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# A unique, Late Oligocene shrew-like marsupial from western Argentina and the evolution of dental morphology

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We describe a new metatherian mammal, *Fieratherium sorex* gen. et sp. nov., found in western Argentina (Quebrada Fiera locality, southern Mendoza Province), in Late Oligocene deposits (Agua de la Piedra Formation, Deseadan age). The only known specimen is a juvenile with fragments of both dentaries, the right maxilla and a fragment of the left premaxilla with dentition. The loci and the number teeth preserved suggest a dental formula of I?3/i3, C1/c1, P3/p3, M?3/m?3. *Fieratherium sorex* has a convergent shrew-like appearance and a unique combination of features among metatherians and other South American mammals of Palaeogene age, including the well-known faunas of Patagonia. An analysis of its phylogenetic affinities suggests that *Fieratherium* is the sister-group of the Paucituberculata. As already described by other authors for several mammalian taxa, the mainly Patagonian South American Palaeogene fossil record offers little information to understanding the evolution of northern lineages. *Fieratherium* may represent a taxon belonging to a lineage that had its origin in Neotropical regions, so far unrecorded in the southern region of South America.

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## Introduction

Interpreting the evolution of the South American mammalian associations during the Palaeogene was classically based on data collected from the southern tip of the continent (i.e. Patagonia; e.g. Simpson 1980; Madden *et al*. 2010; Vizcaíno *et al*. 2012). These data have been complemented with recent fieldwork and further studies in the northern part of the continent (e.g. Kay *et al*. 1997; Cozzuol 2006; Croft 2007; Latrubesse *et al*. 2010; Sánchez Villagra *et al*. 2010) and mostly in Neogene strata. Distinct from both of these areas, Mendoza province, western Argentina, is just north of Patagonia and was the source of the extremely specialized marsupial *Groeberia minoprioi* (Polydolopimorphia, Argyrolagoidea). George G. Simpson (1970) suggested that this species, as well as other peculiar forms, evolved from lineages that were absent in the best-known fossiliferous regions of Patagonia. In fact, several decades later, Goin & Candela (2004) described, from the intertropical lowlands of western Amazonia (Peru), a new Palaeogene marsupial with primitive molar features that predict the pattern of groeberiids. This could indicate that the tropics were the source of some mammalian lineages that later spread into more marginal lands (e.g. Antoine *et al*. 2011).

The palaeontological site of Quebrada Fiera is located in southern Mendoza Province, western Argentina (Fig. 1A), and has been known since the 1970s (Gorroño *et al*. 1979). Preliminary studies on the originally recovered fauna led to it being assigned to the Deseadan South American Land Mammal Age (SALMA), Late Oligocene (Pascual *et al*. 1965; Pascual & Odreman Rivas 1973). Due to the difficult access (Fig. 1B), the site was not prospected for several decades. However, since 2006 new fossil collections have been made during a series of field seasons (Prámparo *et al*. 2006; Cerdeño & Vera 2007; Cerdeño 2011). Currently, fossils known from this locality include phorusrhacids, indeterminate small birds, and numerous remains belonging to several mammalian lineages, many of which are still under description: xenarthrans (sloths, glyptodonts and armadillos), native ungulates (notohippids, archaeohyracids, interatheriids, hegetotheriids, toxodontids, leontiniids, homalodotheriids, litopterns and pyrotheres), a rodent, and metatherians (Bond & Pascual 1983; Gorroño *et al*. 1979; Vera & Cerdeño 2009; Cerdeño & Vera 2010; Cerdeño *et al*. 2010; Cerdeño 2011). Metatherians are known from three specimens belonging to three different taxa: two are the carnivorous sparassodonts *Proborhyaena gigantea* (Proborhyaenidae; Bond & Pascual 1983) and

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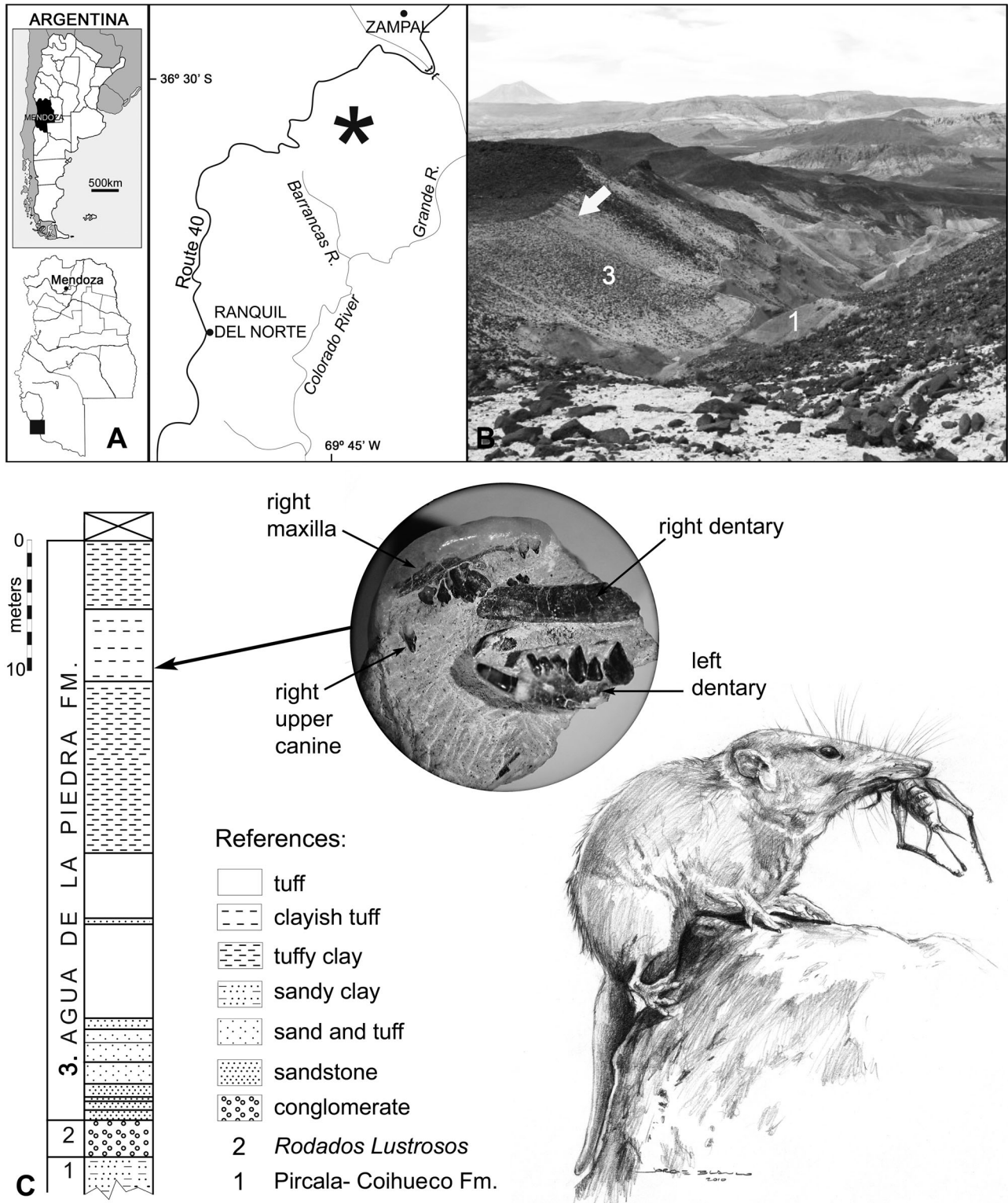
**Figure 1.** Geographical and stratigraphical occurrence of *Fieratherium sorex* gen. et sp. nov. (MCNAM-PV 3958). **A,** location of the Quebrada Fiera fossil site in the south of Mendoza Province, Argentina; **B,** photograph of the site; the numbers correspond to the lithostratigraphical units mentioned in **C**; the arrow indicates the place of finding; **C,** stratigraphical column exposed at Quebrada Fiera; the marsupial *Fieratherium sorex* gen. et sp. nov. comes from the upper levels exposed on the site of the Agua de la Piedra Formation (Late Oligocene; Deseadan SALMA). The life reconstruction of *F. sorex* was created by Jorge Blanco.

**Table 1.** Measurements (mm) of *Fieratherium sorex* gen. et sp. nov. (MCNAM-PV 3958) from the Late Oligocene (Deseadan age) of Quebrada Fiera, Mendoza, Argentina.

| | P2 | DP3 | M1 | M3 | p1 | p2 | dp3 | m1 |
|---|---|---|---|---|---|---|---|---|
| Length | 1.36 | 1.26 | 2.66 | 3.49 | 1.00 | 1.20 | 1.11 | 2.33 |
| Maximum width | 0.73 | 1.10 | 2.33 | 3.02 | 0.81 | 0.93 | 0.66 | 1.40 (tr) |
| | | | | | | | | 1.33 (tal) |

Abbreviations: tal, talonid; tr, trigonid.

*Pharsophorus* sp. (Borhyaenidae; Cerdeño 2011), and the third is the subject of this paper.

Here we describe a new and peculiar metatherian from Quebrada Fiera. The very tiny specimen (Table 1) was discovered while preparing the large dentary of a notoungulate in the laboratory. The scope of this work is to describe the new taxon, examine its phylogenetic affinities, and infer dietary habits. The new mammal adds significant information to the extensive Palaeogene diversity and adaptive radiation of the South American metatherians. Its uniqueness is suggestive of an evolutionary history for its lineage that probably occurred far north of Patagonia, in a different Neotropical context.

## Institutional abbreviation

**MCNAM-PV**: Museo de Ciencias Naturales y Antropológicas 'J. C. Moyano', Vertebrate Paleontology Collection, Mendoza Province, Argentina.

## Anatomical abbreviations

Capital and lower case letters, C/c, canine; I/i, incisor; P/p, premolar; M/m, molar, refer to upper and lower teeth, respectively; D/d refers to deciduous teeth (DP3/dp3).

## Geographical and stratigraphical location

Quebrada Fiera is located about 15 km south of El Zampal, Malargüe Department, Mendoza Province, Argentina (Fig. 1A), at about 1400 m above sea level. The stratigraphical sequence begins with the upper section of the Malargüe Group: the Loncoche and Roca formations (Campanian and Maastrichtian age, respectively), overlain by the early Palaeogene Pircala-Coihueco formations (Gorroño *et al.* 1979; Narciso *et al.* 2004; Combina & Nullo 2002). This sequence is affected by an erosive discordance and it is followed by 2–4 m of clastic conglomerates in a silty matrix: the *Rodados Lustrosos* (Spanish for 'polished pebbles'; Groeber 1946). The *Rodados Lustrosos* are followed by about 40 m of sandstones, clays and tuffs, of whitish, greyish and light brown colour (Gorroño *et al.* 1979; Fig. 1C). The fossil vertebrates collected in the locality of Quebrada Fiera were unearthed from the upper levels exposed in the area, represented by the silty tuffs (Gorroño *et al.* 1979; Fig. 1B, C). The sedimentary sequence of Quebrada Fiera was originally considered as either part of the *Complejo*

*vulcano-sedimentario del Terciario Inferior* (Gorroño *et al.* 1979) or the *Complejo Efusivo Eógeno* (Bettini 1982), but currently it is included in the Agua de la Piedra Formation (e.g. Narciso *et al.* 2004; Combina & Nullo 2008). The deposits of this unit represent an alluvial plain with low energy streams, influenced by strong volcanism (Narciso *et al.* 2004). The sequence of the Agua de la Piedra Formation exposed at Quebrada Fiera represents the basal portions of the unit (Combina & Nullo 2008). The mammalian association suggests that it was deposited during the Late Oligocene (Deseadan age; Gorroño *et al.* 1979; Narciso *et al.* 2004).

## Systematic palaeontology

Class **Mammalia** Linnaeus 1758
Subclass **Metatheria** Huxley 1880
Genus *Fieratherium* nov.

**Type species.** *Fieratherium sorex* sp. nov.

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

**Derivation of name.** *Fiera*- after Quebrada Fiera locality; *-therium*, from the Latin *therion*, beast, common ending of many mammal generic names.

*Fieratherium sorex* sp. nov.
(Figs 1C, 2, 3)

**Diagnosis.** Differs from all other metatherians in the following combination of features: I2–I3 large and labiolingually compressed; i1 hypertrophied and procumbent; reduced canines; p1 single-rooted; p2 with a low principal cusp; M1 with a hypocone-like talon in a basal position, short and wide anterior cingulum, tall and well-defined parastyle, large StB posteriorly placed, narrow paracone, absence of premetacrista and incomplete postparacrista; M3 labially reduced with paracone taller than metacone and wider protocone compared with M1; lower molars with extremely reduced paraconid, low metaconid located close to the protoconid, m1 with spire-like entoconid, circular in cross-section and located at the posterior border of the talonid, hypoconulid absent.

**Derivation of name.** The specific epithet *sorex*, is the Latin meaning for 'shrew', in reference to the shrew-like appearance of the new species.
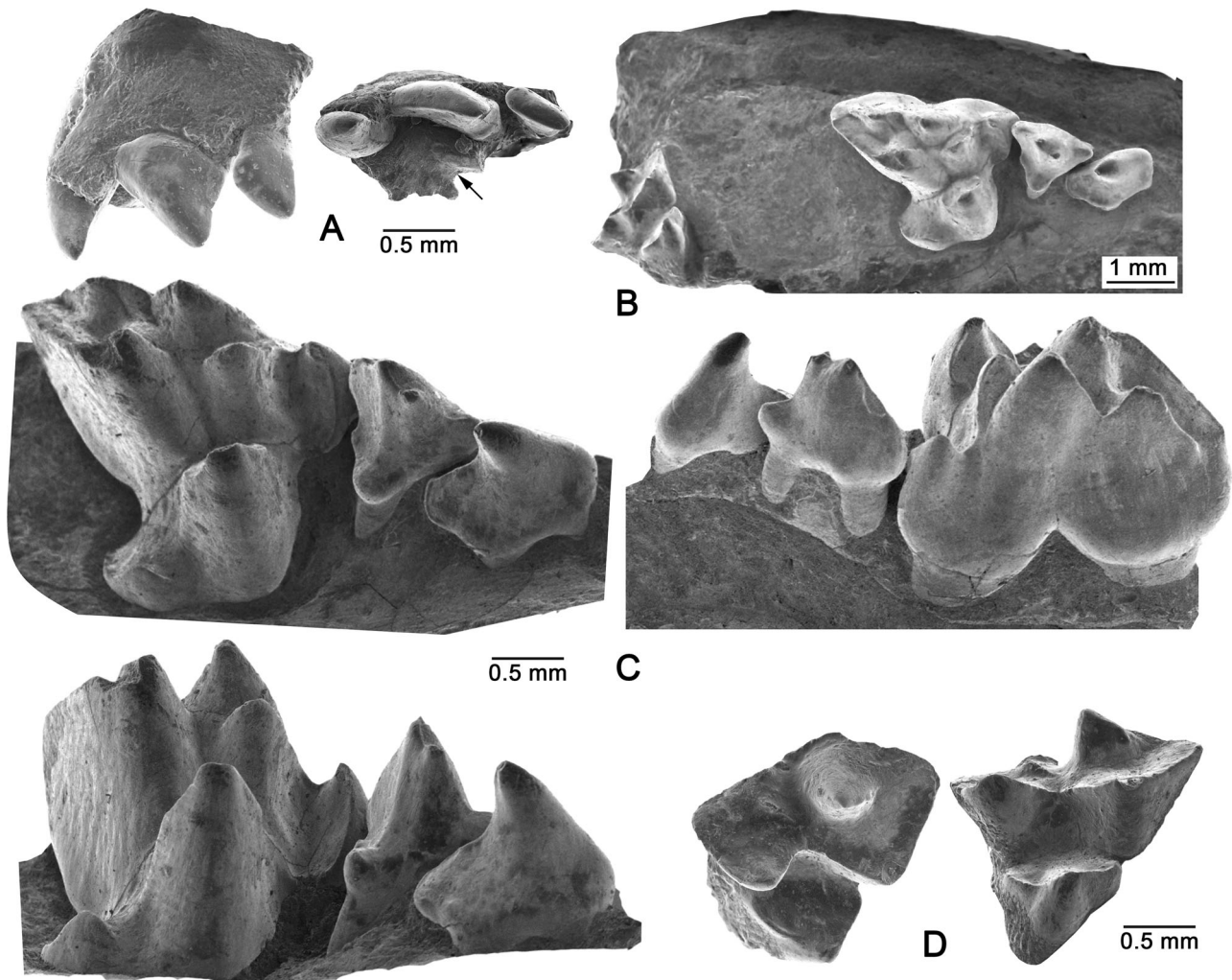
**Figure 2.** *Fieratherium sorex* gen. et sp. nov. (MCNAM-PV 3958) from Quebrada Fiera, Mendoza, Argentina; Deseadan age, Late Oligocene. **A,** fragment of left premaxilla with i1–i3 in lateral and ventral views; arrow indicates the anterior border of the incisive foramen; **B,** right maxilla in occlusal view with P2, DP3, M1, crypta of M2 and M3; **C,** detail of P2, DP3 and M1 in occluso-lingual, labial and lingual views; **D,** detail of M3 in occlusal and occluso-lingual views.

**Holotype.** MCNAM-PV 3958, fragments of both dentaries, right maxilla and fragment of left premaxilla with dentition partially preserved, all belonging to the same, juvenile specimen (Figs 1C, 2, 3).

**Occurrence.** Quebrada Fiera (36°33′13.3″S, 69°42′3.5″W; Fig. 1A), Malargüe Department, southern Mendoza Province, Argentina, from the Agua de la Piedra Formation, Late Oligocene (Deseadan SALMA).

**Description.** MCNAM-PV 3958 is recognized as a juvenile specimen (sensu Anders *et al*. 2011) because of the presence of deciduous teeth (DP3 and dp3), the near absence of wear on the occlusal surface of the teeth, and the early erupting condition shown by several molars. Left M1 and m1–m2 have their crown bases slightly below the

alveolar plane and open alveoli, indicating an incomplete eruption. Left M3 is partially erupted with more than three-quarters of the crown already out of its crypt. The right dentary has the dental crypt, but not the m3, indicating that this molar was still in the process of erupting.

**Premaxilla.** Part of the palatal and facial portions of a left premaxilla have been preserved (Fig. 2A). In ventral view and lingual to the first two incisors, the anterior portion of the left incisor foramen is observed, which is quite small compared with other shrew-like marsupials (e.g. caenolestids). In lateral view, the bone is slightly convex at the level of the root of I1 and appears to be quite high, which is an unusual feature in most marsupials.

**Maxilla.** The palatal portion of the right maxilla is the best preserved part of the specimen. The palate is wide
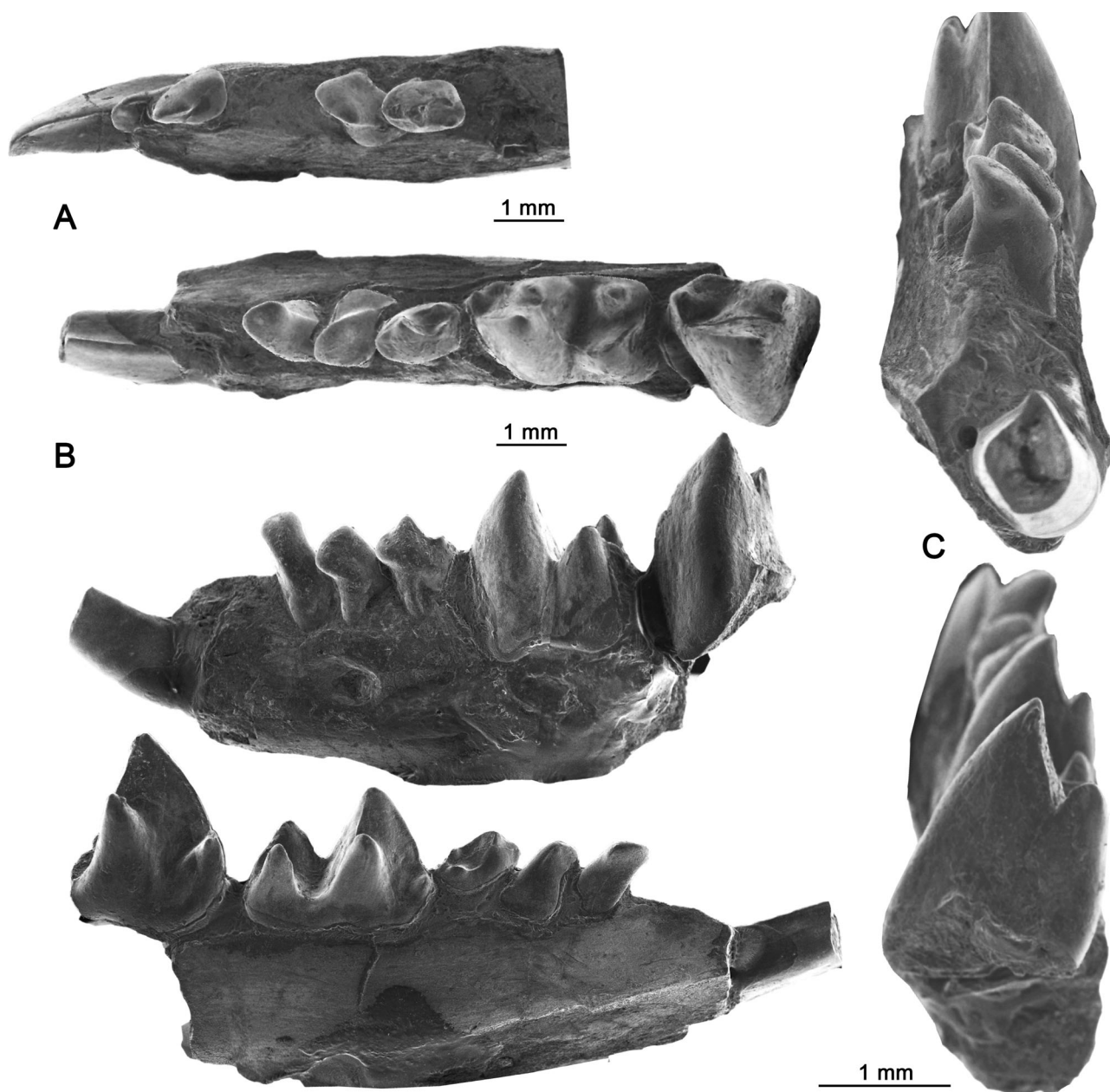
**Figure 3.** *Fieratherium sorex* gen. et sp. nov. (MCNAM-PV 3958) from Quebrada Fiera, Mendoza, Argentina; Deseadan age, Late Oligocene. **A,** right dentary with i1–i3, p2, and dp3 in occlusal view; **B,** left dentary with i1, p1, p2, dp3, m1 and trigonid of m2 in occlusal, labial and lingual views; **C,** same dentary in anterior and posterior views.

at the level of molars, narrowing at the level of DP3 (Fig. 2B). Small vascular foramina open next to the tooth alveoli. It is not possible to assess if palatal vacuities were present, though as with many living marsupials with palatal vacuities, there is a shallow groove anterior and lingual to M1, continuing to a point lingual to the alveolus of P1.

**Dentary.** Both dentaries are partially preserved (Fig. 3A, B). The horizontal ramus is slender and low, even lower than the m1; however, this condition is related to the juvenile stage of the specimen. The labial alveolar border of the dentary is slightly lower than that of the lingual. In lateral view, there are two mental foramina; the anterior is the largest and is located below p2, the second is below m1 (Fig. 3B). The symphysis is smooth and long, with the main axis almost horizontal, extending back to the level of dp3.

**Dental formula.** There were no less than seven antemolar teeth in the upper and lower dentitions, as reconstructed

from the preserved teeth, bones and alveoli. We conclude that the dental formula is best expressed as I?3/i3, C1/c1, P3/p3, M?3/m?3, according to the following analysis.

Three upper incisors are present in the preserved premaxilla (Fig. 2A). Because the premaxilla is broken anteriorly and posteriorly, it is impossible to determine if there were additional incisors. The first incisor is distinctively shaped, compared with the remaining elements (see below), as occurs with the first incisor in many marsupials (e.g. didelphimorphians; Voss & Jansa 2003). If this was also the case in *Fieratherium*, then the anteriormost preserved incisor is likely an I1. An isolated conical tooth is here referred to a right upper canine. Its position in the matrix is vertical and close to the maxilla with its tip pointing downwards with respect to this bone (Fig. 1C). The maxilla has two premolars (P2 and DP3) and an alveolus immediately anterior to P2 (Fig. 2B). Its shape does not match the coronal outline of the upper canine; so, we interpret it as the alveolus of P1. Finally, on the palatal portion of the maxilla, there are two molars (M1 and M3), and the alveoli for an intermediate element (M2). The bone is broken posterior to the M3, in such a way that it is impossible to confirm the existence of an M4. Also, the juvenile state of the material precludes an M4 having erupted, even if one is present in the adult. From these observations, we conclude an upper dental formula of I?3, C, P3, M?3.

Our interpretation of the lower dental formula relies on the combined evidence from both dentaries (Fig. 3A, B). The anteriormost lower tooth is large and procumbent, and is interpreted as the first incisor (i1). It is followed by two small, single-rooted teeth (see the right dentary in Fig. 3A) identified as two additional incisors. Posterior to these, there is the alveolus for a single-rooted tooth identified as a lower canine (right dentary; Fig. 3A). Between this last alveolus and the first molar there are three teeth, here interpreted as p1, p2, and dp3; p2 and dp3 are preserved in both dentaries, whereas p1 is present in the left one (Fig. 3B). The right p1 was preserved detached from the dentary. The right mandible has no molars attached; the left one has the m1 and the trigonid of m2. There is no indication of the final number of molars, though there is the crypt for at least one additional molar posterior to m2 in the right dentary. We infer that the lower dental formula is: i3, c1, p3, m?3.

**Deciduous premolar.** The molariform tooth that is set anterior to the first molar has a complex morphology, as in the deciduous tooth (DP3/dp3) of other metatherians (e.g. Voss & Jansa 2003). Both upper and lower molariform teeth imbricate between P2/p2 and M1/m1 (Figs 2C, 3B), suggesting that the molariform element erupted before the contiguous teeth. A computed tomography (CT) analysis performed on the maxilla revealed the presence of denser material than bone just below the molariform tooth, which most likely represents the P3 inside its crypt. Although the

CT images obtained were low quality and inconclusive. The overall evidence leads us to conclude the molariform upper and lower teeth are deciduous elements.

**Upper teeth.** The first incisor is styliform, stout, and slightly recumbent. The I2 and I3 are triangular in outline and strongly compressed labiolingually. There is a central cusp and a long anterior crest; the posterior crest is more vertical. I2 is larger than I3 (Fig. 2A).

An isolated, single-rooted tooth is identified as a right canine (Fig. 1C). This tooth is short, slightly recumbent and conical at its apex, with a convex labial face and a more flattened lingual one. There is a plane surface at its posterolabial slope, near the crown base, which is probably a fracture. The alternative interpretation as a wear facet seems unlikely; the animal is young and the usual position for the facets in the upper canines is at the lingual side of the tooth.

The teeth preserved in the maxilla are P2, DP3, M1 and M3 (Fig. 2B). The P2 is completely erupted. It has two roots with the anterior slightly smaller than the posterior. The tooth sits obliquely in the maxilla with the anterior root slightly labial and the posterior posterolingual to it. The crown consists of an asymmetrical main cusp followed by a broad posterior cingulum, which is wider lingually. There is a proportionally long crest running from the apex of the main cusp towards the posterior edge of the tooth.

DP3 is small by comparison with M1 and has a complex crown morphology (Fig. 2B, C). It has three thin roots: two labial and one lingual. The antero-labial root is the smallest and the postero-labial is the largest. The crown is triangular in occlusal view and consists of three main cusps: paracone, metacone and protocone, and two smaller: parastyle and metastyle. Paracone and metacone are twinned and the metacone is the tallest. Parastyle, metacone and metastyle are aligned. There is no stylar shelf; instead, the labial border of the tooth forms a vertical wall defined by the already mentioned labial cusps. The protocone is small and low, without a basin. There is a minute cusp just posterior and labial to the protocone and almost at the same horizontal plane.

The M1 is proportionally large, high-crowned and triangular in outline (Fig. 2B, C). The metacone is the tallest cusp of the crown, closely followed by the StB. The paracone and the metacone are triangular in cross-section and with flat labial surfaces. In lingual view, feeble vertical enamel striations are developed on the metacone and protocone (Fig. 2C). The paracone and metacone are close to each other and the StB is wedged between: the lingual slope of the StB is positioned between the paracone and the metacone, in a place usually occupied by the centrocrista. The postparacrista is incomplete and ends at the lingual slope of StB, while the premetacrista is absent. Labial and basal to the metacone there is a small enamel ridge that connects this cusp with the StD. The prepara crista is short,

almost vertical, and ends at the anterior slope of the StB. The postmetacrista is large and oblique to the transversal axis of the tooth. The stylar shelf is narrower at the anterior part of the tooth and widens posteriorly. It bears two main cusps, StB and StD. StB is tall and set labially and posterior to the paracone, almost at the middle of the anteroposterior length of the tooth. StD is smaller than StB and slightly labiolingually compressed. StB has one crest descending posteriorly from its apex, StD has two crests: one anterior and the other posterior to its apex. The anterior crest of StD meets the posterior crest of StB, while its posterior crest tends toward, but does not reach, the metastylar corner of the tooth. The parastylar corner projects forwards and bears a well-defined StA. This cusp is prominent, sharp; it is set lower than the remaining structures of the stylar shelf and, on the contrary, is associated to the anterobasal cingulum. This cingulum is short, broad and lingually oblique. The protocone is narrow and it is set in the crown lower than the paracone and metacone. Its labial face is almost vertical. The paraconule and the metaconule are absent; however, there are preprotoconal and postprotoconal crests slightly swollen and curved at their labial endings. A possible interpretation of this is that these swellings constitute vestiges of the conules. There is a broad posterointernal cusp developed at the base of the crown, much below and immediately behind the protocone (Fig. 2C). This cusp is taller at the lingual border, and descends to the labial border of the tooth. The M2 is not preserved. There are at least two alveoli, with the lingual one much larger than the posterolabial (Fig. 2B). The M3 is well-preserved except that its labial portion is broken (Fig. 2B, D). It is lower and almost half the size of M1. The M3 sits lingual to M1. This position may be post-mortem deformation, but it is placed just below a bony buttress separating the M2 and M3 loci. M3 differs from M1 in that the paracone is taller than the metacone. The paracone and the metacone are more distant from each other and there is a V-shaped centrocrista. The preparacrista is longer than that of the M1. The labial faces of the paracone and metacone are flat. The postero-labial border of the tooth is broken; therefore, the length of the postmetacrista is unknown. The StB is lower and more rounded in section than in the M1. Behind the StB, there is a very small StD. The protocone is proportionally taller and broader, and the preprotoconal and postprotoconal crests are better defined. Other structures of this tooth are lost by fracture.

**Lower teeth.** The first incisor is hypertrophied, procumbent and slightly curved at its distal end (Fig. 3A, B). The tip is laterally compressed, while the rest of the crown is more cylindrical. In the broken left incisor it can be seen that the labial enamel layer is thicker than the lingual one (Fig. 3C). Where the labial and lingual enamel layers join, there is a sharp edge, which runs dorsally and over the whole length of the tooth. The alveolus of this tooth opens at the anterior end of the dentary.

The second and third lower incisors are single-rooted and slightly procumbent (Fig. 3A). The crowns are wide posteriorly. The apices are laterally compressed. In lateral view, the crown of i2 is symmetrical and round, and the crown of i3 is asymmetrical with a longer posterior edge. The second lower incisor is slightly staggered over the i1 and a bony buttress of the dentary raises the labial alveolar base of the i2 above the alveolar base of i3. Because of this staggered condition this tooth is likely homologous to the i3 of other metatherians (following Hershkovitz 1982, 1995), but we refer to it as i2 based on its location. The buttress of the second lower incisor in *Fieratherium* is low and the staggered condition is subtly defined compared with most marsupials. Among them, the morphology of *Fieratherium* resembles living caenolestids: the procumbent first lower incisor (the serially homologous i2) and the following incisors are not as crowded as in other metatherians, consequently, the i3 slightly staggers over the i2 (Hershkovitz 1995).

The p1 is single-rooted and high (Fig. 3B). The crown widens posteriorly at its base; it has one main cusp which is labiolingually compressed. The p2 is double-rooted and slightly lower than p1. It is more obliquely set with respect to the anteroposterior axis of the dentary. The apex of the main cusp is laterally compressed, and its base is wider than p1.

The dp3 has two slender roots and is small with a complex morphology (Fig. 3A, B). This tooth is proportionally smaller than the deciduous tooth of at least some living didelphids (Online Supplementary Material Appendix 1). There is a main cusp, the protoconid, followed posteriorly by a short, basined talonid. The paraconid and the metaconid are absent, as well as the anterior cingulum. The protoconid is blunt and triangular in section. The preprotocristid is short and poorly defined; it descends towards the anterior end of the tooth. A blunt crest connects the apex of the protoconid with the hypoconid. The talonid is short, narrow and basined. There are two similarly sized, laterally compressed cusps, the entoconid (lingual) and the hypoconid (labial); the entoconid is placed posteriorly with respect to the hypoconid. There is no hypoconulid. There is also a short and oblique posthypocristid that directs towards the entoconid.

The m1 is roughly rectangular in outline, with the trigonid higher and slightly wider than the talonid (Fig. 3B). The protoconid is the largest cusp, more than twice the size of the remaining trigonid cusps. The protoconid is triangular in cross-section, with a sharp preprotocristid descending anterior, almost parallel to the anteroposterior axis of the tooth. The paraconid is low, anteroposteriorly compressed, and located slightly laterally. The metaconid is small and twinned to the protoconid. The talonid is shorter than the trigonid. The talonid bears two cusps similar in height: the entoconid and hypoconid. The entoconid is columnar, spire-like, and circular in cross-section; it is located close to the

posterior border of the tooth. There is no pre-entocristid. The hypoconid is triangular in cross-section. The cristid obliqua ends labial to a point below the metacristid notch. The posthypocristid descends medially towards the posterior base of the entoconid. The hypoconulid as such is absent; at the lingual end of the posthypocristid, there is a small swelling that could be interpreted as the vestige of this cusp. The presence of the anterior cingulum cannot be confirmed in m1. There is no posterior cingulum.

The trigonid of m2 is the only structure preserved from this tooth (Fig. 3B, C). It is larger and the general morphology resembles the m1, differing in the proportionally larger paraconid and the more distant position of the metaconid with regard to the protoconid. There is a broad and short anterior cingulum. The metacristid notch is shallow.

## Discussion

### Phylogenetic analysis

The phylogenetic position of *Fieratherium sorex* was tested by a cladistic analysis, using the data matrix of morphological characters of Goin *et al.* (2009). Modifications were made according to the taxa analysed in the present study and new characters were added (Online Supplementary Material Appendices 2 and 3). The taxa scored include 17 metatherians represented by the crown-group Marsupialia (Paucituberculata, Microbiotheria and fossil relatives) and two basal stem marsupials considered as the outgroup (*Alphadon* and *Pucadelphys*). The selection of taxa is concentrated on 'pseudodiprotodont' marsupials. The matrix includes 44 morphological characters that describe the morphology of the dentary and the upper and lower dentition. Of the 44 characters selected, 30 are binary and 14 are multistate of which four are ordered (characters 2, 3, 30 and 38).

An equally weighted parsimony analysis was conducted using TNT 1.1 (Goloboff *et al.* 2008). An exact search produced four most parsimonious trees of 111 steps (consistency index = 0.550; retention index = 0.702). The Bremer support is very low for each node, suggesting that the stability of the tree is weak. The strict consensus and its Bremer values are shown in Fig. 4.

The general topology of the tree resembles the results in Goin *et al.* (2009). The most striking difference concerns the unresolved position of *Pucadelphys* and *Derorhynchus*. In two of the four trees obtained, *Pucadelphys* is located outside the group formed by the common ancestor of Microbiotheria, Paucituberculata, and all of its descendants, in agreement with the majority of the analyses (e.g. Sánchez Villagra *et al*. 2007; Beck *et al*. 2008; Forasiepi 2009; Ladevèze & Muizon 2010). In the two remaining trees, *Pucadelphys* is closer to the Paucituberculata, similar to Goin *et al*. (2009). In this study and in Goin *et al*. (2009),

it is probable that the limited taxon sample of the 'pseudodiprotodont' marsupials and the characters selected are affecting the resolution of the phylogenetic position of *Pucadelphys*. *Derorhynchus* is here found in an unresolved position or closer to the Paucituberculata, as in Goin *et al*. (2009). In an alternative hypothesis (Ladevèze & Muizon 2010), *Derorhynchus* is located outside the crown group Marsupialia. The phylogenetic position of these Palaeogene metatherians is pending further analysis.

*Fieratherium sorex* is resolved in all the trees as a stem Paucituberculata. This clade is supported by two unambiguous synapomorphies: reduced or absent lower canine (character 6 [1]) and reduced or absent hypoconulid (character 13 [1]). In addition *Fieratherium* shares with paucituberculatans the presence of three lower incisors, hypertrophied first lower incisor, large StB, reduction of M3, and lack of paraconules. Some features of the *Fieratherium* dentition resemble basal paucituberculatans, such as *Evolestes* and *Bardalestes* (Goin *et al.* 2007, 2009) in having StB and StD separated from the unreduced paracone and metacone, StB slightly posteriorly located, and a short and wide anterior cingulum (e.g. *Evolestes*; Goin *et al.* 2007).

*Bardalestes hunco* and *Evolestes hadrommatos* are basal paucituberculatans. *Bardalestes* is known from Late Paleocene and Early-Middle Eocene levels (Itaboraian and Paso del Sapo fauna) of Patagonia and *Evolestes* from Oligocene levels (Deseadan) of Bolivia (Goin *et al.* 2007, 2009). According to the characters used in this study (Online Supplementary Material Appendix 2), *Bardalestes* shares with the remaining paucituberculatans three unambiguous synapomorphies: presence of pre-entocristid in m1–m3 (character 14 [0]), laterally compressed entoconid (character 15 [1]), and StC fused to StD (character 41 [2]). *Evolestes* has two additional unambiguous synapomorphies: absence of postcingulum (character 23 [1]) and very large metaconule, hypocone-like (character 38 [2]).

These characters and other features classically used to support the paucituberculatan clade, such as a labially salient hypoconid, StB and StD larger than paracone and metacone, and winged and lingually expanded metaconule (Abello 2007; Goin *et al.* 2007, 2009; see also below) are absent in *Fieratherium* and hence exclude it from this group. In addition, *Fieratherium* has some uniquely derived features, such as M1 with a hypocone-like talon in a basal position, short and wide anterior cingulum separated from the stylar shelf, tall and well-defined parastyle, narrow paracone, M3 with paracone taller than metacone; low metaconid located close to the protoconid, spire-like entoconid, circular in cross-section and located at the posterior border of the talonid, that support the exclusion of *Fieratherium* from the Paucituberculata. The name Paucituberculata is maintained for the group that includes the most recent common ancestor of *Riolestes*, *Bardalestes*, the Palaeothentoidea and Caenolestoidea clade, and all of its descendants (following Goin *et al.* 2009).
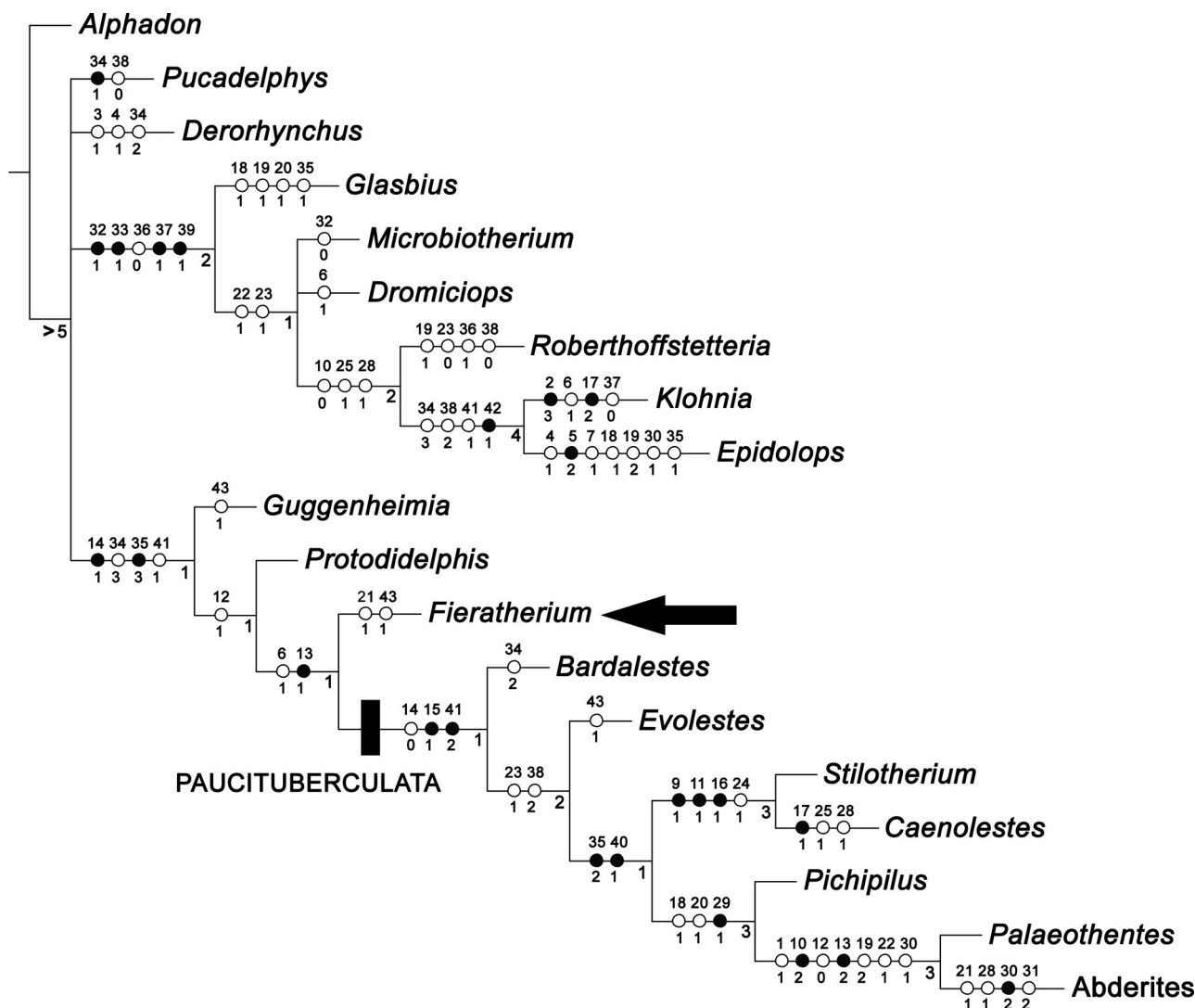
**Figure 4.** Strict consensus cladogram (111 steps, consistency index = 0.550, retention index = 0.702) with unambiguous synapomorphies; black circles indicate autapomorphic features and white circles indicate homoplastic synapomorphies. Numbers at nodes indicate the Bremer support.

The Paucituberculata is an endemic South American clade of marsupials first recognized in the latest Paleocene–Early Eocene (Itboraí and Las Flores formations; Goin *et al.* 2009; see Gelfo *et al*. 2009 for a discussion of the age of the units). The radiation of the group took place in the Early Oligocene (pre-Deseadan ages) and early records are rare and sparse. During the Early Miocene (Colhuehuapian), paucituberculatans diversified with the record of 11 genera distributed into four different clades: Caenolestidae, Pichipilidae, Abderitidae and Palaeothentidae (Marshall 1980; Abello 2007; Abello & Rubilar Rogers 2012). The group declined during the late Neogene and is currently represented by *Caenolestes*, *Lestoros* and *Rhyncholestes*. The phylogenetic position of *Fieratherium* (Fig. 4) suggests that it represents a different lineage closely related

to but placed outside the Paucituberculata. The discovery of *Fieratherium* reinforces the possibility that the diversity of the 'pseudodiprotodont' marsupials during the Cenozoic of South America was wider than previously thought and includes lineages whose early history remains unknown.

*Fieratherium* shares some characters with basal marsupials, such as *Derorhynchus* and protodidelphids. *Derorhynchus*, similar to *Fieratherium*, has a low paraconid in m1, a talonid subequal in length to the trigonid, and a spire-like entoconid (Paula Couto 1952; Marshall 1987; Goin *et al.* 1999). In protodidelphids (e.g. *Protodidelphis* and *Guggenheimia;* Paula Couto 1952; Marshall 1987), the upper molars have large StB slightly posteriorly located and large StD, and tall and spire-like-entoconid. In addition, these basal taxa have a postprotoconal cingulum,

which would represent the homologous structure of the distolingual hypocone-like cusp of *Fieratherium* (see below). *Derorhynchus* is known since the Late Paleocene (Salamanca Formation; Bond *et al.* 1995), while protodidelphids are known since the Early Eocene (Itaboraí and Las Flores formations; Goin *et al.* 1997). The similarities between *Fieratherium* and these early Palaeogene taxa, lacking in other known taxa from the well-studied Deseadan and Colhuehuapian localities from Patagonia and Bolivia, are worth mentioning. Comparisons with these Palaeogene taxa and the analysis of the phylogenetic position of *Fieratherium* allow interpretation of the evolution of character states, such as the occurrence of the hypocone-like cusp in the M1. This cusp is absent from all other known metatherians.
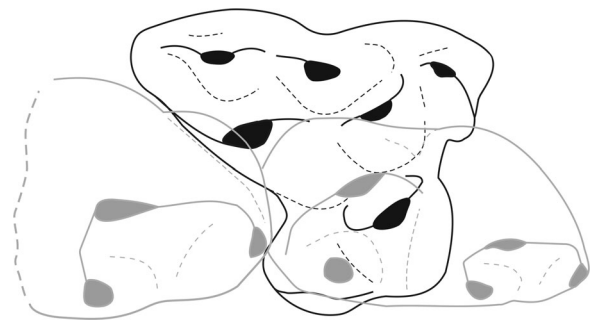
## Upper molars: distolingual cusp

The last common ancestor of eutherians and metatherians does not have a hypocone (e.g. Simpson 1936), but possesses a small metaconule. The metaconule is variably present in several successive therian sister taxa (e.g. *Pappotherium*, *Falepetrus*), some basal eutherians (e.g. *Zalambdalestes*, *Kennalestes*, *Cimolestes*, *Didelphodus*), and metatherians (e.g. *Deltatheridium*, *Alphadon*, *Pediomys*, *Asiatherium*). The hypocone was defined by Osborn (1888) as the posterointernal cusp of the upper molars that originates from an expansion of the postcingulum (Osborn 1897, 1907; see also Gregory 1934; Kielan-Jaworowska *et al.* 2004; Anemone *et al*. 2012). Later, a diverse origin for this cusp was accepted. Simpson (1936) and others concurred that the hypocone is formed by budding or fission on the protocone, overgrowth from the posterior cingulum, enlargement and displacement of the metaconule, or other evolutionary processes (see also Hunter & Jernvall 1995). Hence, the term hypocone was largely used in a topographic sense without considering the homology of its origin. In addition, an enlarged distolingual cusp was independently achieved among different mammalian lineages (e.g. Gregory 1934; Hunter & Jernvall 1995; Anemone *et al*. 2012). In this phylogenetic context, the cusp generally called the hypocone is clearly not homologous between major taxonomic groups that possess the cusp (e.g. Simpson 1936; Van Valen 1994; Sánchez Villagra & Kay 1996).

Among metatherians, paucituberculatans, polydolopimorphians, peramelemorphians, and diprotodont marsupials have an enlarged distolingual cusp. The paucituberculatan cusp is considered homologous to the metaconule (Abello 2007; Goin *et al.* 2007; contra Marshall 1980) and also in Australian forms (e.g. Tedford & Woodburne 1987, 1998; contra Osborn 1907; Sánchez Villagra & Kay 1996; see below). Some diprotodonts (e.g. Pseudocheiridae, Phascolarctidae, Ectopodontidae, among others) have, in addition, a neomorph cusp at the lingual base of the metacone, the neometaconule (Woodburne *et al.* 1987a, b). Consider-

ing the latter structure, accessory distolingual cusps among metatherians derive from different parts of the tooth and are not homologous among the lineages. Because of its uncertain origin, Sánchez Villagra & Kay (1996) suggested that the distolingual cusp be named based on its topography and function, in spite of its origin (see Tedford & Woodburne 1998 for an alternative view). Additionally, occlusion of the metaconule finishes at the end of Phase I of mastication, when the cusp is located between the hypoconid of one molar and the protoconid of the next molar of the tooth row. The hypocone, in turn, occludes with the lingual side of the trigonid basin during Phase I and continues in active occlusion during Phase II of mastication (Sánchez Villagra & Kay 1996).

The enlarged distolingual cusp of *Fieratherium* is not derived from the metaconule. If the swelling of the postprotoconal crest is the vestige of the metaconule, as we suggest in the description, then the distolingual cusp is derived from another tooth structure. The distolingual cusp of *Fieratherium* has no morphological relation with the occlusal surface of the protocone, and is located at the base of the crown, arguing in favour of an origin from the postprotoconal cingulum. This is present in some basal stem marsupials (e.g. *Turgidodon*; Johanson 1996) and in some Paleocene taxa, such as *Protodidelphis* and *Guggenheimia* from Las Flores Formation (Goin *et al*. 1997, personal observations) which represent the sister taxa of *Fieratherium* and paucituberculatans (Fig. 4). Moreover, the distolingual cusp in *Fieratherium* does not occlude with any structure of the lower molars. In occlusion (Fig. 5), it is located between successive lower molars, and mostly at the lingual side of the talonid of the opposite molar. Hence, the distolingual cusp of *Fieratherium* has a different function to that of other metatherians.

In summary, the distolingual cusp of *Fieratherium* undoubtedly represents a novelty for Metatheria. A similar structure, with a homology traceable to the postprotoconal cingulum, has not been previously recognized for any South American taxon (including the well-known Itaboraí



**Figure 5.** Superposition of upper (black line) and lower (grey line) teeth of *Fieratherium sorex* gen. et sp. nov. The distolingual cusp (hypocone) of the upper molar fits lingual to the talonid of the opposite lower tooth.

or Las Flores fossil assemblages with basal stem marsupials; Paula Couto 1952; Marshall 1987; Goin *et al.* 1997; personal observations). *Fieratherium* is the only metatherian in which the postprotoconal cingulum is enlarged to form a cusp, such as the hypocone in some placental mammals.

The presence of an enlarge distolingual cusp in mammals is associated with herbivory, because it allows the processing of vegetable matter. The radiation of mammals with this feature has been dated approximately synchronously in all continents by the Middle Eocene, and is perhaps correlated with the floral turnover associated with cooling and drying climatic trends (Hunter & Jernvall 1995). In *Fieratherium*, even if its distolingual cusp appears to be a post Eocene–Oligocene innovation, it cannot be related in functional terms with herbivory but with an insectivorous diet. The morphology of *Fieraherium* agrees with the taxonomic and ecological diversification that followed the global cooling event of the earliest Oligocene, recognized in Patagonia as the 'Patagonian Hinge' (Goin *et al.* 2010), based particularly on the analysis of the metatherian associations. This evolutionary event encompasses the major taxonomic and ecologic shift in the land-mammal faunas of southern South America at the Eocene–Oligocene boundary (Goin *et al.* 2010). The record of *Fieratherium* in the Oligocene (Deseadan SALMA) of Quebrada Fiera is consistent with this scenario.

## Tooth eruption sequence

The generalized condition among marsupials and basal stem taxa, such as *Alphadon*, *Pucadelphys* and sparassodonts, is that the P3/p3 erupts and emerges at about the same time as the M4/m4 (Cifelli *et al.* 1996; Cifelli & Muizon 1998; van Nievelt & Smith 2005; Astúa & Leiner 2008; Forasiepi 2009). Among South American marsupials, the living Paucituberculata (i.e. Caenolestidae) is peculiar in this regard. The deciduous premolar is rudimentary and non-functional in occlusion and the P3/p3 significantly delays its eruption until long after the eruption of the last molar (i.e. the m4 has almost finished its eruption, whereas the p3 has not begun to erupt; Luckett & Hong 2000). With regard to fossil taxa, in *Stilotherium* there is probably a delay in the eruption of the permanent premolar. As exemplified by specimen MACN-A 8464 of *Stilotherium*, the four lower molars are already erupted while the p3 did not completely finished the process (Luckett & Hong 2000, fig. 12). However, the molar cusps have almost no wear, suggesting that the delay in the eruption of p3 was possibly not as long as in caenolestids.

In *Fieratherium*, the deciduous premolar is attached in the dentary and maxilla, while the M3 and m3 (according to the crypt) are partially erupted (Fig. 2B). If the accumulation of tissue below the DP3 represents the primordial P3 (see comments in the description above), then the eruption of P3 would be after the complete eruption of M3, and

then probably about the same time as the last molar, if this tooth was present as in the crown group marsupials and close relatives. With regards to morphology, the DP3/dp3 of *Fieratherium* is proportionally smaller than the deciduous teeth of most didelphids (Online Supplementary Material Appendix 1), and it is reduced and vestigial in living paucituberculatans (Luckett & Hong 2000). No deciduous premolar has been reported in fossil paucituberculatans comparable to the morphology of *Fieratherium*. Because *Fieratherium* occupies a phylogenetic position basal to paucituberculatans (Fig. 4), it would be likely that the reduction in the size of the deciduous teeth of *Fieratherium* represents the plesiomorphic condition compared with the vestigial DP3/dp3 of caenolestids.

Finally, it is worth mentioning that *Fieratherium* seems to have a peculiar molar eruption rate. In most living marsupials and basal stem taxa (e.g. *Alphadon*, *Pucadelphys* and sparassodonts), when the third molar has more than half of the crown erupted (as in the case of the specimen MCNAM-PV 3958 of *Fieratherium*), the first and the second molars are completely erupted with the crowns at the level of the alveolar line and the alveoli closed around the roots (e.g. Cifelli & Muizon 1998; Astúa & Leiner 2008; Forasiepi 2009). In *Fieratherium*, the molars seem to erupt at about the same time: by the time the third molar has more than half of the crown exposed, the first and second molars are below the alveolar line and the crypts are still opened (Fig. 3B). This pattern could be explained by a heterochronic shift in which either the posterior molars accelerate or the anterior molars retard the eruption with regard to the ancestor. Because *Fieratherium* is only known by an incomplete skull and dentary of a single specimen, it is not possible to support any of these possible causes.

## Morphological convergences with placental mammals

Distinct features classify *Fieratherium* as a metatherian: one single deciduous tooth, a staggered second lower incisor (homologous with i3; Hershkovitz 1982), and a broad stylar shelf with tall stylar cusps (Kielan-Jaworowska *et al*. 2004). In addition, the presence of three premolars is consistent with *Fieratherium* being a metatherian.

The dental morphology of *Fieratherium* argues in favour of an insectivoran diet. The cusps are pointed, the crests are sharp, and there are clear differences in height between trigon/trigonid and talon/talonid. The power stroke is vertical and steep, associated with a carnivorous diet (Butler 2001). In addition, the dentition of *Fieratherium* strongly resembles insectivorous placentals (i.e. eulipotyphlans) in several features suggesting strong convergences. The lower teeth have a large and procumbent first lower incisor (e.g. soricids such as *Crocidura* and *Blarina*, erinaceids such as *Erinaceus*, talpids, and fossil relatives such as *Apternodus*), the anterior premolars are reduced in size, with some

single rooted elements (e.g. antemolars of erinaceids such as *Erinaceus*), and the hypoconulid is reduced or absent (e.g. erinaceids such as *Erinaceus*, and soricids such as *Sorex*) (Repenning 1967; Asher *et al*. 2002). The upper molars have an enlarged distolingual cusp in the posterior base of the protocone (hypocone), as in most eulipotyphlans and fossil relatives such as *Micropternodus*, *Leptacodon*, insectivoran afroriscidans (e.g. Russell 1960; Repenning 1967; McKenna 1968; Asher *et al*. 2002), and the paraconid is markedly smaller than the metaconid (e.g. as in some erinaceids such as *Echinosorex* and *Erinaceus*, some soricids as *Crocidura* and *Blarina*, and *Nesophontes*; Asher *et al*. 2002).

In addition, the morphology of the DP3 of *Fieratherium* resembles the P4 of eulipotyphlans. There is one principal tall cusp (thought to be formed by paracone and metacone appresed to each other in *Fieratherium* and by the paracone in eulipotyphlans), an acute parastyle (e.g. in some soricids such as *Crocidura* and *Blarina*, *Nesophontes*, and fossil relatives such as *Micropternodus borealis*, *Apternodus gregori* and *A. major,* the parastyle projects at a sharp angle from the anterior margin of the tooth; Russell 1960, Asher *et al*. 2002), and a low, lingually projected protocone. The dp3 shares at least with the p4 of some soricids (e.g. *Sorex* and *Crocidura*) the reduction of the paraconid and a relatively large protoconid (Repenning 1967).

Placental 'insectivorans' were absent from South American ecosystems during most of the Cenozoic. Despite some early work arguing in favour of 'insectivorans' (e.g. Ameghino 1894), their presence was later disproved. There are no eulipotyphlans currently in South America, with the exception of the soricid shrew, *Cryptotis*, which is an element of the most recent migration into the continent reaching only the northern tip of the continent (Woodman & Péfaur 2007). The Paucituberculata were up to now the only clade with shrew-like morphological features. *Fieratherium* represents another lineage of shrew-like marsupials, with even stronger 'insectivoran' convergences in the dentition. Both groups would have occupied an ecological role similar to the eulipotyphlans during the Cenozoic in South America, with the paucituberculatans more diverse and abundant.

## *Fieratherium* and the South American biogeographical context

The Late Oligocene Deseadan faunal associations are represented by several well-known and classical localities in Patagonia (e.g. Gran Barranca, Cabeza Blanca, Scarrit Pocket, La Flecha, Chubut and Santa Cruz provinces; Loomis 1914; Chafee 1952; Madden *et al*. 2010). Other Deseadan mammalian associations are known from the Bolivian localities of Salla and Lacayani (Hoffstetter *et al*. 1971; Vucetich 1989; Kay *et al*. 1998), the Fray Bentos Formation in Uruguay and Argentina (Mones & Ubilla 1978; Ubilla *et al*. 1994; Bond *et al*. 1998), the Moquegua

Formation in Peru (Shockey *et al*. 2006), the Tremembé Formation in Brazil (Soria & Alvarenga 1989; Berqvist & Ribeiro 1998; Vucetich & Ribeiro 2003), and the Río Maipo-Abanico Formation in Chile (Croft *et al*. 2008). Among them, the Patagonian and Bolivian associations are the best known and show significant differences. Quebrada Fiera is outside these localities and supports the idea of a mixed faunal association. It includes representatives from the southern and northern associations and exclusive species as a result of the intermediate latitudinal position of Mendoza in the palaeogeographical context of the South American Oligocene (Cerdeño 2011). Together with *Mendozahippus* (Notoungulata, Notohippidae; Cerdeño & Vera 2010), *Fieratherium* is also unique to the Quebrada Fiera association.

Recent biogeographical reviews conducted by Morrone (2002, 2004a, 2004b, 2006; see also Goin *et al*. forthcoming) stressed the dual nature of South American biogeography. The southernmost tip of the continent (Patagonia and the Southern Andes) was regarded as belonging to a distinct region (the Andean Region) of the Austral Kingdom. In turn, the rest of South America was included within the Neotropical Region of the Holotropical Kingdom. Much of our knowledge of mammalian evolution in South America, and especially of its Palaeogene history, comes from evidence from the Andean Region. The Paleocene-Eocene history of the intertropical regions of this continent is still largely unknown. The Quebrada Fiera locality in southern Mendoza Province lies near the boundary between the Andean and Neotropical regions. It is possible to assume that the origin and radiation of the *Fieratherium* lineage occurred north of Patagonia, and that its occurrence in Mendoza Province by Deseadan times corresponds to a relatively marginal area within the Neotropical realm. We suggest that continued prospecting in low latitude Palaeogene localities, such as those of Contamana (mid- to Late Eocene; Antoine *et al*. 2011) or Santa Rosa (?Late Eocene–?Early Oligocene; Goin & Candela 2004), in the Peruvian Amazonia, will offer better clues on the evolution of *Fieratherium* and the Paucituberculata clade.

## Conclusions

A new metatherian, *Fieratherium sorex* gen. et sp. nov., is analysed and described. The specimen comes from the Quebrada Fiera locality, Mendoza Province, Argentina, from Late Oligocene deposits of Deseadan age. *Fieratherium* has a unique combination of features that clearly differentiates it from other metatherians hitherto recovered. The dentition of *Fieratherium* is highly convergent with 'insectivorans', including by the presence of a distolingual cusp (hypocone) derived from a posterobasal cingulum, unrecorded in any marsupial or basal

stem relative. The phylogenetic analysis suggests that *Fieratherium* is the sister-group of the Paucituberculata. Its occurrence in the Late Oligocene of Mendoza Province suggests that the lineage to which it belongs probably has its origin in more typical Neotropical regions.

## Acknowledgements

## Supplemental material

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