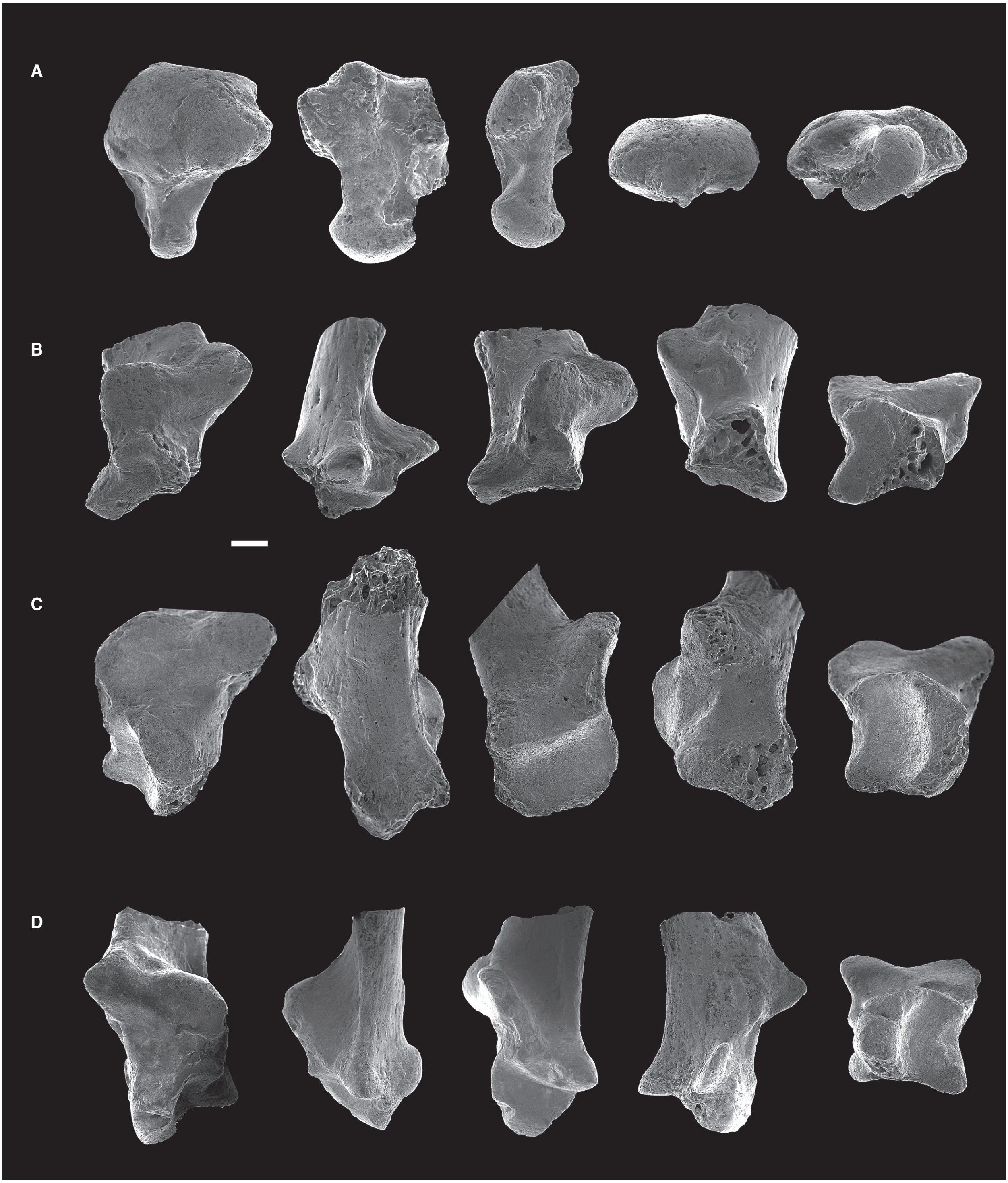

FIG. 3. Scanning electron micrographs of La Barda australidelphian tarsals. A, LIEB-PV 4005, a left astragalus in dorsal, plantar, lateral, proximal and distal views. B–D, dorsal, plantar, medial, lateral and distal views of: B, LIEB-PV 4094, a right calcaneum; C, LIEB-PV 4148, a left calcaneum; D, LIEB-PV 4183, a left calcaneum. Scale bar represents 1 mm. [Correction added on 24 May 2016, after first online publication : Figure 3 replacement]

locomotion. The neck is wider than the head. The dorsal side of the neck is more constricted, forming a wide ridge between the AN and the trochlea. There is a CLAJP with the CaA and the Su halves orientated almost in the same plantar plane. The CaA is shallowly concave and the Su is slightly convex. The Su half of the CLAJP extends to the

AN. The specimen preservation does not allow determination of whether this extension is part of the CLAJP, as in the extended SuAd of *Trichosurus* (Szalay 1994, fig. 7.59G), or if there is an auxiliary facet CaAd, such as in *Dasyurus* (Szalay 1994, fig. 7.37G). However, by its shape, this extension looks more like that present in *Trichosurus.* The ampt is broken but the first part of it was plantar. The morphology of the astragalus, LIEB-PV 4005, is reminiscent of that of the Dasyuromorphia (Szalay 1994; see above).

LIEB-PV 4094 (Fig. 3B) is a left calcaneum. The tc preserves only the distal base, with the major axis medioplantar to laterodorsal. The two components of the CLAJP have almost the same dorsal orientation, with CaA half convex and Su slightly concave. The at is a sharp ridge. The lateral side is slightly broken, but it is preserved enough to indicate than the pp was reduced (also the complete pp in LIEB-PV 4148 is small). Only the CaCum is preserved: it faces distally and it is crescent-shaped more curved than in *Dromiciops* (Szalay 1994). The size of LIEB-PV 4094 and the morphology of its CLAJP are compatible with those of LIEB-PV 4005.

LIEB-PV 4148 (Fig. 3C) is a left calcaneum. It is the largest of the three, but with a difference of less than one mm (with a mean of 1% difference in all measures taken); this could represent intraspecific variation. The tc, the CaCum and the CLAJP are as in LIEB-PV 4094. The at is wider. The CaCul is continuous with CaCum but at an angle of almost 90°. The CaCul is dorsoplantary as large as the CaCum, and has the same width. The lateral side is broken.

LIEB-PV 4183 (Fig. 3D) is a right calcaneum. It is almost the same size as LIEB-PV 4094. The tc, the at, the CaCum and the CLAJP are as in LIEB-PV 4094. The CaCul is narrower than in LIEB-PV 4148. The CaCua is also crescent-shaped, smaller than the CaCum, such as in *Dromiciops* (Szalay 1994) or the calcaneum assigned to *Djarthia* (Beck *et al.* 2008). The pp is complete, reduced and more distal than the CaCum, but not reaching the CaCua, projecting in a small crest, similar to *Murexia* (Szalay 1994, fig. 7.35B, pp not in the figure), more distally placed and larger than in *Dromiciops*, but smaller than in the calcaneum assigned to *Djarthia* (Beck *et al.* 2008).

RESULTS

Specimen assignation

We refer all four specimens here studied to the same taxon for the following reasons: (1) the three calcanea show only minor variation in overall size; (2) all calcanea show a common general morphology; (3) the astragalus matches well, in size and morphology of its articular facets, with the calcanea. Indeed, the calcaneum LIEB-PV 4094 closely matches the articular facets of the astragalus LIEB-PV 4005. Moreover, both show exactly the same preservation features and a similar colour pattern, in such a way that suggests that they could belong to the same individual.

Phylogenetic analysis

The analysis results in six equally parsimonious trees with 980 steps. The Consistency Index (CI) is 0.34 and the Retention Index (RI) is 0.64. The Bremer support has values from 1 to 8 (Fig. 4).

The taxon from Paso del Sapo is nested within Diprotodontia and forms a trichotomy with (*Phascolarctos Vombatus*) and (*Dendrolagus* (*Dorcopsis* (*Thylogale Macropus*))). This clade (Fig. 4) has an absolute Bremer Support of 2 and a relative Bremer Support of 100. It is supported by 17 synapomorphies, two of them corresponding to astragalar features: intermediate angle between: (1) ATim and ATil; and (2) AFi and Atil.

Correlation models

Three linear regression models for different measurements of upper molars were used to evaluate the correlation between tarsal size and molar size (see Tables 1–3 and Figs 5–7). As additional evidence, two living analogues were chosen based on the similar size of the tarsals: *Dasyurus hallucatus* and *Pseudochirulus* cf. *canescens* (Bassarova *et al.* 2009), both species with a mean body mass of c. 500 g (Bassarova *et al.* 2009; Braithwaite & Begg 1995).

DISCUSSION

Australidelphian-shaped tarsals in the La Barda association

The three calcanea and single astragalus here studied, probably belonging to the same taxon, share a unique feature among the metatherian tarsal bones recovered from the La Barda locality, namely fused CaA and Su facets; Szalay (1994) called this the ‘continuous lower ankle joint pattern’ (CLAJP). He considered that the CLAJP evolved early within the stem lineage of Australidelphia, the latter being presently represented by the South American and Antarctic Microbiotheria plus all Australasian lineages. This fusion surely had important anatomical, physiological and evolutionary consequences, as blood vessels and nerves related to the astragalus are displayed throughout

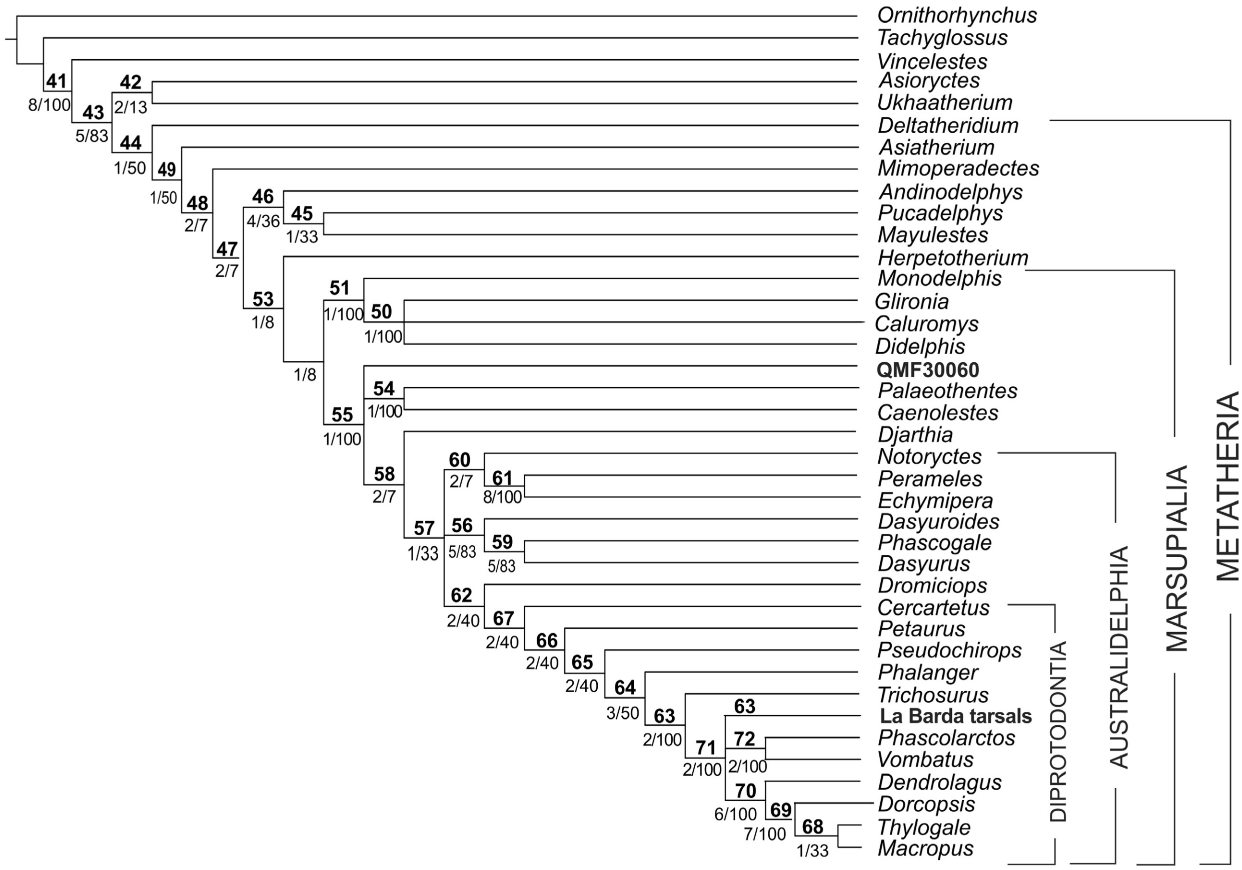

FIG. 4. Strict consensus tree resulting from the phylogenetic analysis (from 6 equally parsimonious trees with 980 steps). Numbers above branches correspond to the nodes (list of synapomorphies in Lorente *et al.* (2016)). Numbers below branches correspond to absolute/relative Bremer supports. CI = 0.34; RI = 0.64.

TABLE 2. Regression models.

Variable X	Variable Y	N	R	Slope	Intercept	PE%					
						Average	Standard Deviation	Minimum	Maximum	−2 SD	2 SD
M1 width	AL	9	0.89	1.26	0.40	3.31	24.85	−34.94	30.04	−46.39	53.02
M2 width	AL	9	0.94	1.37	0.12	2.26	20.70	−24.99	28.93	−39.14	43.66
M3 width	AL	9	0.92	1.37	0.04	2.44	19.23	−21.61	32.92	−36.02	40.89

AL, astragalar length.

the space between the sustentacular and ectal facets in most mammals (e.g. the artery of the sinus tarsi and artery of the tarsal canal; Kelikian & Sarrafian 2011). Szalay (1994, p. 347) suggested that this modification of the sinus tarsi allowed the hyperinversion of the foot, which can be regarded as an arboreal specialization. The changes in the soft anatomy that accompanied this confluence are not yet studied. The fusion is not an exclusive synapomorphy of Australidelphia metatherian, as it also happened in other therians (e.g. the ungulate *Pyrotherium*; Lorente 2015). However, it is extremely rare in other groups and not comparable in detail. It has been described for hyraxes (Barrow *et al.* 2010), but only on the basis of an astragalus that is broken where the sustentacular facet is in extant hyracoids; these also have a hypertrofied ectal facet. The condition has also been reported for the the rodent *Coendu* (Candela & Picasso 2008, fig. 19: A-II; pers. obs. MLP 1084). However, even though the astragalus of this species has confluent facets, there is a clear boundary between the two and there is a

TABLE 3. Results for regression models.

Family	Species	Collection	No	Molar	Width	Predicted	PE%	Average
Gashterniidae	*Gashternia ctalehor*	LIEB-PV	1049	M3	4.06	1.96	−4.79	−10.01
Gashterniidae	*Gashternia ctalehor*	LIEB-PV	1050	M2	4.28	2.11	−11.31	
Gashterniidae	*Gashternia ctalehor*	LIEB-PV	1068	M1	4.06	2.17	−13.93	
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1173	M1	2.73	1.67	11.87	23.56
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1173	M2	2.22	1.21	54.56	
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1174	M1	2.51	1.56	19.45	
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1175	M1	2.48	1.55	20.62	
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1176	M1	2.72	1.66	12.18	
Polydolopidae	*Polydolops* sp. nov. 2	LIEB-PV	1177	M1	2.43	1.52	22.66	
Polydolopidae	*Amphidolops* sp. nov. 2	LIEB-PV	1181	M2	3.42	1.79	3.81	3.69
Polydolopidae	*Amphidolops* sp. nov. 2	LIEB-PV	1182	M2	3.43	1.8	3.58	

The astragalar length of LIEB-PB 4005 was used in every case.

canal below them, such that the passage for blood vessels and nerves is not modified with respect to the pattern seen in other mammals. Finally it has been claimed that some didelphids have a CLAJP (Hershkovitz 1992), although it should be noted that this contradicts the anatomical descriptions of Szalay (e.g. 1982*a*, *b*, 1994).

An additional aspect present in the la Barda calcanea merits further discussion: they display a tripartite, australidelphian-like cuboid facet (i.e. it is divided into three rather that one or two facets; each with a different orientation). Szalay (1994) attributed this feature exclusively to the Australidelphia. Nevertheless, while describing the argyrolagoid pattern, he showed precisely this australidelphian attribute in them (see Szalay 1994, p. 215 and figs 7.27–28). Even though he described the argyrolagoid facets as those of didelphimorphians, they have a quite different orientation and are noticeably stepped, as in the Australidelphia (Fig. 6). Actually, he regarded argyrolagids as highly derived ameridelphians, describing them as ‘closely paralleling the structure found in macropodids’ (Szalay, 1994, p. 215). We see no contradiction in this: as discussed below, we regard argyrolagoids (and all other polydolopimorphians) as australidelphians (Case *et al*. 2005).

Size correlation of the La Barda tarsals

Regression models were used to predict, from size estimations, possible relationships between these tarsals and dentally defined metatherian taxa (those described by Tejedor *et al*. 2009; see Figs 5–7). The following groups have molar teeth smaller than those expected for the tarsals here studied: Microbiotheriidae gen. et sp. indet. ‘D’ and *Eomicrobiotherium* sp.; ?Microbiotheria gen. et sp. indet. ‘F’; Didelphimorphia gen. et sp. indet. A; the Derorhynchidae *Pauladelphys* sp. nov.; Paucituberculata gen. et sp. nov. 4 and gen. et sp. nov. 5; and the Polydolopidae *Polydolops* sp. nov. 1 and sp. nov. 2 (as the curtosis of the models is low because of the small sample size, species should be inside the confidence interval of all regressions to be accepted as possible candidates for La Barda tarsals). On the other hand, the Hathliacynidae gen. et sp. nov. 6 and the Borhyaenidae cf. *Nemolestes* have molar teeth larger than expected.

Taxa that fall within the expected prediction error of the models are: the Gashterniidae *Gashternia ctalehor*; the Protodidelphidae *Protodidelphis* sp. nov. and *Protodidelphis* cf. *P.* sp. nov.; the Polydolopidae *Amphidolops* sp. nov. 1 and *Amphidolops* sp. nov. 2; and Peradectidae gen. et sp. nov. 3. It should also be noted that there are still no upper molar teeth recovered from the Paso del Sapo associations that are referable to: Borhyaenidae, gen. et sp. nov. C; Caroloameghiniidae gen. et sp. nov. 2; *Palangania* cf. *P. brandmayri* and *Palangania* sp.; Sternbergiidae cf. *Itaboraidelphys*; or Polydolopidae *Polydolops* sp. nov. 3, to match the La Barda tarsals in the regression models (values used in the regressions are from Laguna Fría). All of them show similar values in the lower teeth to the species mentioned before; therefore, they can also be regarded as plausible candidates.

Of this dozen metatherian taxa from the Paso del Sapo associations that match in overall dimensions their teeth and tarsals, several of them can be reasonably ruled out as follows.

The Sparassodonta referred by Tejedor *et al*. (2009) to ‘Borhyaenidae, gen. et sp. nov. C’ (LIEB-PV 1093). We refer here to the smallest of the three sparassodont taxa recorded at Laguna Fría and/or La Barda localities. Regarding this specimen, it should be noted that an isolated calcaneum, currently being described elsewhere, can be referred to it. This bone is slightly larger than the tarsals here described; additionally, it preserves a combination of features that relate it to the Sparassodonta (e.g. small peroneal process, extensive fibular contact, nearly vertical orientation of the sustentacular facet; Szalay 1994). Actually, it is quite similar to that of *Arctodictis* cf. *sinclairi* (MLP 85-VII-

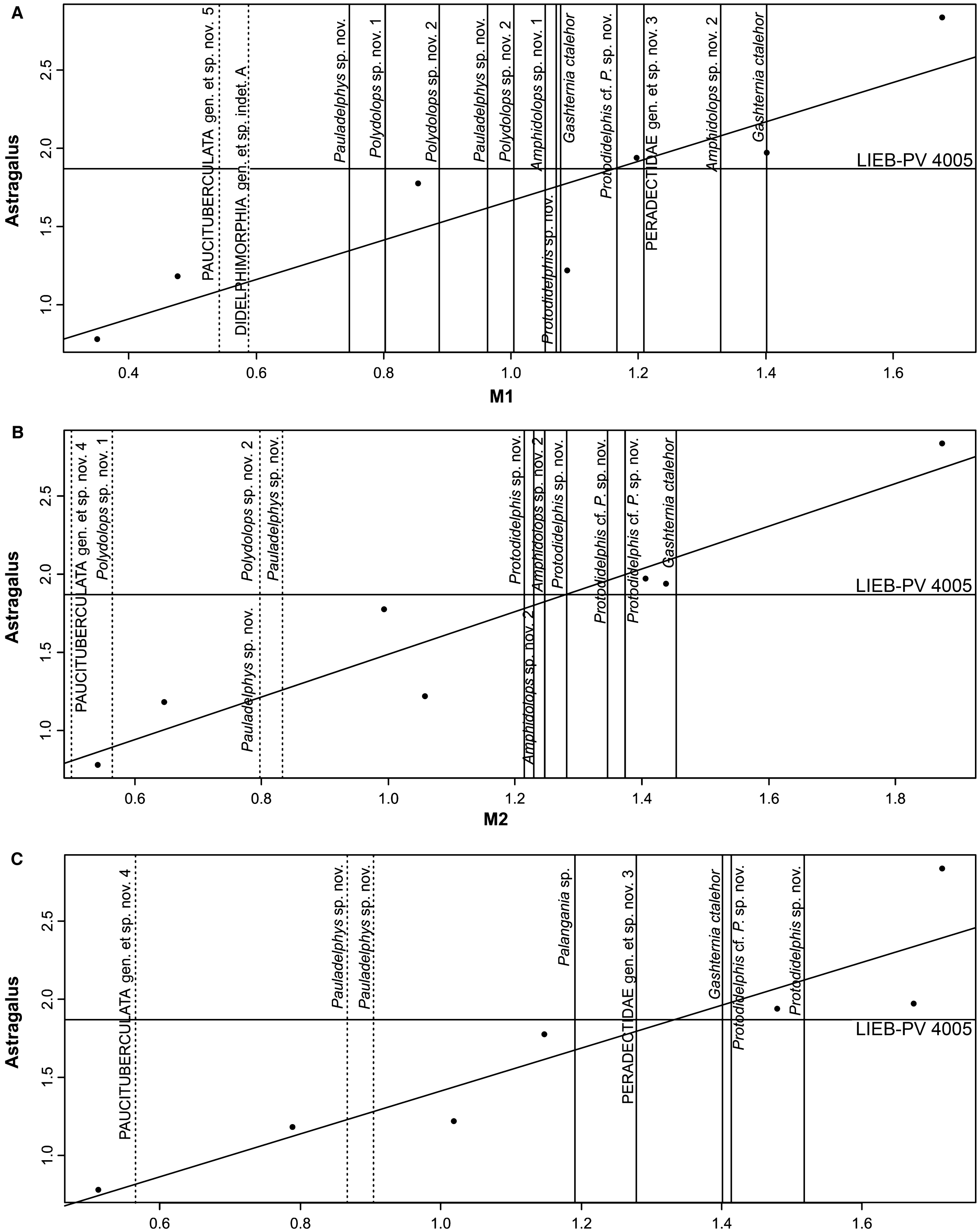

FIG. 5. Linear regression models. Dots correspond to the model specimens (see Table 1). The horizontal line represents the logarithmic value of LIEB-PV 4005 length; vertical lines represent the logarithmic values of the Paso del Sapo metatherian molars per species (maximum and minimum values); solid lines are in the confidence interval; broken lines lie outside the confidence interval. A, log(astragalar length) = 1.26 × log(M1 length) + 0.40. B, log(astragalar length) = 1.37 × log(M2 length) + 0.12. C, log (astragalar length) = 1.37 × log (M3 length) + 0.04.

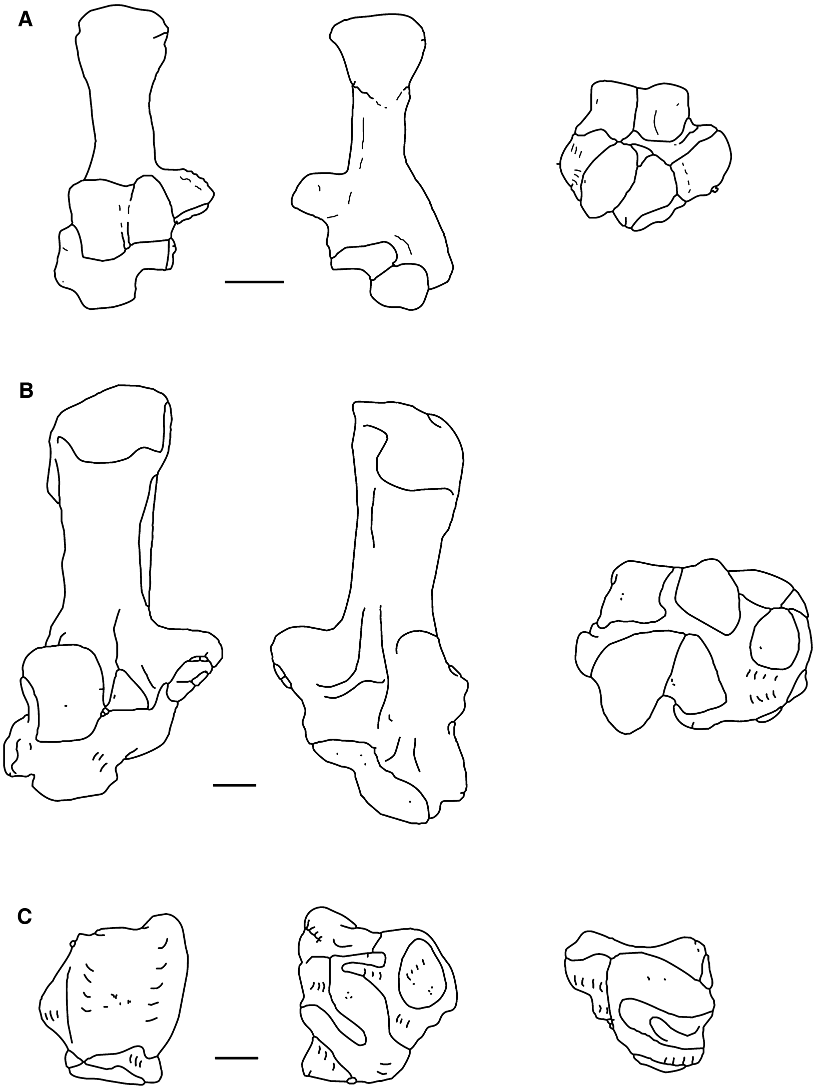

FIG. 6. Argyrolagid tarsals. A, left calcaneum of an indeterminate argyrolagoid from Miocene strata of Gaiman (Chubut Province, Argentina) in dorsal, plantar and distal views (mirror image). B–C, *Argyrolagus scagliai*; dorsal, plantar and distal views of: B, right calcaneum; C, right astragalus. Scale bars represent 1 mm. Modified from Szalay (1994, fig. 7.28).

3-1) from the early Miocene (Forasiepi, 2009), implying that the tarsal morphology characteristic of this order had evolved at least by the late early Eocene.

Two peradectoid taxa (Peradectidae gen. et sp. nov. 3 and Caroloameghinidae gen. et sp. nov. 2) recovered from the Paso del Sapo localities. Peradectians are well known from the Late Cretaceous – Palaeogene of North America where they are represented by abundant tarsal remains. Both dental and tarsal morphology are ameridelphian (Rose *et al.* 2012). On the peradectoid nature of Caroloameghinidae, see Goin (2006).

Both protodidelphids and sternbergiids can be reasonably excluded from the Australidelphia because they have been considered 'Ameridelphia' on the basis of recent reviews of the Itaboraian taxa (Oliveira 1998; Oliveira & Goin 2011, 2012).

All other taxa to which the La Barda tarsals could be referred are assignable to representatives of the order Polydolopimorphia, as follows: *Gashternia, Palangania, Polydolops* and *Amphidolops*. The first two are Gashterniidae and Glasbiidae respectively, while the latter two are Polydolopidae.

The undoubtedly polydolopimorphian tarsals known up to now are those of *Argyrolagus scagliai* (Simpson, 1970). Even though they lack the CLAJP pattern characteristic of australidelphians, the extremely specialized pattern of the argyrolagid tarsals should be noted (Fig. 6). These tarsals have reduced and very close CaA and Su facets, hyperthrophied fibular facet, elongated calcaneal tuber, reduced and distally oriented peroneal process, and, in the astragalus, a mortar-like ATim facet (as in macropodids, see Szalay 1994), and an enlarged trochlea (see Szalay 1994, figs 7.27–28). This morphology is distinctive among metatherians, closely resembling that of hopping kangaroos (e.g. *Thylogale*). Several other features are similar to australidelphians other than Diprotodontia.

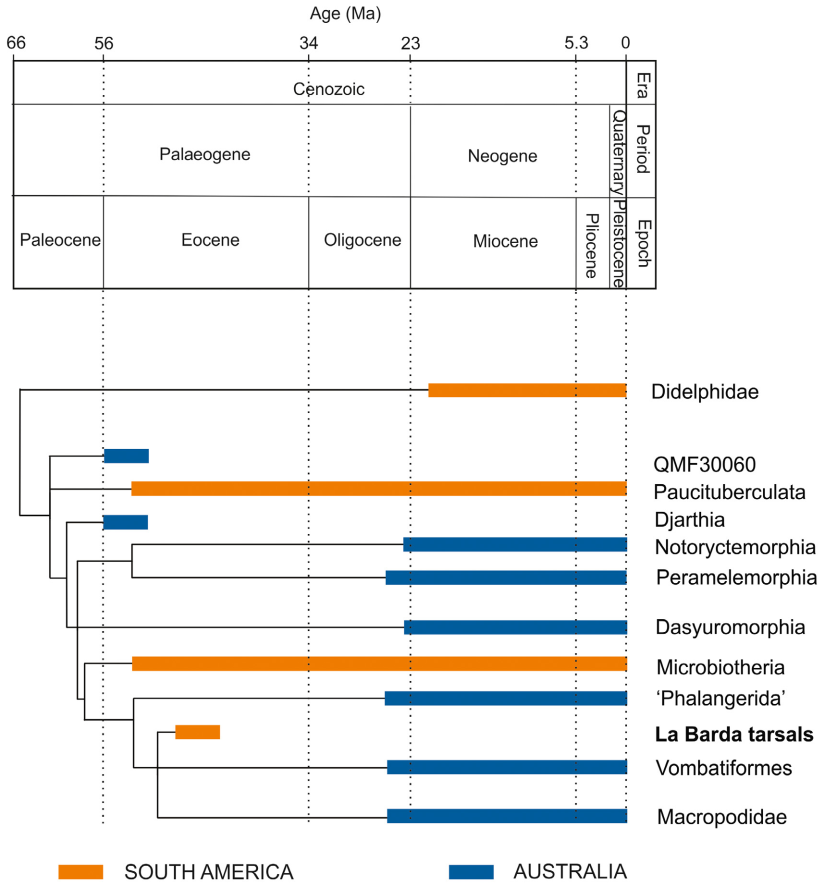

FIG. 7. Strict consensus tree resulting from the phylogenetic analysis and the known record of major lineages studied in this work. Note the position of the La Barda tarsals within the Diprotodontia clade. Colour online.

For instance, the extended navicular facet of the astragalus is much like those of some peramelemorphians (e.g. *Macrotis*, *Echymipera*). These similarities with australidelphian marsupials were noted by Szalay (1994, p. 211–215). Although it lacks a CLAJP, *Argyrolagus* has a tripartite, 'stepped', australidelphian-like calcaneocuboid facet (Szalay 1994, p. 215). We suggest that the separation of the CaA and Su facets could be a secondarily acquired feature, as sometimes occurs in macropodoids and peramelids (Szalay 1994, p. 257).

The Paucituberculata *Palaeothentes* also shows a stepped-like australidelphian-like calcaneocuboid facet (Abello & Candela 2010), but the morphology and the distribution of the facets are different from those of *Argyrolagus*. *Palaeothentes* has large and clearly separated CaA and Su facets, a smaller CaFi facet, and CaCua smaller than CaCum (we suggest than the traditional description of calcaneocuboid facets as CaCup and CaCud facets should be abandoned both for *Argyrolagus* and *Palaeothentes*, as these facets do not show those spatial relationships).

An affinity between the Paucituberculata and the Argyrolagidae has previously been suggested (e.g. Sánchez-Villagra & Kay 1997; Sánchez-Villagra 2001). More recent phylogenetic analysis including several extinct polydolopimorphians has demonstrated that argyrolagids are bonapartheriiform Polydolopimorphia and are related to *Glasbius* and *Microbiotherium* (Goin *et al.* 2009).

Summarizing, *Argyrolagus* tarsals differ from those of other metatherians and their referral to the 'Ameridelphia' or Australidelphia is unsupported by the available evidence. Apart from the (apparent) lack of CLAJP, we note their many, striking similarities with australidelphians.

There are only four possible candidates for the assignation of the La Barda tarsals, all of them referable to the Polydolopimorphia: one gashterniid (*Gashternia*), one glasbiid (*Palangania*), and two polydolopids (*Polydolops* and *Amphidolops*). On the basis of the available evidence we cannot advance further in their designation.

Phylogenetic results and implications

The results of the phylogenetic analysis suggest the presence of australidelphians in the South American Palaeogene (Fig. 7). This was already implicit, as the Paso del Sapo assemblage (at least that of the Laguna Fría fossil locality) includes microbiotherian marsupials.

Notwithstanding the presence of dentally defined microbiotherians among the Paso del Sapo mammals, the tarsals here described are larger than those expected for the Microbiotheria from these sites. The microbiotherian body mass generally ranges within a few tens of grams, usually less than 100 g (Zimicz 2004, 2012); exceptions are *Woodburnodon casei* (Woodburnodontidae) and *Pachybiotherium minor* (Microbiotheriidae) with body masses estimated between 1000 and 1300 g and between 256 and 312 g respectively (Goin *et al.* 2007). The microbiotherian species found at Laguna Fría have body masses of *c.* 32 g (Zimicz 2012).

The calcanea are similar to those of *Dromiciops* (the only microbiotherian with known postcrania), but the astragalus LIEB-PV 4005 differs in the presence of a well-defined neck with a small head; *Dromiciops* has the astragalar head expanded on its medial side, a condition similar to that of didelphimorphians (Szalay 1994). Also the pp and gtpl of these calcanea is more like that of Diprotodontia.

In the La Barda tarsals, the sustentacular half of the CLAJP extends towards and reaches the cuboid facet and the navicular facet, which could indicate the presence of a SuAd, a secondary contact between calcaneum and astragalus that appears in terrestrial and hopping macropodoids (Szalay 1994).

The presence of a tripartite calcaneocuboid facet similar to that of other Australidelphians supports the idea of this trait already existed in the early Eocene of South America. Beck (2012*a*) indicated the presence of an intermediate condition in the early Eocene of Australia in the rather ameridelphian-like calcaneum QM F30060. In calcanea associated to *Djarthia murgonensis* (Beck 2008), from the early Eocene of Australia, the peroneal process is more developed, more like didelphimorphians than that of the La Barda remains, the latter being more similar to extant australidelphians. This indicates that australidelphians already exhibited a great diversification and distribution at least by the late early Eocene (Fig. 7).

Finally, there are several additional corollaries that can be drawn from these results; all of them requiring further testing:

1. If the La Barda tarsals can be effectively referred to the Polydolopimorphia, it would support previous claims concerning the australidelphian nature of representatives of this order (Goin 2003; Case *et al.* 2005; Goin *et al.* 2009).
2. In turn, this would argue in favour of Polydolopimorphia belonging to the Diprotodontia or, alternatively, to a monophyletic group that includes both as sister-groups.
3. If the referral of the La Barda tarsals to the Diprotodontia proves to be correct, they would constitute the oldest known evidence of diprotodontians (*c.* 48 Ma; see Tejedor *et al.* 2009).
4. Regardless of their ultimate place of origin, the cladogenesis of the Australidelphia constitutes an Austral Kingdom event *sensu* Morrone (2004, 2006). The Austral Kingdom concept implies that South America is not a single biogeographical unit but a composite; Patagonia and the Southern Andes are part of a southern, major biogeographical realm together with Antarctica and Australasia. The australidelphian fossil record accurately agrees with it.

Acknowledgements. Field work at Paso del Sapo localities was developed from 1999 to 2007. We thank Mrs 'Coca' San Martín and Mr Rafael Nicolletti for allowing us to work in Estancia 'San Ramón' (Laguna Fría locality), as well as to the late Mr Grenier and family who allowed us to work in Estancia '26 de Mayo' (La Barda locality). We are also grateful to our collaborators in the field and the laboratory: Alejandra Abello, Ariel Humai, Claudia Tambussi, Constanza Koefoed, Viviana Albarracín, María Luisa Pemberton, Leonardo Avilla, and Erika Abrantes. Dr Marcelo Tejedor and students discovered the La Barda locality in 2004. A. Kramarz (MACN), D. Flores (MACN), S. Lucero (MACN), M. Reguero (MLP), M. Tejedor (LIEB), B. Patterson (FMNH), C. de Muizon (MNHN), S. Ladeveze (MNHN), G. Veron (MNHN), and C. Bens (MNHN), kindly allowed us to handle specimens for their study. We thank Marcela Tomeo for the design and composition of the figures that illustrate this work. LC thanks the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2012-0340). FJG thanks the Alexander von Humboldt Foundation (Germany), Agencia (PICTO-Undav 0102, 0105), and CONICET (Argentina, PIPs 5621 and 0361). We thank the Editor Dr Anjali Goswami and the reviewers Sally Thomas, Robin Beck and two anonymous reviewers for their valuable comments and suggestions to improve the quality of the paper.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.k3h00

Editor. Anjali Goswami

REFERENCES

ABELLO, M. A. and CANDELA, A. M. 2010. Postcranial skeleton of the Miocene marsupial *Palaeothentes* (Paucituberculata, Palaeothentidae): paleobiology and phylogeny. *Journal of Vertebrate Paleontology*, **30** (5), 1515–1527. doi: 10.1080/02724634.2010.501437

ARAGÓN, E. and MAZZONI, M. M. 1997. Geología y estratigrafía del complejo volcánico piroclástico del río Chubut medio (Eoceno), Chubut, Argentina. *Revista de la Asociación Geológica Argentina*, **52** (3), 243–256.

—— and ROMERO, E. 1984. Geología, paleoambientes y paleobotánica de yacimientos terciarios del occidente de Río

Negro, Neuquén y Chubut. *Actas 9° Congreso Geológico Argentino*, **4**, 475–507.

—— MAZZONI, M. M. and MERODIO, J. 1987. Caracterización geoquímica de la Ignimbrita Barda Colorada en el Río Chubut medio. *Actas 10° Congreso Geológico Argentino*, **4**, 171–173.

ARCHANGELSKY, S. 1974. Sobre una edad de la flora del Hunco, Provincia de Chubut. *Ameghiniana*, **11** (4), 413–417.

BARROW, E., SEIFFERT, E. R. and SIMONS, E. L. 2010. A primitive hyracoid (Mammalia, Paenungulata) from the early Priabonian (late Eocene) of Egypt. *Journal of Systematic Palaeontology*, **8** (2), 213–244.

BASSAROVA, M., JANIS, C. M. and ARCHER, M. 2009. The calcaneum—on the heels of marsupial locomotion. *Journal of Mammalian Evolution*, **16** (1), 1–23.

BECK, R. M. D. 2008. A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints. *Journal of Mammalogy*, **89**, 175–189.

—— 2012*a*. An ‘ameridelphian’ marsupial from the early Eocene of Australia supports a complex model of Southern Hemisphere marsupial biogeography. *Naturwissenschaften*, **99** (9), 715–729.

—— 2012*b*. Data from: An ‘ameridelphian’ marsupial from the early Eocene of Australia supports a complex model of Southern Hemisphere marsupial biogeography. *MorphoBank*, P739. doi: 10.7934/P739

—— GODTHELP, H., WEISBECKER, V., ARCHER, M. and HAND, S. J. 2008. Australia’s oldest marsupial fossils and their biogeographical implications. *PloS One*, **3** (3), e1858.

BRAITHWAITE, R. W. and BEGG, R. J. 1995. Northern quoll *Dasyurus hallucatus* Gould, 1842. 65–66. *In* STRAHAN, R. (ed.). *The mammals of Australia: national photographic index of Australian wildlife*. Reed Books, Sydney.

CANDELA, A. M. and PICASSO, M. B. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in *Miocene porcupines*. *Journal of Morphology*, **269** (5), 552–593.

CASE, J. A., GOIN, F. J. and WOODBURNE, M. O. 2005. “South American” marsupials from the Late Cretaceous of North America and the origin of marsupial cohorts. *Journal of Mammalian Evolution*, **12** (3–4), 461–494.

FORASIEPI, A. M. 2009. Osteology of *Arctodictis sinclairi* (Mammalia, Metatheria, Sparassodonta) and phylogeny of Cenozoic metatherian carnivores from South America. *Monografías del Museo Argentino de Ciencias Naturales nueva serie*, **6**, 1–174.

GOIN, F. J. 2003. Early marsupial radiations in South America. 30–42. *In* JONES, M., DICKMAN, C. and ARCHER, M. (eds). *Predators with pouches: the biology of carnivorous marsupials*. Commonwealth Scientific & Industrial Research Organization, Sydney.

—— 2006. A review of the Caroloameghiniidae, Paleogene South American “primate-like” marsupials (?Didelphimorphia, Peradectoidea). *Palaeontographica A*, **278**, 57–67.

—— ZIMICZ, N., REGUERO, M. A., SANTILLANA, S., MARENSSI, S. A. and MOLY, J. J. 2007. New mammal from the Eocene of Antarctica, and the origins of the Microbiotheria. *Revista de la Asociación Geológica Argentina*, **62**, 597–603.

—— CANDELA, A. M., ABELLO, A. and OLIVEIRA, E. O. 2009. Earliest South American paucituberculatans and their significance in the understanding of “pseudodiprotodont” marsupial radiations. *Zoological Journal of the Linnean Society*, **155**, 867–884.

—— GELFO, J. N., CHORNOGUBSKY, L., WOODBURNE, M. O. and MARTIN, T. 2012*a*. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. 20–50. *In* PATTERSON, B. D. and COSTA, L. P. (eds). *Bones, clones, and biomes: an 80-million year history of recent Neotropical mammals*. University of Chicago Press.

—— TEJEDOR, M. F., CHORNOGUBSKY, L., LÓPEZ, G. M., GELFO, J. N., BOND, M., WOODBURNE, M. O., GUROVICH, Y. and REGUERO, M. 2012*b*. Persistence of a Mesozoic, non-therian mammalian lineage (Gondwanatheria) in the mid-Paleogene of Patagonia. *Naturwissenschaften*, **99**, 449–463.

GOLOBOFF, P., FARRIS, J. and NIXON, K. 2003. TNT: Tree Analysis Using New Technology, v. 1.1. http://www.lillo.org.ar/phylogeny/tnt/

HERSHKOVITZ, P. 1992. Ankle bones: the Chilean opossum *Dromiciops gliroides* Thomas, and marsupial phylogeny. *Bonner Zoologische Beiträge*, **43**, 181–213.

HOROVITZ, I., MARTIN, T., BLOCH, J., LADEVÈZE, S., KURZ, C. and SÁNCHEZ-VILLAGRA, M. R. 2009. Cranial anatomy of the earliest marsupials and the origin of opossums. *PloS One*, **4** (12), e8278.

—— and SÁNCHEZ-VILLAGRA, M. R. 2003. A morphological analysis of marsupial mammal higher-level phylogenetic relationships. *Cladistics*, **19**, 181–212.

KELIKIAN, A. S. and SARRAFIAN, S. K. (eds) 2011. *Sarrafian’s anatomy of the foot and ankle: descriptive, topographic, functional*. Lippincott Williams & Wilkins, 760 pp.

LAGE, J. 1982. Descripción geológica de la Hoja 43C, Gualjaina. Provincia del Chubut. *Boletín del Servicio Geológico Nacional*, **189**, 1–72.

LORENTE, M. 2015. Desarrollo de modelos de asociación y clasificaciones de restos postcraneanos aislados de ungulados nativos del Paleoceno – Eoceno de América del Sur. PhD thesis, Facultad de Ciencias Naturales y Museo de La Plata, Universidad de La Plata.

—— CHORNOGUBSKY, L. and GOIN, F. 2016. Data from: The existence of non-microbiotherian Australidelphian marsupials (Diprotodontia) in the Eocene of Patagonia. *Dryad Digital Data Repository*. doi: 10.5061/dryad.k3h00

MAZZONI, M. M. and ARAGÓN, E. 1985. El complejo volcánico piroclástico de la Formación Huitrera (Paleoceno-Eoceno), en el área del Río Chubut medio, República Argentina. *Actas 4° Congreso Geológico Chileno*, **3**, 275–300.

MAZZONI, M., MARAGÓN, E. and MERODIO, J. 1989. La Ignimbrita Barda Colorada del Complejo Volcánico Piroclástico del Río Chubut medio. *Revista de la Asociación Geológica Argentina*, **44** (1/4), 246–258.

MORRONE, J. J. 2004. Panbiogeografía, componentes bióticos y zonas de transición. *Revista Brasileira de Entomologia*, **48** (2), 149–162.

—— 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annual Review of Entomology*, **51**, 467–494.

OLIVEIRA, E. V. 1998. Taxonomia, filogenia e paleobiogeografia de marsupiais "poliprotodontes" do Mesopaleoceno da Bacia de Itaboraí, Rio de Janeiro, Brasil. PhD Dissertation, Universidade Federal do Rio Grande do Sul.

—— and GOIN, F. J. 2011. A reassesment of bunodont metatherians from the Paleogene of Itaboraí (Brazil): systematics and age of the Itaboraian SALMA. *Revista Brasileira de Paleontologia*, **14**, 105–136.

—— —— 2012. Marsupiais do Início do Paleógeno no Brasil: diversidade e afinidades. 275–307. *In* CACERES, N. C. and MONTEIRO FILHO, E. L. A. (eds). *Os Marsupiais do Brasil: Biologia, Ecologia e Conservaçao*. 2nd edn. Editora UFMS (Universidade Federal de Mato Grosso do Sul), Campo Grande.

PETERSEN, C. S. 1946. Estudios geológicos en la región del Río Chubut medio. *Boletín de la Dirección General de Minas y Geología (Buenos Aires)*, **59**, 1–137.

RAPELA, C., SPALLETTI, L., MERODIO, J. and ARAGÓN, E. 1984. El vulcanismo Paleoceno-Eoceno de la provincia volcánica Andino-Patagónica. *Relatorio 9° Congreso Geológico Argentino*, **1** (8), 189–213.

REGUERO, M., GOIN, F., HOSPITALECHE, C. A., MARENSSI, S. and DUTRA, T. 2013. West Antarctica: tectonics and paleogeography. 9–17. *In Late Cretaceous/Paleogene West Antarctica terrestrial biota and its intercontinental affinities*. Springer.

ROSE, K. D., CHEW, A. E., DUNN, R. H., KRAUS, M. J., FRICKE, H. C. and ZACK, S. P. 2012. Earliest Eocene mammalian fauna from the Paleocene-Eocene Thermal Maximum at Sand Creek Divide, southern Bighorn Basin, Wyoming. *Papers on Paleontology*, **36**, 1–122.

SÁNCHEZ-VILLAGRA, M. R. 2001. The phylogenetic relationships of argyrolagid marsupials. *Zoological Journal of the Linnean Society*, **131**, 481–496.

—— and KAY, R. F. 1997. A skull of *Proargyrolagus*, the oldest argyrolagid (Late Oligocene Salla Beds, Bolivia), with brief comments concerning its paleobiology. *Journal of Vertebrate Paleontology*, **17** (4), 717–724.

SIMPSON, G. G. 1970. The Argyrolagidae, extict South American marsupials. *Bulletin of The Museum of Comparative Zoology*, **139**, 1–86.

SZALAY, F. S. 1982*a*. A new appraisal of marsupial phylogeny and classification. 621–640. *In* ARCHER, M. (ed.). *Carnivorous marsupials*, Vol 2. Royal Zoological Society of New South Wales, Sydney.

—— 1982*b*. Phylogenetic relationships of the marsupials. *Geobios*, **6**, 177–190.

—— 1994. *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge University Press, , 496 pp.

TEJEDOR, M. F., GOIN, F., GELFO, J. N., LÓPEZ, G. M., BOND, M., CARLINI, A. A., SCILLATO-YANÉ, G. J., WOODBURNE, M. O., CHORNOGUBSKY, L., ARAGÓN, E., REGUERO, M. A, CZAPLEWSKI, N. J., VINCON, S., MARTIN, G. M. and CIANCIO, M. R. 2009. New early Eocene mammalian fauna from western Patagonia, Argentina. *American Museum Novitates*, **3638**, 1–43.

VOLKHEIMER, W. and LAGE, L. 1981. Descripción geológica de la Hoja 42C, Cerro Mirador, provincia del Chubut. *Boletín del Servicio Geológico Nacional*, **181**, 1–71.

WOODBURNE, M. O., GOIN, F. J., BOND, M., CARLINI, A. A., GELFO, J. N., LÓPEZ, G. M., IGLESIAS, A. and ZIMICZ, A. N. 2014*a*. Paleogene Land Mammal Faunas of South America; a response to global climatic changes and indigenous floral diversity. *Journal of Mammalian Evolution*, **21**, 1–73.

ZIMICZ, A. N. 2004. *Paleoecología y extinción de los marsupiales con dentición plagiaulacoide de América del Sur: un estudio basado en los cambios en el tamaño corporal*. Tesis de Licenciatura, Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, 182 pp.

—— 2012. *Ecomorfología de los marsupiales paleógenos de América del Sur*. PhD thesis, Universidad Nacional de la Plata, 413 pp.