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# The bizarre 'metatherians' *Groeberia* and *Patagonia*, late surviving members of gondwanatherian mammals

Nicolás R. Chimento[a]*, Federico L. Agnolin[a,b] and Fernando E. Novas[a]

[a]*Laboratorio de Anatomía Comparada y Evolución de los Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia',
Buenos Aires, Argentina;* [b]*Fundación de Historia Natural 'Félix de Azara', Departamento de Ciencias Naturales y Antropología,
CEBBAD – Universidad Maimónides, Buenos Aires, Argentina*

Cenozoic mammalian faunas from South America contrast with those of the other continents by the great diversification of metatherian mammals. Among the later, a wide range of morphological disparity have been reported, and several bizarre mammals have been assigned to such clade, based mainly on biogeographical grounds. Outstanding examples of bizarre mammals referred to as Metatheria are the Eocene *Groeberia* and the Miocene *Patagonia*. Recent discoveries indicate that South America possessed a more diverse faunal composition than previously thought, and it became evident that many Mesozoic holdovers (e.g. australosphenidans, gondwanatherians and dryolestoids) surpassed the K/T boundary, thus forming part of the Cenozoic faunas. The Cenozoic taxa *Patagonia* and *Groeberia* exhibit several similarities with the Gonwanatheria, including rodent-like jaws with enlarged incisives, molariform cheek-teeth, anteriorly extended masseteric fossa and palinal mastication among other features. The inclusion of Gondwanatheria, *Patagonia* and *Groeberia* within an abarcative phylogenetic analysis resulted in close phylogenetic relationships among these taxa. Such hypothesis indicates that Cretaceous relics in the Cenozoic of South America were more diversified than previously thought.

**Keywords:** *Groeberia*; *Patagonia*; Gondwanatheria; South America

## Introduction

Cenozoic mammalian faunas from South America contrast with those from the Northern Hemisphere by the great diversification of metatherians (Sánchez-Villagra 2013). More than 100 metatherian species have been described from this continent, ranging from ossifrage bear-sized borhyaenoids to minute omnivorous paucituberculates (Patterson and Pascual 1972). Within this range of morphological disparity have been historically included some highly modified mammalian taxa which do not comfortably fit into any of the previously known marsupial clades. Among these bizarre taxa are *Groeberia* and *Patagonia*, documented in Eocene and Miocene beds of Argentina, respectively. Available fossil evidence for these forms is currently fragmentary, and consists of partial skulls and jaws with teeth. *Groeberia* and *Patagonia* were small sized, short-faced mammals, with rodent-like jaws.

*Groeberia* is represented by two species: *Groeberia minoprioi* Patterson, 1952 and *Groeberia pattersoni* Simpson, 1970, both from the Middle Eocene Divisadero Largo Formation of Mendoza province, western Argentina (López 2010). *Groeberia* was originally described by Patterson (1952) who interpreted this taxon as belonging to caenolestoid metatherians after comparing it with other taxa, including some rodent-like prosimians. Later, Clemens and Marshall (1976) and Flynn and Wyss

(1999) thought *Groeberia* as phylogenetically closer to diprotodont marsupials, particularly to the South American argyrolagoids. However, Simpson (1970a, 1970b) published new materials and novel data on *Argyrolagus* and *Groeberia*, concluding what both taxa show remarkable differences, and thus placed the Groeberidae as Marsupialia *incertae sedis*. More recently, Pascual et al. (1994), based on a more complete specimen, concluded that *Groeberia* may be included within Metatheria, but its aberrant nature warranted the erection of an order for its own, Groeberida. In contrast to previous authors, Pascual et al. (1994) did not recognise special relationships of the Order Groeberida with any metatherian clade, but considered them as Metatheria *incertae sedis*, in agreement with Simpson's (1970b) proposal. Moreover, some authors questioned the metatherian affinities of *Groeberia* (Reig 1981), emphasising not only on its aberrant anatomy, but also on the absence of clear marsupial-like features. In particular, McKenna (1980) expressed that the referral of *Groeberia* to the Metatheria constitutes 'an act of faith' based on its geography provenance and stratigraphic position, rather than on morphological attributes.

*Patagonia peregrina* Pascual & Carlini, 1987 is known for its lower mandibles and isolated upper and lower teeth documented in beds of the Lower Miocene Sarmiento

*Corresponding author. Email: nicochimento@hotmail.com

Formation (Trelew Member) of Chubut province, southern Argentina (Pascual and Carlini 1987; Goin and Abello 2013). It was originally described by Pascual and Carlini (1987), and interpreted as a metatherian on the basis of a combination of negative and positive evidence. As recognised by Pascual and Carlini (1987), *Patagonia* exhibits many peculiarities that are 'differently developed or completely absent' in other marsupials, including extremely short and deep mandible, unfused subvertical dentary symphysis, dorsally positioned masseteric fossa, rodent-like rootless incisors that extend lingually along ventral border of dentary up to the level of m3, and rectangular and continuously growing cheek-teeth arranged in a close sequence. The striking anatomical and functional similarities of *Patagonia* with the extant South American rodent *Ctenomys* lead Pascual and Carlini (1987) to call *Patagonia* as the 'marsupial tuco-tuco'. As a means to emphasise the unique combination of characters, Pascual and Carlini (1987) coined the monotypic ranks Patagonioidea and Patagoniidae. Although some authors interpreted *Patagonia* as allied with the metatherian clade Argyrolagoidea (e.g. von Koenigswald and Pascual 1990; Flynn and Wyss 1999; Goin and Abello 2013), no synapomorphies have been cited in support for this phylogenetic interpretation. Interestingly, although Pascual and Carlini (1987) included *Patagonia* within Metatheria, they cautiously considered that the genus could also be regarded as an extinct South American representative of the eutherian–marsupial dichotomy (Pascual and Carlini 1987).

It is worth mentioning that *Groeberia* and *Patagonia* were originally described and interpreted in the context of the South American fossil record for metatherians and eutherians. However, discoveries produced in the last years demonstrated that such Tertiary faunas were much more diverse than previously thought. In fact, it became evident that many Mesozoic holdovers (e.g. australosphenidans, gondwanatherians and dryolestoids) surpassed the K/T boundary, surviving well into the Cenozoic (Scillato-Yané and Pascual 1985; Pascual et al. 1992; Bonaparte et al. 1993; Gelfo and Pascual 2001; Goin et al. 2006, 2012; Chimento et al. 2012; Rougier et al. 2012).

Perhaps the most striking example of a Late Mesozoic mammalian clade which attained a wide palaeobiogeographical distribution is the Gondwanatheria (Wilson et al. 2007). Gondwanatherians are currently represented by more than a half dozen genera of rodent-like mammals documented in Late Cretaceous of Patagonia, India, Madagascar as well as in the Early Tertiary of Patagonia and Antarctica (Bonaparte et al. 1993; Krause and Bonaparte 1993; Goin et al. 2004, 2006, 2012; Gurovich 2005). Most gondwanatherians are characterised by rodent-like lower jaws with enlarged and open rooted incisors, and hypsodont musticusped molariform cheek-

teeth (Krause and Bonaparte 1993). Interestingly enough, the rodent-like jaws, with enlarged incisives, and molariform cheek-teeth of gondwanatherians recall the condition of the enigmatic mammals *Groeberia* and *Patagonia*. In order to explore their possible phylogenetic relationships, we review the anatomical characteristics supporting their inclusion into Metatheria and Marsupialia, as well as a close inspection of the dental and cranial similarities shared with gondwanatherians.

## Materials and methods
### *Reviewed material*
First hand studies specimens are *G. minoprioi* (MMP, 738, holotype; MLP 85-IX-24-1), *G. pattersoni* (MLP 68-VI-27-1, holotype) and *P. peregrina* (MACN-CH-869, holotype).

### *Systematic terminology*
Gondwanatheria is defined as the clade composed of *Ferugliotherium*, *Sudamerica*, its common ancestor, and all of its descendants. Within this clade we recognise the basal ferugliotheriids *Ferugliotherium windhauseni* Bonaparte, 1986b, and *Trapalcotherium matuastensis* Rougier, Chornogubsky, Casadio, Arango & Giallombardo, 2009, *Greniodon sylvaticus* Goin, Tejedor, Chornogubsky, López, Gelfo, Bond, Woodburne, Gurovich & Reguero, 2012, and the derived clade Sudamericidae. The Sudamericidae includes all taxa more nearly related to *Sudamerica* than with *Ferugliotherium* or *Trapalcotherium*. Among sudamericids, different authors have recognised the following taxa: *Sudamerica ameghinoi* Scillato-Yané & Pascual, 1984, *Gondwanatherium patagonicum* Bonaparte, 1986a, *Lavanify miolaka* Krause, Prasad, von Koenigswald, Sahni & Grine, 1997 and *Bharattherium bonapartei* Prasad, Verma, Sahni, Krause, Khosla & Parmar, 2007.

*B. bonapartei* is here considered as a senior synonym of *Dakshina jederi*, following the arguments expressed by Verma et al. (2012). In fact, *B. bonapartei* Prasad et al. (1 March 2007) has priority on *D. jederi* Wilson, Das Sarma & Anantharaman (1 June 2007). Besides, we follow the convincing arguments pointed out by Gurovich and Beck (2009) interpreting *Argentodites coloniensis* Kielan-Jaworowska, Ortiz-Jaureguizar, Vieytes, Pascual & Goin (2007) as junior synonym of *F. windhauseni* Bonaparte, 1986b.

Some authors considered gondwanatherians as basal allotherians (i.e. Pascual and Ortiz-Jaureguizar 2007), or even as Mammalia *incertae sedis* (Pascual et al. 1999; Kielan-Jaworowska et al. 2004; Wilson et al. 2007). Nevertheless, until more exhaustive studies become available, we accept the most recently published review
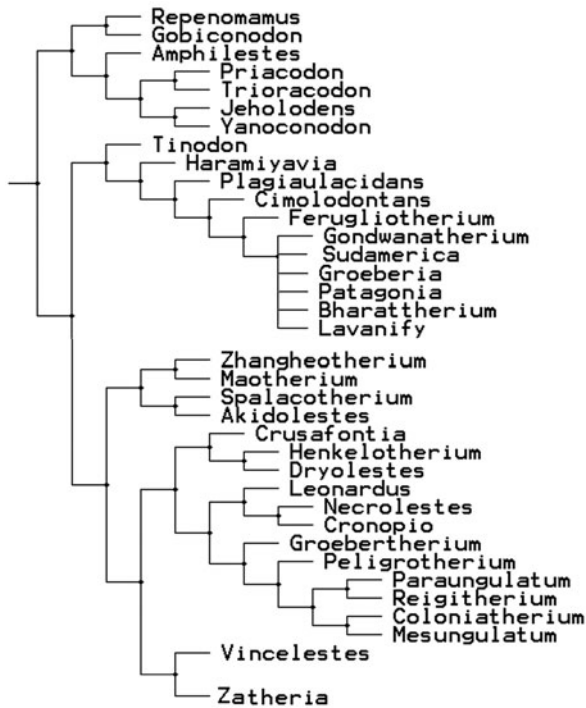
Figure 1.   Cladogram depicting the phylogenetic relationships of *Groeberia* and *Patagonia* within Mammalia.

### Cladistic analysis

We employ the data-set analysed by Chimento et al. (2012) which is a modified version from that of Luo et al. (2007). Aside from characters 1 through 458 from Chimento et al. (2012), we add here characters 459 through 481 taken from different sources (e.g. Rougier et al. 2007; Gurovich and Beck 2009). Present data matrix is also novel in the inclusion of the gondwanatherians *S. ameghinoi* Scillato-Yané and Pascual, 1985, *G. patagonicum* Bonaparte, 1986a, *F. windhauseni* Bonaparte, 1986b, *L. miolaka* Krause et al. 1997 and *B. bonapartei* Prasad et al., 2007. We employ most of the codifications and concepts about gondwanatherian mammals proposed by Gurovich and Beck (2009). Finally, we included the argyrolagids *Proargyrolagus*, *Hondalagus* and *Argyrolagus*, because they belong to a metatherian group of controversial relationships which have frequently been linked to *Patagonia* and *Groeberia* (Flynn and Wyss 1999; Goin and Abello 2013).

The phylogenetic analysis was carried out using TNT 1.1 (Goloboff et al. 2008). All characters were equally weighted and treated as unordered. Heuristic searches were carried out after 1000 pseudoreplicates of WAG + TBR search strategy, with 10 random addition sequences after each search and 100 trees were saved at each replicate. The phylogenetic analysis resulted in the recovery of 290 most parsimonious trees, of 2453 steps, with a consistency index of 0.26, and a retention index of 0.788 (Figure 1).

### Institutional abbreviations

MACN, Colección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Departamento Científico Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina; MMP, Museo Municipal de Ciencias Naturales 'Galileo Scaglia', Mar del Plata, Argentina.

of the Gondwanatheria by Gurovich and Beck (2009), in which gondwanatherians are considered as multituberculates, as previously proposed by Krause and Bonaparte (1993), Krause et al. (1992), Krause and Bonaparte (1993), Kielan-Jaworowska and Bonaparte (1996) and Gurovich (2005, 2008).

### Dental terminology

We follow the concepts of von Koenigswald et al. (1999) and Gurovich (2005). Cheek-teeth of sudamericids and *Patagonia* are here referred as to molariforms (MR/mr) as their hypsodonty makes it difficult to distinguish premolars from molars (Gurovich 2008). However, in basal Gondwanatheria (e.g. *Ferugliotherium*, *Trapalcotherium*) and *Groeberia* only the incisors were hypsodont while post-incisives were brachydont. Following Van Valen (1960), hypsodonty is defined as teeth higher than long. Besides, the term protohypsodonty is applied for rooted teeth, and euhypsodonty for rootless teeth (*sensu* Mones 1982). Regarding mastication, in order to identify palinal jaw movement, we follow von Koenigswald et al. (1999) in distinguishing the trailing from the leading occlusal edges. Palinal jaw movement is identified following von Koenigswald et al.'s (1999) criteria based on topographical distinctions of the trailing and leading occlusal edges.

### Descriptive and comparative anatomy

*Groeberia* and *Patagonia* have been described in detail in previous studies (e.g. Pascual and Carlini 1987; Pascual et al. 1994), so, this section will address on the reinterpretation of some particular anatomical traits of these taxa.

### Dentition of Groeberia

The most recent interpretation of the dental formula of *Groeberia* was performed by Pascual et al. (1994). These authors indicated two different ways in which the tooth number of *Groeberia* may be interpreted: either as I 2/1, C 1/1, P 3/1, M 4/4, or most probably as I 2/1, C 1/0, P 3/2,
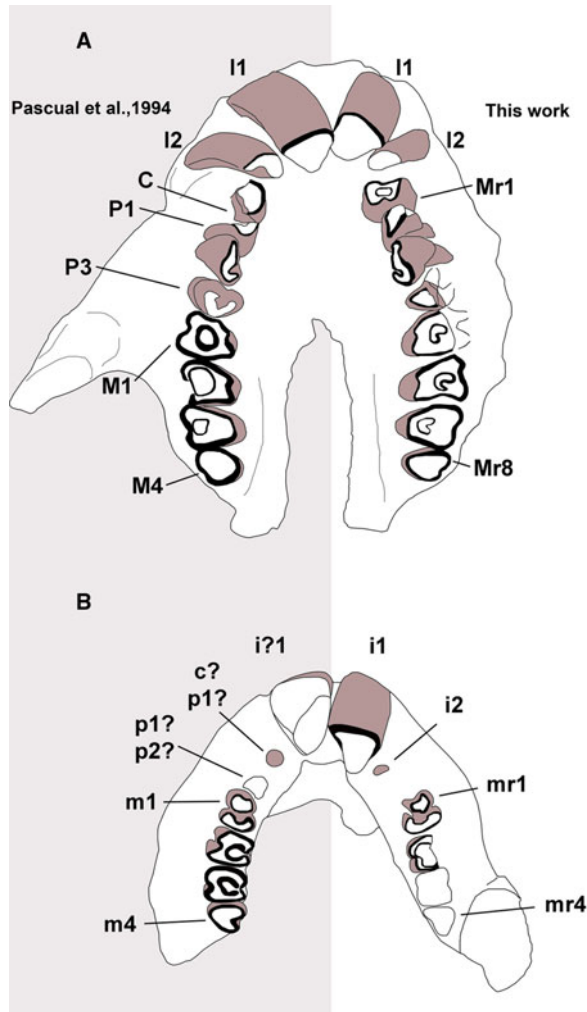
Figure 2.    (Colour online) Dental formula of *G. minoprioi*. (A) Palatal view of upper dentition and (B) occlusal view of lower dentition. At left interpretation made by Pascual et al. (1994), at right the interpretation of this paper.

M 4/4. Pascual and collaborators based their assumptions in the most complete and better preserved specimen of *G. minoprioi* (MLP 85-IX-24-1), which exhibits a complete dental formula. The difference between both formulae mainly relays on how the first lower post-incisive tooth is interpreted. Pascual et al. (1994) referred it as a possible canine or, less probably, as the first premolar. Such dental element of *Groeberia* consists of a single-cusped and single-rooted element, which shows a subcircular cross-section, and lacks a shearing surface. It is separated from the cheek-teeth by a small diastema and is nearly appressed to the anterior incisives. We believe that the location of this tooth may be better interpreted as a second incisive (Figure 2), in agreement with Marshall et al. (1989).

Pascual et al. (1994; Figure 1C) described another single-rooted and single-cusped element on the left
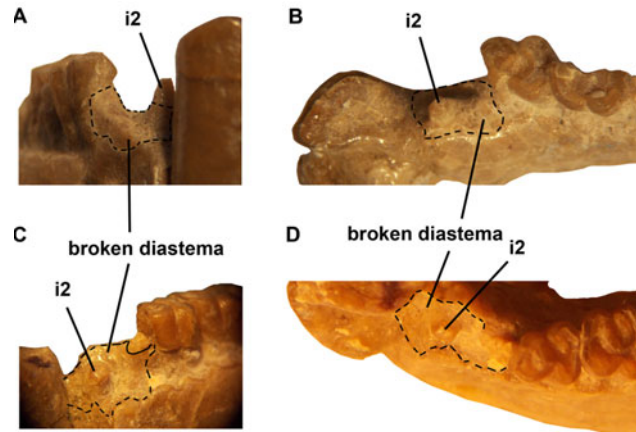


Figure 3.    (Colour online) Dentary of *G. minoprioi* (MLP 85-IX-24-1). (A and B) Detail of anterior portion of right mandible in (A) anterolateral and (B) occlusal views and (C and D) detail of anterior portion of left mandible in (C) anterolateral and (D) occlusal views.

mandibular ramus. It consists of a fragmentary first cheek-tooth, which these authors interpreted as the first or second lower premolar. However, close inspection of this element reveals that it is not a tooth, but a scrap of bone removed from the posterior portion of the shelf-like post-incisive diastema. This new interpretation is supported by the absence of dental tissues (e.g. dentine, enamel), as well as by the absence of alveolus or roots. Moreover, the post-incisive diastema on the right jaw is devoid of a tooth equivalent in position to the element originally described by Pascual et al. as a second lower premolar (Figure 3). In sum, the lower dental formula of specimen MLP 85-IX-24-1 of *G. minoprioi* is here reinterpreted as having two incisives and four molariforms (Figure 2).

In contrast with MLP 85-IX-24-1, the holotype of *G. minoprioi* (MMP 738) lacks any tooth between the first incisors and the cheek-teeth series, and its dental formula was originally interpreted as having one lower incisor and four lower molariforms (Patterson 1952). This may suggest that presence or absence of a second lower incisor may be variable within the species. This variation may reflect ontogenetic or sexual dimorphism, but this hypothesis requires to be tested on the basis of new specimens (Figure 4).

Regarding the upper dental formula of *G. minoprioi*, which is only known in specimen MLP 85-IX-24-1, Pascual et al. (1994) interpreted the first post-incisive element as a canine. It is a mesiodistally compressed tooth, subrectangular in cross-section, which shows a flat occlusal surface with a small central enamel islet. This morphology contrasts with the canine of virtually all of the remaining mammals in which the canine is acute, single-cusped and lacking of enamel islets (Figure 5). In addition, the mammalian canine is usually mesiodistally elongate and subcircular to ellipsoidal in crosss-section. Because
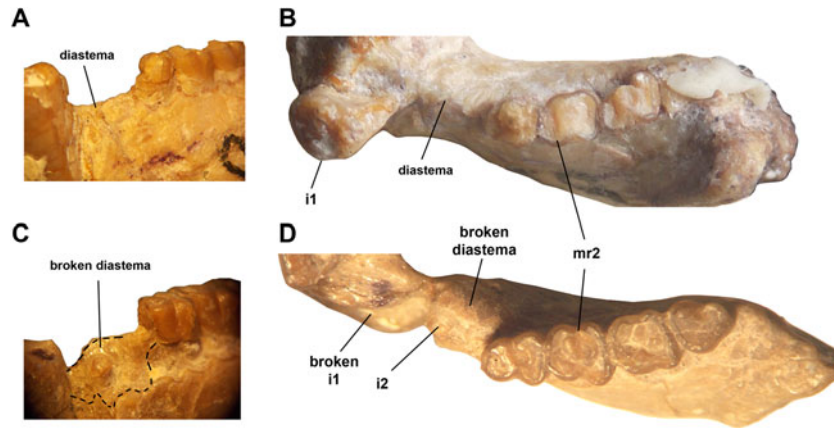
Figure 4.   (Colour online) Dentary of *G. minoprioi*. (A and B) Detail of anterior portion of left mandible of specimen MMP 738 (holotype), in (A) anterolateral and (B) occlusal views; (C and D) detail of anterior portion of left mandible of specimen MLP 85-IX-24-1 in (C) anterolateral and (D) occlusal views.

the putative upper canine of *Groeberia* sharply differs from the normal canine design, and contrarily it exhibits traits of a molariform tooth, we better interpret this element as the first molariform.

In addition, specimen MLP 85-IX-24-1 shows a small gap between I2 and the first post-incisive tooth. Although poor preservation avoids recognising the premaxillary–maxillary suture, the above-mentioned gap may represent the boundary between these two bones (see Supplementary Figure 1). If this interpretation is correct, the first post-incisive element of *Groeberia* results entirely located on the maxilla, being separated from the I2 by a gap, and in a position immediately contiguous with the molariform series. Such spatial relation reinforces the molariform nature of the first post-incisive element of *Groeberia*. Interestingly, in MLP 85-IX-24-1, the dental piece that we interpret as the first upper molariform (the 'canine', as originally interpreted by Pascual et al. (1994)) differs from more posterior cheek-teeth in being transversely expanded. This contrasts with more posterior elements, which are subrectangular and with a mesiodistally elongate main axis. Such differences in tooth shape may suggest that the first post-incisive tooth may represent a
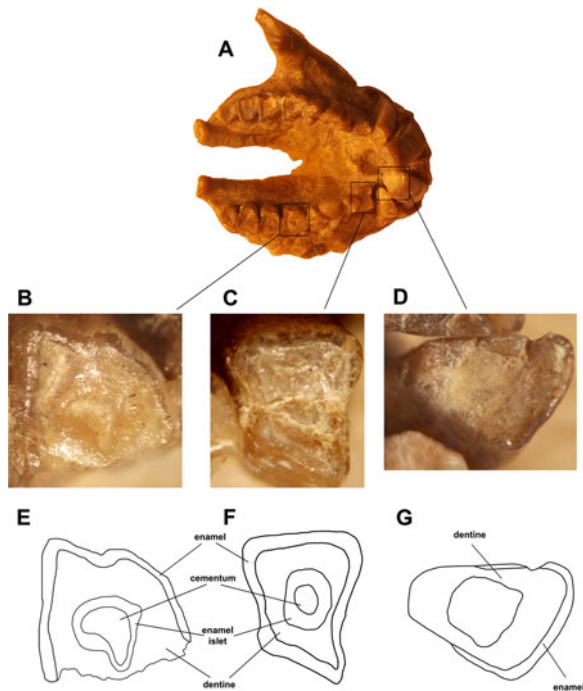


Figure 5.   (Colour online) Upper dentition of *G. minoprioi* (MLP 85-IX-24-1). (A) Complete dental arcade, (B) occlusal view of fifth molariform tooth, (C) occlusal view of first molariform tooth (interpreted as a canine by Pascual et al. (1994)), (D) detail of first incisive crown, (E) sketch of occlusal view of fifth molariform tooth, (F) sketch of occlusal view of first molariform tooth and (G) sketch of first incisive crown.
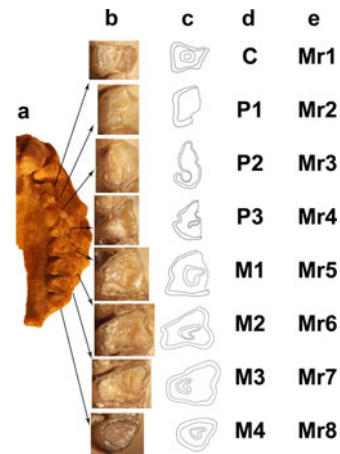


Figure 6.   (Colour online) Right upper dentition of *G. minoprioi* (MLP 85-IX-24-1). (A) General view, (B) detail of each tooth crown, (C) sketch of teeth crowns, (D) tooth identity as interpreted by Pascual et al. (1994) and (E) tooth identity as interpreted in this paper.
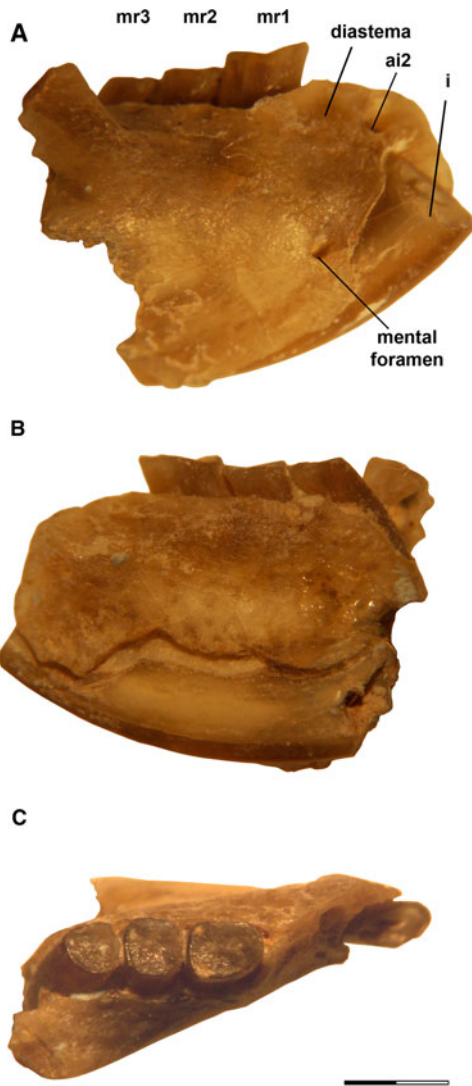
Figure 7.  (Colour online) Right lower jaw of *P. peregrina* (MACN-CH 869, holotype) in lateral (A), medial (B) and occlusal (C) views. Scale bar: 2 mm.

premolar. Additional evidence, however, is required to test this possibility. In sum, the dental formula of *Groeberia* is here reinterpreted as i 2/2, mr 8/4 (Figure 6).

### Dentition of Patagonia

Similar to *Groeberia*, the dental formula of *Patagonia* is not free of uncertainties. Having this problem in mind, Pascual and Carlini (1987) determined the dental formula of *Patagonia* on the basis of comparisons with several extinct metatherian clades. Pascual and Carlini (1987) interpreted the lower dental formula of *Patagonia* as i1, c1, p0, m3. These authors considered that the incisive is posteriorly bordered by a very shallow and conical alveolus set on an oblique angle. Because this alveolus resembles that of the procumbent canine of Epidolopidae

and Prepidolopidae metatherians (Pascual 1980; Pascual and Carlini 1987), Pascual and Carlini (1987) interpreted for *Patagonia* the presence of a reduced canine. More recently, Goin and Abello (2013) considered this element as a canine with doubts, although recognised it as strikingly 'incisiviform'. Sánchez-Villagra et al. (2000) coded the presence of only one lower incisor for *Patagonia* (character 17: state 2), following the dental formula 1.1.0.3 reported by Pascual and Carlini (1987) but questioned the presence of a lower canine adding 'the study of more complete material might modify this interpretation (so the dental formula would include 2 incisors and no canine)'. Thus, Sánchez-Villagra et al. (2000) proposed that *Patagonia* probably had two incisors, and the presumed canine may correspond, to an i2. The element resembles an incisor in being highly adpressed to the anterior incisive and is separated from remaining elements by a diastema. If the latter interpretation is proved, then the morphology and number of incisors and the absence of canines in *Patagonia* result in agreement with that inferred for *Groeberia*.

The three cheek-teeth of *Patagonia* are rectangular in cross-section, and although clear homologies of these teeth cannot be determined with certainty, Pascual and Carlini (1987) identified them as molars. We opt to refer these teeth as molariforms because their morphology and replacement are unknown and preclude clear identification of premolars or molars (Figure 7).

### Review of the anatomical evidence supporting the referral of Groeberia to Metatheria

The phylogenetic position of *Groeberia* remained uncertain since its original description by Patterson (1952). This author assigned *Groeberia* to Marsupialia on the basis of a medially inflected angular process of the mandible, after comparing with rodents, prosimians and other taxa. He also referred *Groeberia* to the Caenolestoidea with doubts, but this hypothesis was heavily criticised by Simpson (1970b), who dismissed the caenolestoid affinities of *Groeberia*. Simpson (1970b) agreed with Patterson (1952) in the uniqueness of *Groeberia*, however, he regarded the Groeberidae as Marsupialia *incertae sedis* (we must emphasise here that the Gondwanatheria was not known at that time; see Pascual et al. 1994). Simpson (1970b) concluded that Patterson based his proposal mostly on negative evidence and on the presence of an inflected angle of the mandible. Simpson (1970b) himself expressed that an inflected mandibular angle was not a conclusive feature in support of the marsupial affinities of *Groeberia*. Notwithstanding, Simpson maintained the referral of *Groeberia* to the Marsupialia because this genus is devoid of features that would make reference to the Marsupialia impossible or
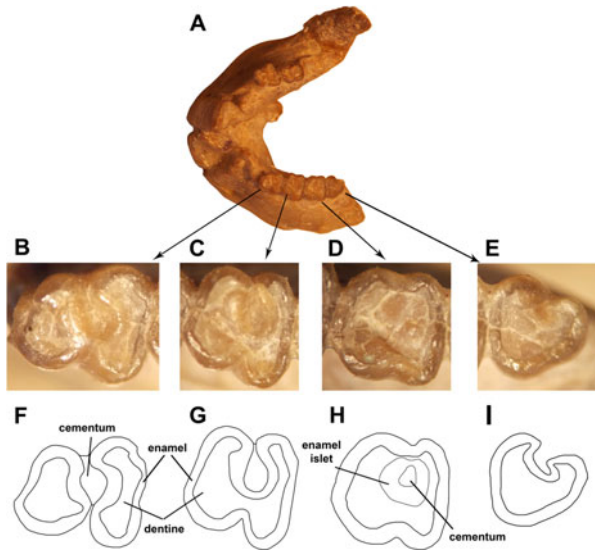
Figure 8. (Colour online) Lower dentition of *G. minoprioi* (MLP 85-IX-24-1). (A) Complete lower dentition in occlusal view, (B) first molariform in occlusal view, (C) second molariform in occlusal view, (D) third molariform in occlusal view, (E) fourth molariform in occlusal view, (F) sketch of first molariform in occlusal view, (G) sketch of second molariform in occlusal view, (H) sketch of third molariform in occlusal view and (I) sketch of fourth molariform in occlusal view.

highly improbable. In defence of his argument, Simpson excluded placental affinities for *Groeberia* because of the absence of possible ancestral placentals in the Cenozoic of South America. Some authors (McKenna 1980; Reig 1981) criticised this hypothesis, because *Groeberia* lacks any clear derived character that may allow including it within Marsupialia and even Metatheria, and they suggested that the advocated metatherian affinities for this taxon were mainly based on biogeographical reasons.

Pascual et al. (1994) referred *Groeberia* to Metatheria and Marsupialia on the basis of some features that these authors interpreted as synapomorphies of these therian clades. They recognised two derived metatherian synapomorphies (i.e. facial opening of the lacrimal canal, and dental formula with P3 M4/4) plus three characters diagnostic of Marsupialia (i.e. lately replaced P3; occurrence of palatal vacuities; and inflected mandibular angle). However, these features deserve the following comments:

(1) Presence of a foramen on the facial process of lacrimal is doubtfully a diagnostic feature of Metatheria + *Groeberia* (contrary to Pascual et al. 1994), because in metatherians and eutherians the presence, location and development of this foramen are highly variable. The lacrimal foramen may be located on the facial process (as it occurs in *Kulbeckia*, *Pucadelphys*, *Asiatherium*, *Maelestes* and *Kennalestes*; Kielan-Jaworowska 1981;

Averianov and Archibald 2003; Wible et al. 2009; Rougier et al. 2012), or within the orbit (as is the case in *Deltatheridium*, *Asioryctes*, *Vincelestes* and Dryolestoidea; Kielan-Jaworowska et al. 2004). Moreover, the facial opening of the lacrimal canal is a very frequent trait in many marsupials, but is also present and variable in several metatherian groups and in the eutherians: in dasyuromorphans (e.g. *Dasyurus*, *Myrmecobius*; NRC personal observation) and paucituberculates (e.g. *Caenolestes*; NRC personal observation) the lacrimal canal lacks a facial exposure, and in didelphids this condition is highly variable among individuals and species, and in several taxa at least two facial foramina are present (e.g. *Monodelphis, Didelphis*; Wible 2003). Within multituberculates the presence of a lacrimal canal is also variable, with specimens lacking this canal, whereas in others it is present and well developed (e.g. *Kryptobaatar*; Wible and Rougier 2000; Kielan-Jaworowska et al. 2004). In addition, in the basalmost living eutherians (i.e. xenarthrans), the rostrum exhibits a large facial exposure (Wible and Gaudin 2004). The presence and degree of exposure of the lacrimal foramen is very variable among mammals and precludes interpreting this feature as an ambiguous characteristic uniting *Groeberia* with metatherians.

(2) Presence of three premolars and four molars has been commonly regarded as a metatherian synapomorphy (Luo et al. 2004). However, as expressed above in this paper, the lower dental formula for *Groeberia* is i2 c0 mr4, a dental pattern that is atypical for metatherians.

(3) Late replacement of P3/p3 is a feature traditionally considered as diagnostic of Marsupialia or Metatheria (Cifelli et al. 1996; Rougier et al. 1998). Pascual et al. (1994) regarded the P3 of *Groeberia* (a tooth here interpreted as the fourth molariform) as recently replaced due to the presence of a poorly developed wear occlusal surface. However, it is worth mentioning that the tooth interpreted by Pascual et al. as P2 (here considered as the third molariform) shows an even less-developed wear occlusal surface, suggesting that this tooth was replaced later than the putative P3. In addition, these teeth may possess different degrees of hypsodonty. Moreover, in MLP 85-IX-24-1 the tooth described by Pascual et al. (1994) as m1 is composed of two reniform columns separated by a transverse groove, indicating that the crown of this tooth was less abraded than other molariform crowns (Figure 8). If this element corresponds to a m1 (as Pascual and coauthors originally thought), then it sharply differs from the

condition seen in metatherians, in which the m1 is the most abraded and larger molariform (in metatherians it is the first cheek-teeth to erupt of the series, and lacks any replacement; Cifelli et al. 1996; Cifelli and de Muizon 1998; Luckett and Hong 2000; van Nievelt & Smith 2005). In sum, evidence at hand argues against a marsupial-like tooth replacement for *Groeberia*.

(4) Pascual et al. (1994) proposed that presence of 'two elongate palatal vacuities, laterally limited by strong, rod-like prominences' may constitute an apomorphy uniting *Groeberia* with marsupials. Although these structures are clearly present in the holotype of *G. pattersoni* as well as in extant and living metatherians (Marshall 1987), their presence is also corroborated in some multituberculates (Kielan-Jaworowska 1971; Rougier et al. 1997). In sum, the presence of palatal vacuities does not constitute an unambiguous apomorphy particularly linking *Groeberia* with metatherians.

(5) *Groeberia* exhibits a strongly inflected angular process of mandible, which is even much more developed than in many marsupials (e.g. Macropodidae, Argyrolagidae; Pascual and Carlini 1987). The angular process has been usually considered as a metatherian synapomorphy (see discussion in Sánchez-Villagra and Smith (1997)) and no known placental has such an extended and upturned flange-like inflection. However, this trait is not unique to metatherians, but constitutes a widespread feature among basal eutherians (e.g. *Gypsonictops*, *Cimolestes*, *Asioryctes*, *Barunlestes*; Lillegraven 1969; Kielan-Jaworowska 1975), australosphenidans (e.g. *Asfaltomylos*; Martin and Rauhut 2005), dryolestoids (e.g. *Cronopio*; Rougier et al. 2011) and basal zatherians (e.g. *Vincelestes*; Bonaparte and Rougier 1987). In addition, and more importantly, a similarly developed inflected ventral margin of the dentary has also been reported for the sudamericid *Sudamerica* (Pascual et al. 1999). In consequence, the presence of an inflected angular process of mandible does not warranty the metatherian affinities for *Groeberia*. In addition, Pascual et al. (1999) reported that the ventromedial border of the dentary forms a sharp and slightly inflected margin, and appears to be different from the more developed inflected angle in *Groeberia*. Therefore, this feature should be analysed in the light of new fossil specimens.

The only numerical phylogenetic analysis regarding the affinities of *Groeberia* within metatherians was carried out by Marshall et al. (1989). These authors proposed that Groeberiidae is the sister group of Argyrolagidae,

sustaining this hypothesis on the basis of eight characters interpreted as derived. Pascual et al. (1994) analysed these characters in detail, and concluded that six of them are partially or completely absent in *Groeberia*, and that the remaining two (i.e. upper incisors gliriform and hypselodont, and first lower incisor with restricted enamel band) were of questionable significance. Furthermore, these authors added other features (first lower incisor with enamel only on ventrolabial surface) that are rather different in argyrolagids and groeberiids. On this basis, Pascual et al. (1994) precluded to assign *Groeberia* to any metatherian subclade and concluded that 'as far as we know, most of the singular features of the Groeberida are unknown among other marsupials and eutherians'. We concur with Pascual et al. (1994) in their criticism to the interpretation of Marshall et al. (1989).

The most recent analysis in which argyrolagoid affinities were proposed for *Groeberia* is that by Flynn and Wyss (1999). They recognised the following four features that are shared by both taxa: I1 recumbent and recurved backward (their character number 21), I1 triangular in cross-section (their character number 23), lower and upper incisors with enamel restricted to anterolabial face (their character number 25) and absence of cristid oblique (their character number 16). Nevertheless, the first three characters are documented not only in *Groeberia* and *Patagonia*, but also in multituberculates and gondwanatherians (Krause and Bonaparte 1993; Pascual et al. 1999; Kielan-Jaworowska et al. 2004; Gurovich and Beck 2009). Moreover, in none of these taxa a clear separation of the talonid and trigonid by a cristid oblique is present. However, such morphology may represent a truly plesiomorphic condition, or alternatively, it may be due to the heavy wear of the crown (a derived feature present in many rodents, marsupials and other taxa). This is in sharp contrast with argyrolagids (including *Klohnia*; Pascual and Carlini 1987; Flynn and Wyss 1999; Zimicz 2011) in which trigonid and talonid are very well developed and separated by a cristid. Aside from these problems with the distribution of characters among mammals, the analysis conducted by Flynn and Wyss (1999) has serious methodological flaws, mainly because these authors restricted their character survey to *Groeberia*, *Patagonia* and to the argyrolagoids, without expliciting outgroups (in other words, the only possible result is that *Groeberia* and *Patagonia* are deeply nested within Argyrolagoidea). In sum, no clear synapomorphies unite *Groeberia* with the Argyrolagoidea marsupials, as previously noted by Simpson (1970a, 1970b) and Pascual et al. (1994).

In conclusion, the supposed metatherian, marsupialian and argyrolagoid affinities of *Groeberia* lack empirical support, and the features cited by previous authors as shared by these groups are here regarded as equivocal or acquired by convergence.

### Review of the anatomical evidence supporting referral of Patagonia *to Metatheria*

Pascual and Carlini ([1987](#)) considered *Patagonia* as a metatherian because of its unique combination of characters, which is unknown among eutherians, and because no features are present in this taxon to preclude its reference to Metatheria (Pascual and Carlini [1987](#)). The only character cited in support of the metatherian affinities of *Patagonia* is the inflected ventral border of the mandible and probably the related inflected angular process (Pascual and Carlini [1987](#)). However, such a feature is widely present among basal mammalian clades (see above). No other unambiguous metatherian synapomorphies have been currently identified in the available specimens of *Patagonia*.

*Patagonia* has been particularly related to the Argyrolagoidea among metatherians (e.g. Pascual and Carlini in von Koenigswald and Pascual [1990](#); Flynn and Wyss [1999](#); Goin et al. [2010](#)), although no unambiguous synapomorphies have been cited in support for such relationships. von Koenigswald and Goin ([2000](#)) recognised the presence of small-sized enamel prisms (< 3 μm) as a derived feature uniting *Patagonia* with argyrolagoids. Nevertheless, small-sized enamel prisms are not uniquely shared by these two taxa, but this condition has also been reported for derived multituberculates and gondwanatherians (Krause and Carlson [1987](#); Krause et al. [1992](#); Krause and Bonaparte [1993](#); Wood and Stern [1997](#)). Gondwanatherians (e.g. *Ferugliotherium*, *Gondwanatherium* and *Sudamerica*) show parameters of enamel microstructure resembling those of *Patagonia*, including low prism diameter (< 4.7 μm) and large prism density (> 39/mm$^2$; Krause et al. [1992](#); von Koenigswald et al. [1999](#)).

Flynn and Wyss ([1999](#)) considered that both *Patagonia* and *Groeberia* were related to argyrolagoids. However, these authors compared both taxa exclusively with argyrolagoids. The list of characters recognised by Flynn and Wyss ([1999](#)) to link *Groeberia*, argyrolagoids and *Patagonia* includes a reduced m1, absence of talonid on cheek-teeth and simplified cheek-teeth (Flynn and Wyss [1999](#)). However, these features are ambiguous: presence of a reduced peg-like first lower molar cannot be checked in *Patagonia* because the reduced tooth anterior to the cheek-teeth appears to be the incisive, rather than a premolar (Sánchez-Villagra et al. [2000](#)). As discussed above, simplified molariforms without signs of talonid are present in allotherians and other basal mammals, in contrast to argyrolagoids, in which the talonids are still retained (although some derived therians possess great reduction of the talonid, as for example the Chrysochloridae and some Rodentia). In this way, argyrolagoid affinities for *Patagonia* lack empirical support. In addition, Flynn and Wyss ([1999](#)) conclude, on the basis of their preliminary phylogenetic analysis that *Patagonia* is most closely

related to the putative argyrolagoid *Klohnia* (see Goin et al. ([2010](#)) for a different phylogenetic proposal), although they recognised that *Patagonia* is highly distinct morphologically from *Klohnia*. This sister group relationship was sustained on the basis of three features, namely: a medially positioned lower gliriform incisor with the posterior end curving dorsally, presence of a premolar-incisor diastema in the lower jaw and absence of m4 (Flynn and Wyss [1999](#)). Although all these features are present in both *Klohnia* and *Patagonia*, they are also present in most (if not all) multituberculates. In fact, in most multituberculates and gondwanatherians the presence of a gliriform incisor has been usually considered as a synapomorphy uniting both clades (Krause and Bonaparte [1993](#); Pascual et al. [1999](#)). However, Pascual et al. ([1999](#)), analysing the form and structure of the incisor of Gondwanatheria and Multituberculata, stated that: 'incisors of this form evolved independently within Multituberculata as well as in a variety of non-multituberculate mammalian taxa.' In conclusion, such feature is here considered of ambiguous phylogenetic significance. In the same way, the presence of a postcanine diastema widely occurs in multituberculates (Kielan-Jaworowska et al. [2004](#)), being also present in the gondwanatherians *Ferugliotherium*, *Gondwanatherium* and *Sudamerica* (Kielan-Jaworowska and Bonaparte [1996](#); Pascual et al. [1999](#); Gurovich and Beck [2009](#)). Finally, the absence of m4 applies to all non-sudamericid multituberculates, probably including *Ferugliotherium* (Kielan-Jaworowska and Bonaparte [1996](#); Gurovich [2005](#); Gurovich and Beck [2009](#)), being diagnostic of such clade. As explained above, the identity of cheek-teeth in the sudamericid *Sudamerica* is still uncertain, but contrasting with the remaining multituberculates it shows four lower molariforms (Pascual et al. [1999](#); but see discussion in Gurovich and Beck [2009](#)).

In sum, the analysis offered above demonstrates that most of characters recognised in support that *Groeberia* and *Patagonia* are members of Metatheria (or Argyrolagoidea) are problematic, at least, and that some of the features interpreted as unique to *Groeberia* and *Patagonia* are also present in multituberculates and gondwanatherians.

### Phylogenetic affinities of Groeberia *and* Patagonia *within Mammalia*

As explained in previous pages, features originally thought as supporting metatherian affinities for *Groeberia* and *Patagonia* are dubious at least. As follows, we review the morphological evidence cited in support of their therian affiliation.

As recognised in the original description of *Patagonia* (Pascual and Carlini [1987](#)), the cheek-teeth of this taxon
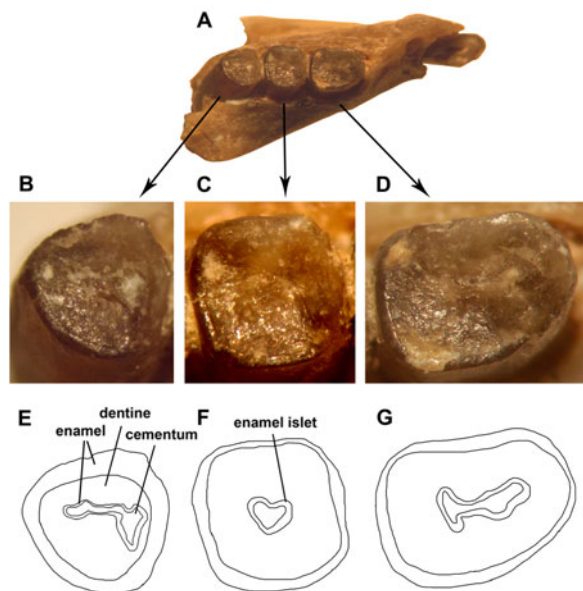
Figure 9. (Colour online) Lower dentition of *P. peregrina* (MACN-CH 869, holotype) in occlusal view. (A) Complete mandible, (B) first molariform in occlusal view, (C) second molariform in occlusal view, (D) third molariform in occlusal view, (E) sketch of first molariform in occlusal view, (F) sketch of second molariform in occlusal view and (G) sketch of third molariform in occlusal view.

are not strictly lobate and lack trigonid, talonid or original cusps, a condition which can be alternatively considered as plesiomorphic or derived within mammals. In the case of *Groeberia*, the teeth also lack clearly defined trigonid and talonid, as previously observed by Flynn and Wyss (1999). Moreover, the lower molariforms of *Groeberia* lack any sign of trigonid cusps, including the cristid obliqua, a morphology that recalls pretribosphenic mammals (see Kielan-Jaworowska et al. 2004). In this way, both *Groeberia* and *Patagonia* retained the absence of talonid or trigonid. Tribosphery is considered as a key character of therian mammals (Patterson 1956; Fox 1975; Butler 1990; Cifelli 1993; Sigogneau-Russell 1998, 2003; Luo et al. 2002, 2007), but a talonid-like structure has been acquired convergently in other groups, such as Australosphenida (Luo et al. 2001). Apparently, the presence of the tribosphenic molariforms is absent in both *Patagonia* and *Groeberia*.

In addition, *Patagonia* contrasts with most therian mammals in that the lower molariforms have the labial side taller than the lingual side, whereas in tribosphenic mammals the reverse condition occurs: the lingual side (which bears the paracone cusp in eutherians, and the metacone cusp in metatherians) constitutes the taller region of the lower teeth (Gelfo and Pascual 2001; Rougier et al. 2011; Chimento et al. 2012). In *Patagonia*, as in pretribosphenic taxa (for example, the gondwanatherians *Bharattherium* and *Sudamerica*) the occlusal surface of the

lower cheek-teeth forms a very shallow and broad, mesiodistally oriented valley, with its labial rim being distinctly taller than the lingual one (Figure 9). Also, the relative extent of the enamel on the lingual surface of the crown is greater than it is on the buccal surface (Bonaparte 1986a; Krause et al. 1992; von Koenigswald et al. 1999; Pascual et al. 1999). Gurovich (2005) indicates that in upper molariforms of gondwanatherians the enamel of the lingual surface of the crown was dorsoventrally lower than in the buccal surface.

*Groeberia* differs from *Patagonia* in that the lower molariforms show the inner margin taller than the lateral margin, a condition resembling that of tribosphenic taxa (including metatherians). However, it is worth mentioning that in the gondwanatherians *Greniodon* (Goin et al. 2012) and *Trapalcotherium* (Rougier et al. 2009), such kind of molariform occlusion occurs, suggesting that this condition may not be unique of tribosphenic mammals.

Dentary bone morphology of both *Groeberia* and *Patagonia* does not fit well with the generalised patterns of a tribosphenic mammal. This may indicate that these taxa are highly derived mammals (as some rodents), or may be plesiomorphic mammals in this respect. In both *Patagonia* and *Groeberia*, only the base of the coronoid process has been preserved (Pascual and Carlini 1987; Pascual et al. 1994). This process appears to be confined to a dorsal position, as indicated by the masseteric crest situated close to the alveolar level. This could indicate that the angular process was dorsally positioned. Such morphology differs from that in most boreosphenidans (including metatherians) and stem zatherians, in which the angular process of the jaw is in line with the ventral margin of the horizontal ramus of the dentary (Martin and Rauhut 2005). In this regard, *Groeberia* and *Patagonia* retained a primitive condition which is also present in australosphenidans (e.g. *Asfaltomylos*, *Bishops*; Luo et al. 2002; Martin and Rauhut 2005), as well as in the zatherian *Mozomus* (Li et al. 2005). Interestingly, this condition appears to be present in the incompletely known dentary of the gondwananatherian *Sudamerica* (Pascual et al. 1999).

In sum, *Patagonia* and *Groeberia* resemble teeth and dentary morphology of basal mammals, being rather different from that of most tribosphenic taxa, including almost all metatherians.

On the other hand, the gross morphology of the dentary of *Groeberia* and *Patagonia* is similar to that of multituberculates, particularly taeniolabidoids (e.g. *Taeniolabis*, *Catopsbaatar*; Kielan-Jaworowska and Hurum 1997), and gondwanatherians (e.g. *Sudamerica*; Pascual et al. 1999). In these taxa, the dentaries are very short and deep, a distinct pre-molariform diastema is present, a large and anteriorly extended pterygoid fossa is developed and the coronoid process originates far anteriorly (Pascual et al. 1999; Krause et al. 2003). In addition, presence of a large, procumbent, laterally compressed lower central

incisor with a large and long alveolus that passes ventrally to the cheek-teeth is also a feature shared by *Groeberia*, *Patagonia* and multituberculates (Pascual et al. 1999; Krause et al. 2003). In addition, *Groeberia* presents a ventromedial position of the lower incisors with respect to the cheek teeth due to the presence of a symphyseal shelf.

Moreover, the combination of rectangular shaped, hypsodont molariform-like teeth with cementum-filled vertical furrows and flat occlusal surface and absence of plagiaulacoid p4 has been considered as unique to Gondwanatheria (Pascual et al. 1999; Krause et al. 2003). Notably, these characters are also present as a whole in *Patagonia* and in *Groeberia*.

In this way, we carried out a numerical phylogenetic analysis with the aim to recognise the phylogenetic affinities of *Groeberia* and *Patagonia*.

## Phylogenetic results

The clear-cut morphological distinctions between *Groeberia* and *Patagonia* with metatherians, in addition to the absence of therian synapomorphies, invite to test their affinities in the context of a comprehensive cladistic analysis of Mammalia.

The phylogenetic analysis here carried out resulted in the inclusion of *Groeberia* and *Patagonia* within Gondwanatheria. This allowed us to identify many features that *Groeberia* and *Patagonia* share with allotherians, multituberculates, cimolodontans and gondwanatherians, which are listed and commented in the following pages. Character definition is preceded by character number (as listed in the character list; Supplementary material: Appendix 1), and its corresponding character state (as scored in the data matrix; Supplementary material: Appendix 2). Complete list of unambiguous synapomorphies is shown in Supplementary material: Appendix 3.

In addition, we run phylogenetic analyses including interpretations of previous authors regarding dental formula of both *Groeberia* and *Patagonia*, with the aim to test robusticity of present phylogenetic hypothesis. These analyses are congruent in the gondwanatherian affiliation of *Groeberia* and *Patagonia* (Supplementary material: Appendix 4).

## *Synapomorphies of Allotheria present in* Groeberia *and* Patagonia

*167(2) Well-developed diastema in the lower incisor–canine region*. The presence of a diastema in the lower premolariform region of dentary (167-2) was here recovered as diagnostic of Allotheria. In fact, the presence of an enlarged diastema was traditionally considered as diagnostic of Multituberculata (Clemens and Kielan-

Jaworowska 1979). Its presence in *Sudamerica* and *Ferugliotherium* was considered as a feature uniting gondwanatherians and multituberculates (Kielan-Jaworowska and Bonaparte 1996; see also Pascual et al. 1999), and was proposed as an unambiguous synapomorphy uniting both groups by Gurovich and Beck (2009). The occurrence of a large lower diastema in the dentition of plesiomorphic allotherians, including *Haramiyavia* (Jenkins et al. 1997), *Megaconus* (Zhou et al. 2013) and *Arboharamiya* (Zheng et al. 2013), indicates that this feature may be considered as diagnostic of Allotheria. In *Patagonia* and *Groeberia*, a post-canine diastema is also present (although different from each other), although it is more anteroposteriorly restricted than in most allotherians, with the single exception of very basal taxa such as *Megaconus* (Zhou et al. 2013) and *Arboharamiya* (Zheng et al. 2013).

Presence of a well-developed lower diastema is also convergently present in several small metatherians, including argyrolagoids (Flynn and Wyss 1999) and other pseudodiprotodont taxa (Goin et al. 2010; Goin and Abello 2013).

*448(1) Coronoid ridge on dentary subvertical*. A nearly vertical coronoid process on dentary has been reported in *Groeberia*, and was formerly considered as a unique feature of Groeberida (Pascual et al. 1994). However, the presence of a strong, salient and nearly vertical coronoid process of mandible is typical of multituberculates, particularly taeniolabidoids (e.g. *Taeniolabis*, *Catopsbaatar*; Kielan-Jaworowska and Hurum 1997). In the basal allotherians *Haramiyavia* (Jenkins et al. 1997), *Megaconus* (Zhou et al. 2013) and *Arboharamiya* (Zheng et al. 2013), the coronoid process is also nearly vertical. In *Sudamerica*, the ascending process of the mandible is highly incomplete, although the preserved portion of this process indicates that it was nearly vertically oriented. In *Patagonia*, there is no complete coronoid process on the dentary, but the base is preserved and clearly indicates that the ascending process was very vertical (Pascual and Carlini 1987; Goin and Abello 2013).

## *Synapomorphies of Multituberculata present in* Groeberia *and* Patagonia

Within Allotheria, we here recovered the presence of five unambiguous multituberculte synapomorphies: mandibular foramen located within the pterygoid fossa but not associated with meckelian sulcus, less than two lower incisors, crested diastema anterior to the lower incisors, coronoid separated from the tooth row by a retromolar basin and coronoid process of the dentary with its root beneath the m2. These characters are discussed as follows.
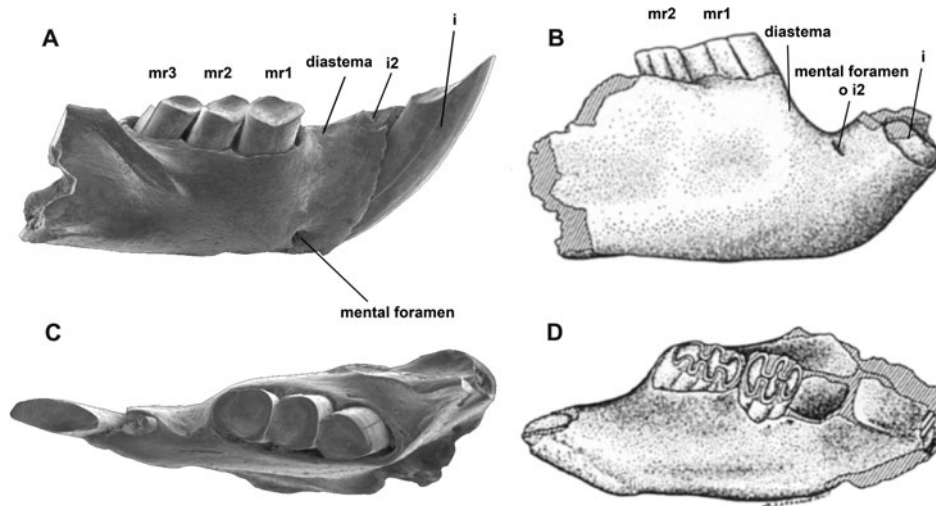
Figure 10.    Comparison between lower jaw of *P. peregrina* and *S. ameghinoi*. (A) Lateral view of right dentary of *P. peregrina*, (B) lateral view of left dentary of *S. ameghinoi*, (C) occlusal view of right mandible of *P. peregrina* and (D) occlusal view of right mandible of *S. ameghinoi*. (A and C) Modified from Goin and Abello (2013) and (B and D) modified from Pascual et al. (1999).

*13(3) Location of mandibular foramen (posterior opening of the mandibular canal) on the pterygoid fossa but not associated with Meckel's sulcus.* Medially, a well-marked trough and overlying ridge extend posteriorly from the mandibular foramen to the condyle in basal mammalian taxa, as for example symmetrodontans (e.g. *Spalacotherium*, *Spalacolestes*; Simpson 1928; Kielan-Jaworowska et al. 2004). These features reflect the presence of postdentary elements (i.e. articular, prearticular, angular, surangular) that remained attached to the medial surface of the dentary. In basal allotherians, as *Haramiyavia* (Butler 2000) and *Megaconus* (Zhou et al. 2013), the mandibular foramen is related to the meckelian groove. On the contrary, in multituberculates, and in therian mammals the mandibular foramen is not associated with the Meckel sulcus (Kielan-Jaworowska et al. 2004), a condition also present in *Patagonia* (Pascual and Carlini 1987). The present analysis indicates that the presence of an independent mandibular foramen was convergently acquired by multituberculates and therian mammals.

In *Groeberia*, the poorly preserved medial margin of the dentary forbids recognition of both the medial foramen and pterygoid fossa.

*142(4) Two or fewer lower incisors.* Multituberculates are characterised for the presence of rodent-like anterior lower incisors (Clemens and Kielan-Jaworowska 1979). In basal allotherians, such as *Haramiyavia* (Butler 2000), three lower incisors are present. In contrast, in all known multituberculates a single lower incisor is present (Kielan-Jaworowska et al. 2004). Similarly, a single rodent-like lower incisor alveolus has been reported in the dentaries of the gondwanatherians *Ferugliotherium* and *Sudamerica* (Pascual et al. 1999; Gurovich and Beck 2009), and also probably *Gondwanatherium* (Gurovich 2005).

We have recognised two lower incisors for *Groeberia* (see above), and although in *Patagonia* the number of lower incisors is not certain, evidence at hand suggests the presence of two incisors (Sánchez-Villagra et al. 2000) (Figure 10).

Following Kielan-Jaworowska et al. (2004), the presence of less than three anterior lower incisors constitutes a synapomorphy of Multituberculata that is also present in gondwanatherians, *Groeberia* and *Patagonia*.

*466(1) Crested diastema posterior to lower incisors.* Pascual and Carlini (1987) described that the dorsal margin of the lower diastema in front of the molariforms in *Patagonia* ended in an acute crest-like ridge. Although this portion of the jaw is poorly preserved in *Groeberia*, a condition can be corroborated in the holotype of *G. minoprioi* (Patterson 1952). Similarly, the diastema below the lower incisor is transversely compressed and dorsally crested in most genera of cimolodontan multituberculates (e.g. *Mesodma*, *Cimolodon*, *Stygimys*; Clemens 1963; Sloan and Van Valen 1965). A similar conformation has also been reported in the gondwanatherian *Sudamerica* (Pascual et al. 1999) and *Ferugliotherium* (Kielan-Jaworowska and Bonaparte 1996), as well as on indeterminate sudamericid from Antarctica (Goin et al. 2006). A similar pattern is also present in the much smaller diastema seen in 'paulchoffatoids', which show a deep ridge on the dorsal margin of the diastema (e.g. *Paulchoffatia*, *Kuehneodon*; Hahn 1969). On the contrary, in the basal non-multituberculate allotherian *Haramiyavia*, the diastema is plesiomorphic in being dorsally rounded and smooth (Jenkins et al. 1997).

*467(1) Coronoid process of dentary forms a strong, salient lamina that is separated from the tooth row by a*

*deep diagonal valley (retromolar basin).* Pascual and Carlini (1987) paid attention to the presence of a very wide and oblique basin posterolateral to the tooth row, and internal to the coronoid process in the lower jaw of *Patagonia*. This conspicuous diagonal valley is formed between the coronoid and the alveolar border behind m3. A similar structure has also been observed in *Groeberia*, in which the retromolar space is very well developed and extends anteriorly to the level of the third lower molariform. This condition has also been observed in some Theria, as some Australian diprotodonts (Potoroinae), and some rodents (Pascual and Carlini 1987).

This basin is called as the 'retromolar basin' and it is also known for most mutituberculates (Clemens and Kielan-Jaworowska 1979; Kielan-Jaworowska et al. 2004). In the sudamericid *Sudamerica*, the retromolar basin is still more developed and conforming a laterally expanded shelf that also extends to the level of m3 (Pascual et al. 1999).

*468(1) Coronoid process of dentary has its root beneath m2.* Interestingly, the coronoid process in *Patagonia* and *Groeberia* rises at level of m2 (Pascual and Carlini 1987; Pascual et al. 1994). A similar condition is also present in the gondwanatherian *Sudamerica* in which the coronoid process is located opposite to the second molariform cheek-tooth (Pascual et al. 1999). In most multituberculates the coronoid process rises at level of m2 or even more anteriorly. Thus, conforming a derived feature of multituberculates (Kielan-Jaworowska et al. 2004), which is absent in basal allotherians (e.g. *Haramiyavia*, Jenkins et al. 1997).

A well-developed, nearly vertical and anteriorly positioned coronoid process, together with its very deep masseteric fossa, and retromolar basin are features that suggest a voluminous external adductor muscle in *Patagonia* (Pascual et al. 1986), and also *Groeberia*. This muscle is related to adduction movements as well as retraction of the dentary, and is very well developed in taxa with palinal mastication (Kielan-Jaworowska et al. 2004; see details in Pascual et al. 1986), including multituberculates.

### Synapomorphies of Cimolodonta present in Groeberia and Patagonia

Within multituberculates, *Groeberia* and *Patagonia* exhibit some resemblance with Cimolodonta in the common presence of reduced number of lower premolars, base of alveolus of lower incisors prominent, external enamel band conformed by two fields of enamel and a mid-neutral zone, main axis of lower incisor oblique to teeth row:

*153(3) Less than two lower premolars.* In contrast with basal allotherians (e.g. *Haramiyavia*, Paulchoffatiidae and

Plagiaulacidae; Butler 2000; Kielan-Jaworowska et al. 2004), cimolodontan multituberculates (e.g. *Nemegtbaatar*, *Mesodma*; Clemens and Kielan-Jaworowska 1979; Kielan-Jaworowska et al. 2004) exhibit a reduced number of lower premolars with two or one, and when present the p3 is small and peg-like, hidden below an enlarged p4. In gondwanatherians, a single lower premolar has been reported for *Ferugliotherium* (Kielan-Jaworowska and Bonaparte 1996). In *Sudamerica*, the presence or absence of a premolar is uncertain. This genus shows four cheek-teeth, and the first of these teeth can be interpreted alternatively as a first molar (Pascual et al. 1999) or a p4 (see Gurovich and Beck 2009). In *Patagonia* only three cheek-teeth have been reported, and there is no sign of a lower premolar, resembling cimolodontans in this aspect. Similarly, in *Groeberia*, molariform teeth are similar to each other. As explained above, we interpret that the first molariform of *Groeberia* may belong to a premolar tooth. It is worth mentioning here that the presence of a single premolar has been reported in *Klohnia* and *Argyrolagus* (probably two premolars in *Proagyrolagus* and *Hondalagus*) (Simpson 1970a; Pascual et al. 1994; Flynn and Wyss 1999), and was considered as a feature uniting *Groeberia* and *Patagonia* with these metatherian taxa (Flynn and Wyss, 1999). On the basis of the present analysis we consider that the reduction in the number of cheek-teeth occurred independently in Patagonia and derived Taeniolabidoidea. The reduction of lower premolars may represent a synapomorphy uniting *Groeberia*, *Patagonia*, sudamericids and cimolodontans.

*465(1) Base of the alveolus of lower incisor shapes a prominence.* A very well-developed prominence at the base of the alveolus is present in most cimolodontan multituberculates (e.g. *Catopsbaatar, Taeniolabis, Lambdopsalis*; Kielan-Jaworowska and Hurum 1997). In the same way, in *Sudamerica* such prominence is also well developed, and consequently, the dorsal margin of the post-incisive diastema acquires an 'S'-shaped margin. Pascual and Carlini (1987) mentioned that in *Patagonia* the base of the alveolus of the first lower incisor conforms to a dorsal superficial elevation similar to that of hystricognathous rodents.

On the contrary, in non-cimolodontan taxa, there is no elevation at the base of the incisor alveolus, representing plesiomorphic condition present in *Paulchoffatia* and *Haramiyavia*, for example (Hahn 1969; Jenkins et al. 1997).

In *Groeberia*, the incisive teeth are vertically oriented, and the presence of a basal prominence cannot be conclusively detected due to its strong morphological modification. In this way we coded this character in *Groeberia* as inapplicable (?).

*477(1) External enamel band on incisors conformed to two fields of tangential enamel separated by a neutral zone of radial enamel (von Koenigswald et al. 1999).* von

Koenigswald et al. (1999) described in detail the enamel of the incisors in the gondwanatherian mammals *Sudamerica* and *Gondwanatherium*. In the cross-section, the lower incisors show a peculiar arrangement of enamel micro-structure. In the above-mentioned gondwanatherians, the schmelzmuster is composed of tangential and radial enamel, of which the tangential enamel shows a different disposition of prisms between its lateral and mesial parts (von Koenigswald et al. 1999). The incisors show two fields of tangential enamel with prisms oriented in opposite direction separated by a neutral area of radial enamel. A similar composition of the incisor enamel has been mentioned for several ptilodontoid multituberculates (Sahni 1979). Two fields of tangential enamel have been reported in incisors of *Groeberia* (von Koenigswald et al. 1999; von Koenigswald and Goin 2000). In *Patagonia*, there are also two fields of tangential enamel in its lateral extension. In the mesial portion, the prisms point mesially whereas on the lateral part they point laterally (see von Koenigswald and Goin 2000). Although von Koenigswald and Goin (2000) indicated the absence of neutral area, presence of a neutral area near the incisor ventral corner may be still recognised (see Figure 15A in von Koenigswald and Goin 2000). In this way, *Patagonia* shares with gondwanatherians and multituberculates the presence and position of a neutral area, two layers of tangential enamel, specific orientation in each layer and predominance of interprismatic matrix in the external layer (von Koenigswald and Goin 2000). Its occurrence has also been observed in some diprotodont and polydolopimorph marsupials (von Koenigswald and Goin 2000; von Koenigswald and Pascual 1990), and few placentals (e.g. cricetids and soricids; von Koenigswald and Goin 2000).

*478(1) Main axis of anterior lower incisor oblique to the cheek-teeth row (Pascual et al. 1999).* The dentary of *Sudamerica* resembles closely that of multituberculates, and particularly taeniolabidoids (e.g. *Taeniolabis*, *Catops-baatar*; Kielan-Jaworowska and Hurum 1997) in having a large and long alveolus of the anterior lower incisor that passes inferior to the cheek-teeth and lies oblique to the longitudinal axis of the cheek-tooth row (Pascual et al. 1999). A similar condition has been described for *Patagonia*, in which the lower incisor lies obliquely in the jaw, its root passing medial and ventral to the roots of the first cheek-tooth but directly ventral to those of the last cheek-tooth (Pascual and Carlini 1987; see also Flynn and Wyss 1999).

It is worth mentioning here that the disposition and direction of the lower incisor in *Groberia* is strikingly different from any known mammalian taxon, including *Patagonia* (Pascual et al. 1994). Due to the verticalisation of the incisives its condition is difficult to check in *Groeberia*. However, preserved portion of dentary suggests that the base of incisives in *Groeberia* was also

obliquely developed with respect to the main cheek-teeth row axis.

As a conclusion, presence of incisive teeth oblique to the cheek-teeth rows may be proposed as a synapomorphy uniting multituberculates, gondwanatherian *Patagonia* and *Groeberia*.

### Synapomorphies of Gondwanatheria present in Groeberia *and* Patagonia

Two unambiguous synapomorphies are also present in *Groeberia*, *Patagonia* and Gondwanatheria:

*144(1) Lower anterior-most incisor enamel restricted anteriorly.* Krause and Bonaparte (1993) indicated that rodent-like lower incisors with anteriorly restricted enamel may be a feature of gondwanatherians. Although the Taenolabidoidea are generally considered as being derived in having enamel restricted to the ventral aspect (Sloan and Van Valen 1965; Krause et al. 1992; Kielan-Jaworowska et al. 2004), it should be noted that in taenolabidoids the apex of the incisors is usually unworn and may be capped with enamel (Krause et al. 1992).

In Gondwanatheria (e.g. *Ferugliotherium*, *Sudamer-ica*, *Gondwanatherium*; Krause and Bonaparte 1993; Pascual et al. 1999), the enamel is limited to the ventral aspect of the tooth but ascends further dorsally on the lateral side than on the medial side (*Ferugliotherium*; Krause et al. 1992). This combination of characters is also present in the genera *Groeberia* (von Koenigswald and Goin 2000) (Figure 5). In *Patagonia*, the enamel surrounds all the tooth, however, it is extremely thin in the posterolabial portion and the lingual face (Goin and Abello 2013).

As explained by Krause et al. (1992), gondwanather-ians, including *Groeberia* and *Patagonia*, exhibit a combination of characters on its lower incisors that are absent as a whole in multituberculates (Jepsen 1937), including enamel extending to the base of the root, and tip of the crown not totally covered by enamel. Although these characters are also present in rodent incisors (Jepsen 1937), gondwanatherians and *Groeberia* and *Patagonia* differ from them in lacking any sign of prism decussation (Krause et al. 1992; see also von Koenigswald and Goin 2000).

*145(1) Lower anterior-most incisor with open root.* Gondwanatherians, *Groeberia* and *Patagonia* exhibit a combination of characters on its lower incisors that are absent as a whole in multituberculates (Jepsen 1937), including evergrowing roots (Krause et al. 1992). While the incisor is rodent-like in shape, in *Sudamerica* (Pascual et al. 1999) as well as in *Patagonia* (Pascual and Carlini 1987), and probably also in *Ferugliotherium* (Kielan-Jaworowoska and Bonaparte 1996), it is oriented differently from that in rodents, extending along the
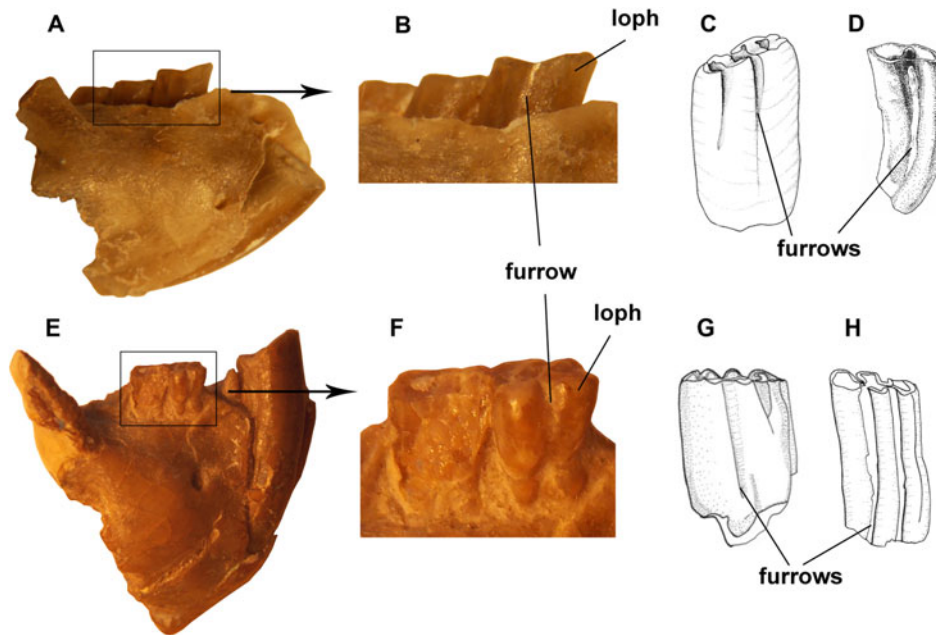
Figure 11. (Colour online) Detail of crown morphology of *Patagonia* and *Groeberia* and comparisons with other gondwanatherians. (A) Right dentary of *P. peregrina* in lateral view vista labial, (B) detail of right mr1–mr2 in lateral view, (C) molariform of *G. patagonicum* in lateral view (modified from Bonaparte (1986b)), (D) molariform of *D. jederi* in lateral view (modified from Wilson et al. (2007)), (E) right dentary of *G. minoprioi* (MLP 85-IX-24-1) in lateral view, (F) detail of right mr1–mr2 in lateral view, (G) molariform of *G. patagonicum* in lateral view (modified from Gurovich (2005)) and (H) molariform of *S. ameghinoi* in lateral view (modified from Gurovich (2008)).

ventral border of the horizontal ramus, first below the m1, then lingually to other molars and conforming the ventral margin of the mandible (Pascual and Carlini 1987). This peculiar conformation of the open rooted lower incisors is not matched by any other mammal and may be unique to gondwanatherians.

Although the present phylogenetic analysis lacks resolution within gondwanatherians, *Patagonia* looks more derived than *Ferugliotherium* and *Groeberia* in the following features, which are present in several sudamericids:

*173(1) Open-root end of the postcanines*. In the basal gondwanatherians (e.g. *Ferugliotherium, Trapalcotherium, Greniodon*; Kielan-Jaworowska et al. 1992; Rougier et al. 2009; Goin et al. 2012), the molariforms are low-crowned and rooted, being typically brachyodont. On the contrary, in more derived gondwanatherians (e.g. *Gondwanatherium, Lavanify, Bharattherium, Sudamerica*; Krause et al. 1997; Wilson et al. 2007), and *Patagonia* (Pascual and Carlini, 1987) the molariforms are proto-hypsodont and show dorsoventrally tall roots (von Koenigswald et al. 1999).

On the other hand, the molariforms were described as low and brachyodont by Pascual et al. (1994). However, the teeth crowns are higher than long, matching the definition of hypsodont teeth (Van Valen 1960). The roots resemble those of hypsodont mammals in being very tall,

transversely expanded and anteroposteriorly compressed (Pascual et al. 1994). Due to the presence of closed distal end of roots, the teeth are here interpreted as proto-hypsodont (*sensu* Mones 1982). In spite of its hypsodont nature, the teeth of *Groeberia* are different from *Patagonia* and sudamericids, which show open-rooted molariforms, and may represent an intermediate condition from brachyodont low-crowned ferugliotherids and euhypsodont-like sudamericids.

In sum, the shared presence of hypsodont cheek-teeth in sudamericids and *Patagonia* is here considered as a synapomorphy uniting these taxa.

*470(1) Vertical furrows on the margins of the molariforms crown*. Presence of deep and dorsoventrally extended grooves filled with cementum on the lateral surface of molariforms crowns conforms a peculiar feature shared by *Sudamerica*, *Gondwanatherium*, *Barattherium* and *Lavanify*, and considered as diagnostic of gondwanatherians (Bonaparte 1986b; Krause et al. 1997; Gurovich 2005; Wilson et al. 2007). In *Ferugliotherium* and *Trapalcotherium*, such grooves are clearly absent (Wilson et al. 2007; Rougier et al. 2009). In *Gondwanatheriun* they are dorsoventrally restricted and not extended towards the base of the crowns (Wilson et al. 2007). On the contrary, such furrows are extended along the crown in *Sudamerica*, *Bharattherium* and *Lavanify* (Prasad et al. 2007; Wilson et al. 2007). However, in the
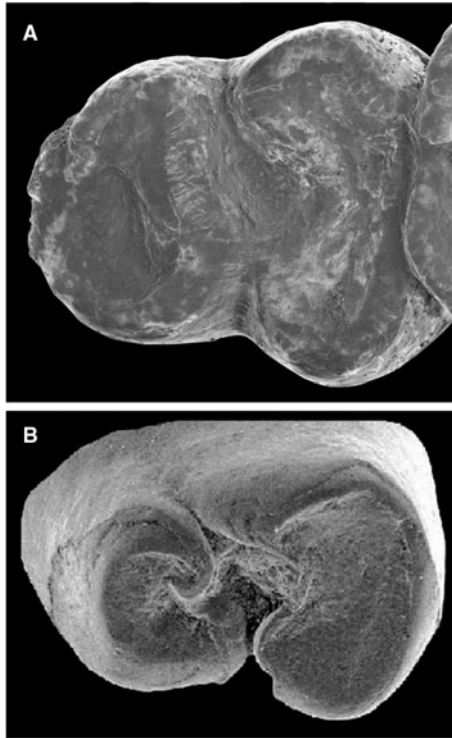
Figure 12.    (A) Occlusal view of mr1 of *G. minoprioi* (MLP 85-IX-24-1) and (B) occlusal view of mr1 of an unnamed Sudamericidae from India (modified from Verma et al. (2012)).

latter two taxa, the grooves are restricted to the lingual side of the crown, whereas in *Sudamerica* and *Gondwanatherium* these grooves are present on both lingual and labial surfaces (Wilson et al. 2007).

Remarkably, *Patagonia* closely resembles derived gondwanatherians in having molariforms with dorsoventrally tall vertical furrows which are filled with cementum on both lateral and medial surfaces of molariform crowns

(Pascual and Carlini 1987; von Koenigswald and Pascual 1990; von Koenigswald and Goin 2000). This contrasts with the smooth surface known for *Groeberia* (Pascual et al. 1994) (Figures 11–13).

As a conclusion, the presence of molariforms with vertical furrows filled with cementum may be considered as a synapomorphy of Sudamericidae, including *Patagonia*.

*475(1) Crowns and roots of m2 oblique to the occlusal plane (Krause and Bonaparte 1993).* Krause and Bonaparte (1993) recognised that the second lower molar of both *Sudamerica* and *Gondwanatherium* shares a distally sloping occlusal surface, a feature probably related to hypsodonty (Krause and Bonaparte 1993). In fact, in contrast to the basal gondwanatherian *Ferugliotherium* (Krause et al. 1992), sudamericids show an elongate crown that is oblique to the occlusal plane, whereas in the former the occlusal plane is perpendicular to the crown and root (Krause and Bonaparte 1993). In *Patagonia*, the occlusal plane is also oblique with respect to the dorsoventral axis of the crown and roots (Pascual and Carlini 1987), being a derived condition shared with sudamericids.

In addition, there are several features that *Patagonia* shares with South American sudamericids. For example, the enamel of cheek-tooth in *Gondwanatherium* and *Sudamerica* is very thick and formed solely by radial enamel (von Koenigswald et al. 1999). This pattern is also documented in *Patagonia*, whereas in *Lavanify* and *Barattherium* the enamel is much thinner and shows well-developed perikymata (Prasad et al. 2007).

In spite of these similarities, *Patagonia* differs from the sudamericid *Sudamerica* in having only three lower molariforms, whereas in the latter there are only four cheek-teeth (Pascual et al. 1999; von Koenigswald et al. 1999). This feature may represent an autapomorphy of *Patagonia*.
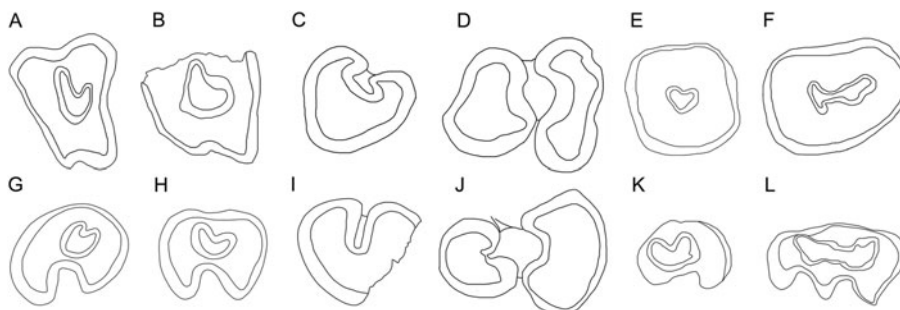


Figure 13.    Comparison of selected gondwanatherian molariform teeth. (A–D) *G. minoprioi* (MLP 85-IX-24-1): (A) sixth upper molariform, (B) fifth upper molariform, (C) fourth lower molariform and (D) first lower molariform. (E and F) *P. peregrina* (MACN-CH 869): (E) second lower molariform and (F) first lower molariform. (G) Lower molariform (modified from Prasad et al. (2007)), (H) possible fourth lower molariform (modified from Wilson et al. (2007)), (K) lower molariform (modified from Prasad et al. (2007)), (L) possible first lower molariform (modified from Wilson et al. (2007)). (I) Possible lower molariform of *L. miolaka* (modified from Krause et al. (1997)) and (J) possible first lower molariform of unnamed Sudamericidae from India (modified from Verma et al. (2012)).

## Discussion

### *Mastication in* Groeberia *and* Patagonia*, and their similarities with multituberculates*

Allotherians are mammals with molariform teeth showing two longitudinal cusp rows, which occlude in such a way that the labial lower row bites into the valley extending between the upper cusp rows. Occlusion of these teeth is bilateral, and the mandibular movement is orthal or palinal, but not transverse (Butler 2000). Most mammals differ from allotherians in that the teeth functioned in unilateral occlusion with the labial surfaces of the lower cusps shearing against the lingual surfaces of the upper cusps, involving transverse movement (Kielan-Jaworowska et al. 2004). Krause (1982) argued that the palinal jaw movement is unique to multituberculates (allotherians herein) among mammals, and later Krause and Bonaparte (1993) proposed the presence of this kind of mastication also for gondwanatherians, constituting an important character uniting both clades (Gurovich and Beck 2009). In fact, wear patterns indicate that both *Ferugliotherium* (Krause et al. 1992) and sudamericids (Pascual et al. 1999; von Koenigswald et al. 1999) had a palinal power stroke, as in undoubted multituberculate mammals. Zimicz (2012) recently proposed that a similar masticatory type was present in some metatherians, including diprotodonts and argyrolagids.

The palinal movement of the dentary in most taxa is sustained on the basis of three main lines of evidence present on molar teeth: (1) anteroposterior orientation of wear striations, (2) development of leading and trailing enamel edges on dentine and (3) presence of anteroposterior wear groove (Krause and Bonaparte 1993). These three characters are present in *Patagonia* and *Groeberia*, and clearly points to a palinal jaw movement in these taxa (see also Pascual et al. 1986).

Regarding the identification of leading and trailing enamel edges, it must be said that the degree of wear of the dentine in herbivorous mammals is asymmetrical with respect to the direction of jaw movement (Rensberger 1973). Leading and trailing edges on molariform occlusal surfaces can be distinguished based on differentially worn dentine. On the leading edge, the dentine is protected by enamel and thus, it remains continuous with the enamel; on the trailing edge, the dentine is unprotected and it erodes below the level of the enamel (Wilson et al. 2007). *Patagonia* and *Groeberia* show a similar pattern as in *Sudamerica*, with the mesial edge (leading) abraded more deeply than that of the distal (trailing). This indicates that the mandible was pulled backwards (palinally) during the power stroke of the masticatory cycle (von Koenigswald et al. 1999).

In addition, the anterior lower molariforms of *Patagonia* and *Groeberia* are much more elongate than the most posterior molariforms; since the position of enlarged molars indicates the most effective zone during mastication, its anterior position constitutes another anatomical evidence in support of palinal mastication (von Koenigswald et al. 1999).

The muscular system reconstructed for *Patagonia* matches well with the palinal jaw movement. The detailed study of Pascual et al. (1986) indicates that *Patagonia* exhibits a mandibular musculature with well-developed and dorsally located external adductor, expanded and reflected superficial masseter, prominent external adductor and internal pterygoid, suggesting mainly a palinal mastication for this taxon. Moreover, as characteristically occurs in multituberculates (Kielan-Jaworowska et al. 2004), the external mandibular fossa is anteriorly extended, and surpasses the level of the anterior margin of the posteriormost molariform, a condition also shared with *Groeberia*.

As a concluding remark, *Patagonia* and *Groeberia* share with allotherians the apomorphically palinal mastication.

### *Brief comparisons between* Groeberia *and* Patagonia

Pascual and Carlini (1987) in their detailed description of *Patagonia* pointed out several similarities shared by this genus and *Groeberia*. However, they interpreted that such similarities were the result of convergent evolution. Here we present some brief comparisons of the lower jaw of both taxa, detailing gross differences between these genera.

Although both *Patagonia* and *Groeberia* share a rodent-like aspect in having enlarged anterior incisives and reduced number of post-incisive teeth, a number of remarkable differences allow proposing that they may represent different evolutionary radiations within Gondwanatheria. In *Patagonia*, the dental formula consists of two possible lower incisors and three molariforms (see Pascual and Carlini 1987; Sánchez-Villagra et al. 2000), whereas in *Groeberia*, as interpreted here, there are two lower incisors and four molariforms. Furthermore, *Patagonia* differs from *Groeberia* in having euhypsodont rectangular cheek-teeth (Pascual and Carlini 1987), whereas in *Groeberia* the teeth are more brachyodont or protohypsodont (Pascual et al. 1994) (Figures 12 and 13). In *Patagonia*, the palate is entirely solid, whereas *Groeberia* shows palatal vacuities (Pascual et al. 1994; Goin and Abello 2013).

In *Groeberia*, the lower incisor extends inside an odd medial posterior projection of the symphysis, whereas in *Patagonia* the intra-alveolar portion is rodent-like, in being extended along the horizontal ramus (Pascual and Carlini 1987). Finally, the schmelzmuster of the incisor in *Groeberia* shows crack-stopping mechanisms underlying the outer radial enamel, a convergence with rodents, a

feature that is absent in *Patagonia* (von Koenigswald and Pascual 1990).

In *Patagonia*, the mandibular symphysis is subvertical and unfused, instead of fused and forming an apomorphic medial platform of *Groeberia* (Pascual et al. 1994).

In this way, *Patgonia* shares presence of intra-alveolar portion of lower first incisor extended along the horizontal ramus of the mandible, and a poorly defined mandibular symphysis with the derived gondwanatherian *Sudamerica* (Pascual et al. 1999). On the contrary, the retention of brachyodont or protohypsodont molariforms and fused dentary symphysis are plesiomorphies present in *Groeberia*.

## Groeberia *and* Patagonia*, and cranial morphology in gondwanatherians*

The recognition of *Groeberia* and *Patagonia* as Gondwanatheria adds important data to the knowledge of this enigmatic mammalian clade. Gondwanatherians are up to the date only known by sparse remains, mainly consisting of isolated cheek-teeth and incisors (e.g. Bonaparte 1986a, 1986b, 1990; Bonaparte et al. 1993; Gurovich and Beck 2009; Wilson et al. 2007; Verma et al. 2012), and a still unpublished associated skeleton (Krause et al. 2012). In this way, the skull of *Groeberia* offers information on cranial morphology of Gondwanatheria in the Tertiary. As a whole, we here point out main features of the *Groeberia* skull in order to characterise the gondwanatherian skull. *Groeberia* shares with the Malgasy Cretaceous Gondwanatheria briefly reported by Krause et al. (2012) the following features: very short and tall skull (with possibly vaulted braincase), very tall and laterally convex zygoma with a ventrally oriented blade-like jugal process and two pairs of upper incisors.

The snout of *Groeberia* is very short and tall, showing very well-developed premaxillary bones (Pascual et al. 1999), a condition that characterises multituberculates (Kielan-Jaworowska et al. 2004). The orbits were probably rounded and anteriorly oriented. The lacrimal bone was reduced and the lacrimal foramen was very wide. The palate was strongly arcuate, transversely wide and anteroposteriorly short. In *Groeberia*, the palatal vacuities were present and elongate at the rear of the palate, whereas in *Patagonia* the palate was solid. Anterior palatine foramina were very well developed and rounded in contour, a condition shared with most multituberculates (Kielan-Jaworowska et al. 2004). The mandible was rather short and deep, and occurs in multituberculates and *Sudamerica*, *Groeberia* and *Patagonia* show anteriorly extended masseteric fossa and the coronoid process was subvertically oriented (Kielan-Jaworowska et al. 2004). This combination of characters may allow the recognition of main gondwanatherian skull characters.

## Evolutionary implications of Groeberia *and* Patagonia *in the early radiation of Cenozoic mammals from the southern continents*

A series of stepwise global cooling events, beginning by the middle Eocene, may have played a role in the decline and subsequent extinction of several Mesozoic mammal relics in South America (Goin et al. 2012). On this continent, in contrast with other landmasses, the fossil record indicates a Late Cenozoic survival of several Mesozoic lineages. Well-documented provincialism of mammals in the Mesozoic of South America includes highly distinctive taxa related to Jurassic forms of the northern continents (Bonaparte 1990).

By Eocene and Oligocene times several multituberculate gondwanatheres were recovered from Patagonia and Perú (Goin et al. 2006, 2012; Antoine et al. 2012). In addition, dryolestoids are documented from Paleocene and Miocene beds of Patagonia (Bonaparte et al. 1993; Gelfo and Pascual 2001; Chimento et al. 2012; Rougier et al. 2012). The existence of such atavisms, coexisting with metatherians and derived placental mammals during the Cenozoic, was considered as a 'mixture fauna', a pattern different from that seen in the northern continents (Rougier et al. 2012). The increasing number of Mesozoic lineages now known to survive in the Cenozoic of South America demonstrates the integration of these basal mammals into the eutherian and metatherian faunas of the Cenozoic.

In Antarctica, together with placental and marsupial mammals remains of gondwanatherians were also reported (Goin et al. 2006), suggesting a similar pattern to that seen in South America. This is also evident in Australia, New Zealand and adjacent islands (see Fooden 1972). In fact, monotremes constitute a surviving mesozoic australosphenidan lineage, and its fossil record is known from the Late Mesozoic, through the Cenozoic, to Recent times in Australasia (Luo et al. 2001), coexisting with marsupial and possibly placental mammals. Moreover, a recent finding of a Mesozoic ghost lineage in New Zealand indicates a more complex scenario of Australasian mammalian faunas than previously thought (Worthy et al. 2006), suggesting a condition similar to that of South American Tertiary.

It is striking that the inferred insectivorous and fossorial habits of the Miocene dryolestoid *Necrolestes*, perhaps akin to African golden moles, have no close analogue among Cenozoic South American mammals (Rougier et al. 2012), and may allow the survival of this small mammal until Neogene times. In addition, the equally relictual modern monotremes, which occupy a highly specialised niche since the Early Miocene at least, lack any analogue in the Australian continent (Phillips et al. 2009). The same hypothesis may also be applied to the propalinal rodent-like gondwanatherians *Groeberia*

and *Patagonia*, which also probably occupied an empty ecological niche in South America, before the arrival of rodents by Late Eocene times (Vucetich et al. 2010). This is especially evident in *Patagonia*, which shares striking convergent similarities with burrowing rodents (Pascual et al. 1986). In this way, the survival of these archaic mammals may also be considered the result of the absence of useful competitors of its niche.

## Conclusions

Numerical phylogenetic analysis here carried out allowed to recognise a new hypothesis regarding phylogenetic affinities of the enigmatic genera *Groeberia* and *Patagonia*. These taxa may be nested within gondwanatherian multituberculates on the basis of several features including very short and deep dentaries with distinct pre-molariform diastema, large and anteriorly extended pterygoid fossa and presence of large, rodent-like anterior incisives, among other features. Recognition of *Groeberia* and *Patagonia* as gondwanatherians adds significant information regarding skull morphology in such poorly known clade. *Groeberia* and a briefly reported Malgasy Cretaceous Gondwanatheria (Krause et al. 2012) share a very short and tall skull (with possibly vaulted braincase), strong and laterally convex zygoma with a large and ventrally oriented blade-like jugal process and two pairs of upper incisors of which the anterior incisor is rodent-like. This allows reconstructing the skull in Tertiary Gondwanatheria.

Gondwanatherians are a group of rodent-like mammals mostly known in Cretaceous beds, with the exception of some Paleogene findings in Patagonia (Scillate Yané and Pascual 1985; Bonaparte 1986b; Bonaparte et al. 1993; Goin et al. 2006, 2012). The persistence of some gondwanatherians in Late Paleogene and Early Neogene (i.e. *Groeberia*, *Patagonia*) is surprising and is nearly unknown in any other continent (although few multituberculates survived into the Oligocene of North America). Recent reports in Patagonia of survival of dryolestoids and monotremes well into the Tertiary indicate that the mammalian faunistic composition of the continent was more complex than previously thought. Evidence at hand suggests that the existence of such atavistic taxa, coexisting with more modern metatherians and derived placental mammals during the Cenozoic, may allow recognising these South American communities as part of a 'mixture fauna'.

It was proposed that the survival of these archaic mammals may be considered as the result of the absence of competitors of its niche (Chimento et al. 2012; Rougier et al. 2012). This may also be applied to *Groeberia* and *Patagonia*, which probably occupied an empty ecological niche in South America, before the arrival of rodents by Late Eocene times. In this way, the survival of gondwanatherians may also be considered the result of the absence of useful competitors of their niche.

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