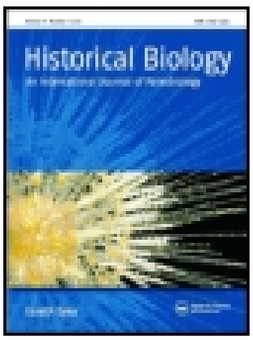

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The Interatheriinae from the Late Oligocene of Mendoza (Argentina), with comments on some Deseadan Interatheriidae

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ABSTRACT

This contribution discusses the interatheriids from Quebrada Fiera, a Late Oligocene locality in the south of Mendoza Province. In addition, the taxonomic status of the Deseadan interatheres *Plagiarthrus clivus*, *Argyrohyrax proavus*, *Argyrohyrax proavunculus*, ?*Argyrohyrax acuticostatus*, *Progaleopithecus fissurelatus*, *Progaleopithecus tournoueri*, and *Notohyrax conicus* is discussed. We recognise in Quebrada Fiera *A. proavus* and *Progaleopithecus* sp. A possible third taxon is represented by one specimen that shows a combination of features that do not permit accurate assignment. These new remains, in combination with a systematic study of Deseadan interatheres, allow for a better definition of each recognised taxon, extended diagnoses, and clarification of some long-standing taxonomic misconceptions. Indeed, the priority of *A. proavus* over *P. clivus* is established, and the latter is proposed as a *nomen dubium*. Associated deciduous and permanent dentition and some limb bones provide new data on the ontogenetic variation and postcranial morphology of *Argyrohyrax*. Phylogenetic analysis supports the taxonomic determinations and places *A. proavus* in a basal position with respect to *Archaeophylus* or *Progaleopithecus*. Documented fossil records of *Argyrohyrax* and *Progaleopithecus* in Mendoza extend the known range to middle latitudes in central west Argentina; these taxa expand the list of mammals from Quebrada Fiera with Patagonian affinities.

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KEYWORDS
Interatheres; Deseadan; Quebrada Fiera; Patagonia; South America

Introduction

Interatheriidae is a group of small-to-medium-sized native ungulates from South America classified within the Suborder Typotheria, Notoungulata (Simpson 1945, 1967; Reguero & Prevosti 2010) as the sister taxon of the clade Typotherioidea (including *Campanorco inauguralis*, 'Archaeohyracidae', Hegetotheriidae and Mesotheriidae) diagnosed by five unequivocal synapomorphies (Reguero & Prevosti 2010). Conventionally, Interatheriidae have been divided into two groups (Simpson 1945, 1967), the Notopithecinae, which includes small brachydont forms from the Middle–Late Eocene Casamayoran and Mustersan South American land mammal ages (SALMAs) (Simpson 1967; Hitz et al. 2006; Vera 2012a, 2012b, 2013a, 2013b, 2016; Vera & Cerdeño 2014), and the Interatheriinae, a group characterised by its hypsodont cheek teeth and a simplified coronal pattern, known from the Tinguiririan SALMA, Late Eocene–Early Oligocene (Hitz et al. 2000; Flynn et al. 2003) to the Late Miocene (lower member of the Ituzaingó Formation; Cione et al. 2000). Although both Interatheriidae and Interatheriinae have been traditionally considered as monophyletic assemblages (Cifelli 1993; Reguero et al. 1996, 2003; Hitz et al. 2000, 2006), a recent analysis by Vera (2016) proposed a different interpretation, regarding Notopithecinae as a family level taxon, phylogenetically positioned outside Interatheriidae *sensu lato*, in which some basal members (such as *Johnbell hatcheri* and *Ignigena minisculus* Hitz et al. 2006) previously identified as notopithecines are included. In this sense, the traditional definition of the Family Interatheriidae should be re-examined.

At present, seven genera and eight species of Interatheriinae are known for the Deseadan SALMA (Late Oligocene) from Argentina, Bolivia and Uruguay. *Plagiarthrus* (Ameghino 1896), *Archaeophylus* Ameghino 1897, *Progaleopithecus* Ameghino 1904, and *Cochilius* Ameghino 1901 (with *Argyrohyrax* considered as a junior synonym of *Plagiarthrus*) were recorded in Patagonia, reaching their greatest diversity (Reguero et al. 2003); meanwhile, the extra-Patagonian records correspond to *Brucemacfaddenia boliviensis* and *Federicoanaya sallaensis* Hitz, Billet and Derryberry 2008 from Salla-Luribay (Bolivia), *Eopachyrucos ranchoverdensis* Reguero, Ubilla and Perea 2003 from the Fray Bentos Formation in Canelones (Uruguay), and *Plagiarthrus* and an indeterminate Interatheriinae also from Fray Bentos Formation in Corrientes Province (Argentina) (Bond et al. 1998). In addition, *Plagiarthrus* has also been identified, but not described, from central-west Argentina by Reguero (1999) and Cerdeño (2011).

The fauna at Quebrada Fiera, in the central-west of Argentina, has been recognised as being of Deseadan age based on its faunal

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assemblage, which includes genera known only from this mammal age. These comprise *Pyrotherium* Ameghino 1889 (Gorroño et al. 1979), *Proborhyaena gigantea* Ameghino 1897 (Bond & Pascual 1983), and *Trachytherus* (Cerdeño 2014). Nevertheless, the age of these fossiliferous beds remains imprecise as absolute dating is lacking. The original description of the geological sequence outcropping in this area was presented by Gorroño et al. (1979; see also Narciso et al. 2004), and has been further summarised in recent papers that deal with this site (Forasiepi et al. 2014, and references therein).

The first mention of Interatheriidae in Mendoza was by Reguero (1999), who referred two specimens from Quebrada Fiera (Museo de La Plata, MLP 79-XII-18-32 and MLP 79-XII-18-33) to *Plagiarthrus clivus*. Other specimens in the MLP from the same site are labelled as *Argyrohyrax* sp. Later, Cerdeño (2011) mentioned the presence of *Plagiarthrus* at Quebrada Fiera, as well as a probable new taxon of interatheriines.

In this paper, the interatheres from the Quebrada Fiera are described in detail for the first time. This study also provides a general systematic review of a number of Deseadan taxa, shedding light on taxonomic issues and improving diagnoses. A phylogenetic analysis focusing on the Deseadan interatheres is also presented here, based on the matrix in Vera (2016), modified and enhanced with new data.

Material and methods

The bulk of the interatheres from the Quebrada Fiera locality (Malargüe Department, Mendoza Province, Argentina) has been recovered over the course of several field seasons since 2006 and are curated at the Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano' (MCNAM), Mendoza, Argentina. A number of other specimens were recovered in 1979 and 1996 by staff of the Museo de La Plata (MLP; Buenos Aires Province), and are also curated in this institution.

One of us (BV) viewed collections of interathere specimens for comparative purposes, housed at Amherst College Museum of Natural History (ACM), Amherst, Massachusetts, USA, the American Museum of Natural History (AMNH), New York, USA, the Field Museum of Natural History (FMNH), Chicago, Illinois, USA, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN), Buenos Aires, Argentina, Museo de La Plata (MLP), La Plata, Argentina, the Deseadan collection of the Muséum national d'Histoire naturelle (MNHN-DES), Paris, France, the University of Florida, Florida Museum of Natural History (UF), Gainesville, Florida, USA, and the Yale Peabody Museum, Vertebrate Paleontology Princeton University Collection (YPM-VPPU), New Haven, Connecticut, USA.

Within the Quebrada Fiera sample, there are two individuals with associated upper and lower dentition, a juvenile (MCNAM-PV 3968) and an adult (MCNAM-PV 3967). A third individual has associated lower dentition and postcranial bones (MCNAM-PV 4697), while the rest of the sample is composed of isolated teeth and very fragmentary upper and lower jaws, which makes comparisons difficult. In general, lower dentitions are more abundant, 30 specimens versus nine with upper teeth.

All specimens mentioned in the text are listed in Appendix 1. These include material from the collections listed above, many unpublished but catalogued, and others previously published as Deseadan interatheres (e.g. *Plagiarthrus*, *Progaleopithecus*, *Archaeophylus*, *Argyrohyrax*, and *Cochilius*). Appendix 1 also lists interathere remains from Quebrada Fiera. The geographic location of Deseadan localities is shown in Figure 1.

Figure 1. Geographic location of Deseadan localities. (1) Salla-Luribay (Bolivia); (2) Arroyo María Grande (Corrientes Province, Argentina); (3) Santa Lucía Basin, Canelones Department (Uruguay); (4) Quebrada Fiera (Mendoza Province, Argentina); (5) Rocas Bayas (Río Negro Province, Argentina); 6–13, Chubut Province, Argentina; (6) Bajada del Diablo; (7) El Pajarito; (8) Las Cascadas; (9) Rinconada de los López; (10) Oeste Río Chico (Ameghino's *Pyrotherium* beds); (11) Scarritt Pocket; (12) Cabeza Blanca; (13) Gran Barranca; (14) Santa Cruz Province, Argentina: La Flecha.

For teeth, the mesial and distal faces refer to the front and back of the head, respectively; Figure 2 shows a comparative scheme for the molars of *Argyrohyrax* (Figure 2(a)–(d)), *Progaleopithecus* (Figure 2(b)–(e)) and *Archaeophylus* (Figure 2(c)–(f)). Based on tooth measurements (length and width of M/m1), a bivariate graph compares the sizes of Deseadan taxa (Appendix 2).

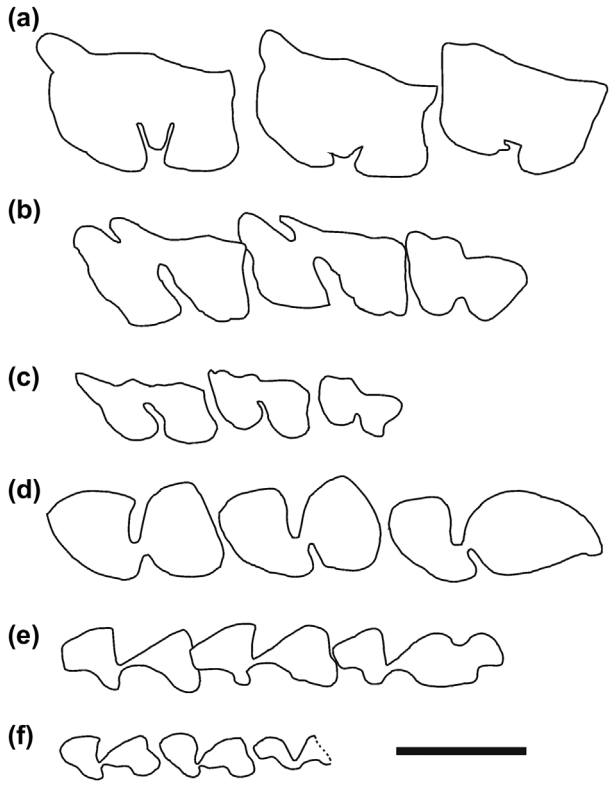

Figure 2. Comparative schemes of upper and lower molars. (a, d) *Argyrohyrax* (based on MACN A52-472 and ACM 3055), (b, e) *Progaleopithecus* (based on AMNH 29603) and (c, f) *Archaeophylus* (based on MACN A52-483 and MACN A52-485). Scale bar is 5 mm.

Phylogenetic analysis was conducted using the computer program TNT 1.1 (Goloboff et al. 2008), on the basis of a data matrix of 16 terminal taxa and 46 dental and cranial characters (Appendices 3 and 4), and applying a similar search protocol to that used by Vera (2016). Maximum parsimony under equal weights was assumed. Terminal taxa were chosen as the most completely preserved species of the Notostylopidae, Olfieldthomasiidae, and Notopithecidae, as well as Tinguiririan, Deseadan, Colhuehuapian, and Santacrucian interatheres. Polarisation of the characters was based on outgroup comparison criterion, using *Simpsonotus praecursor* Pascual, Vucetich and Fernández 1978 (Henricosborniidae) as outgroup. All characters were treated as unordered, referred to in brackets with character states in superscript.

Abbreviations: a.f, antorbital foramen; C/c, upper/lower canine; dc, distal cingulum; df, distal fossette; DP/dp, upper/lower deciduous teeth; en, entoconid; hy, hypocone; hyd, hypolophid; I/i, upper/lower incisor; L, length; M/m, upper/lower molar; ls, lingual sulcus; mf, mesial fossette; P/p, upper/lower premolar; pr, protocone; W, width.

Systematic paleontology

Order Notoungulata Roth 1903
Family Interatheriidae Ameghino 1897
Genus *Argyrohyrax* Ameghino 1897

1897. *Plagiarthrus* Ameghino, p. 344, Fig. 21; Loomis (1914, p. 62–63); Simpson (1932a, 1932b); Patterson (1940); Chaffee (1952, p. 522); Reguero et al. (2003, p. 452).

1901. *Notohyrax* Ameghino, p. 111

Type species. *Argyrohyrax proavus* Ameghino 1897

Distribution and age. Sarmiento Formation (Santa Cruz and Chubut provinces, Argentina), base of the Agua de la Piedra Formation (Mendoza Province) and Fray Bentos Formation (Corrientes Province), Argentina, Deseadan SALMA, Late Oligocene.

Diagnosis (amended). *Argyrohyrax* is the largest Deseadan interatheriine, characterised by P/p1–2 rooted and P/p3–M/m3 hypsodont with roots present only in very old individuals, and thick layer of cementum when it occurs. Differs from *Progaleopithecus*, *Archaeophylus* and *Cochilius* on the basis of P1 overlapped by C and P2, well-developed and very ephemeral distal cingulum in P4–M2, single sulcus in M1–2, and a very prominent descending process of the maxilla (shared with *Cochilius*), p1 not overlapped by c and p2, well-developed protoconid fold in p2 (shared with *Progaleopithecus*), postmetacristid in p3–4, quadrangular trigonid and subcircular talonid in m1–2. This taxon differs from *Progaleopithecus* because of its P3–4 rectangular, with protoloph shorter than metaloph and a middle small lobe, M1–2 with a hypocone lingually protruding with respect to the protocone (less evident than in *Archaeophylus*), simple and very short i1 (not bifid), i1–2 less procumbent, p1 caniniform, m3 with rounded trigonid and talonid and a smoother labial sulcus on the talonid, and moderately expanded root of the zygomatic arch. *Argyrohyrax* contrasts with *Brucemacfaddenia* and *Federicoanaya* in having molarized P3–4, less pronounced parastyle on P3–M3 and rounded talonid on lower molars. Differs from *Interatherium* and *Protypotherium* because of a moderately expanded root of the zygomatic arch, radius with oval, slightly concave distal articular surface, and an ulna with humeral articulation less concave and more vertically oriented.

Argyrohyrax proavus Ameghino 1897
Figure 2(a)–(d), Figures 3–5, Figure 6(a)–(q).

1895. *Clorinda cliva* Ameghino, p. 624–625; Ameghino (1896).

1897. *Plagiarthrus clivus* Ameghino, p. 344; Loomis (1914, p. 62–63); Simpson (1932a, 1932b, 1945); Patterson (1940); Chaffee (1952, p. 522); Reguero et al. (2003, p. 452).

1897. *Argyrohyrax proavunculus* Ameghino, p. 345; Loomis (1914, p. 83); *Plagiarthrus proavunculus* Reguero (1999, in Reguero et al. 2003).

1901. *Notohyrax conicus* Ameghino, p. 111.

Holotype. MACN A52-472, palate with left I1–M3 and isolated right I1–3, C, P1, P3–M3.

Referred material. All specimens identified as *Argyrohyrax proavus* from both Quebrada Fiera (Mendoza) and Patagonian localities are detailed in Appendix 1. The following description is based on the whole sample.

Distribution and age. Sarmiento Formation (Santa Cruz and Chubut provinces), base of the Agua de la Piedra Formation (Mendoza Province) and Fray Bentos Formation (Corrientes Province), Argentina, Deseadan SALMA, Late Oligocene.

Taxonomic background

Before discussing *Argyrohyrax*, it is necessary to explain some issues in relation to the earlier description of *Plagiarthrus*. Within his Protypotheriidae (= Interatheriidae) from Deseadan age, Ameghino (1895, p. 624–625) described the species *Clorinda*

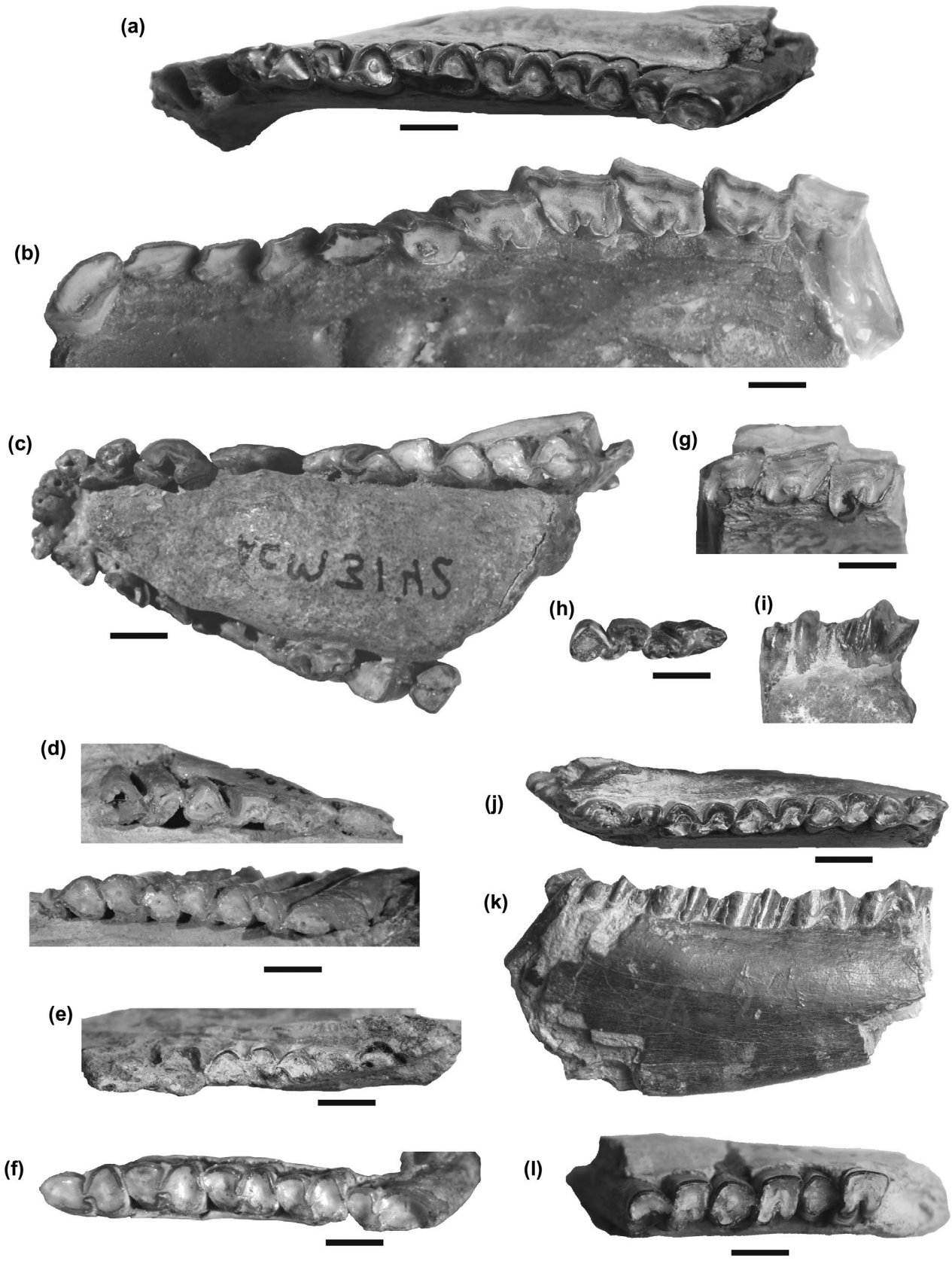

Figure 3. *Argyrohyrax proavus*: (a) MACN A52-474, mandible with right p2–m3; (b) MACN A52-472, palatal fragment with left I1–M3 (holotype); (c) ACM 3142, mandible with left c, p1–4, roots of i1–3, and right p2–3 and roots of i1–c; (d) AMNH 29606, mandible with left p2–4, separated from right p4 (broken)–m3; (e) MACN A52-480, lower jaw with m1–3 (syntype of *Argyrohyrax proavunculus*); (f) ACM 3055, mandible with right p3–m3; (g) MACN A52-478, maxilla with right P4–M2 (syntype of *Argyrohyrax proavunculus*); (h–i) MLP 93-XI-21-21, mandibular fragment with left p2–3, (h) occlusal and (i) lingual views; (j–k) MACN A52-479, lower jaw with dp3–dp4–m1–3, (j) occlusal and (k) lingual views (syntype of *Argyrohyrax proavunculus*); (l) MACN A52-473, mandible with left p4–m2 (holotype of *Notohyrax conicus*). Scale bar is 5 mm.

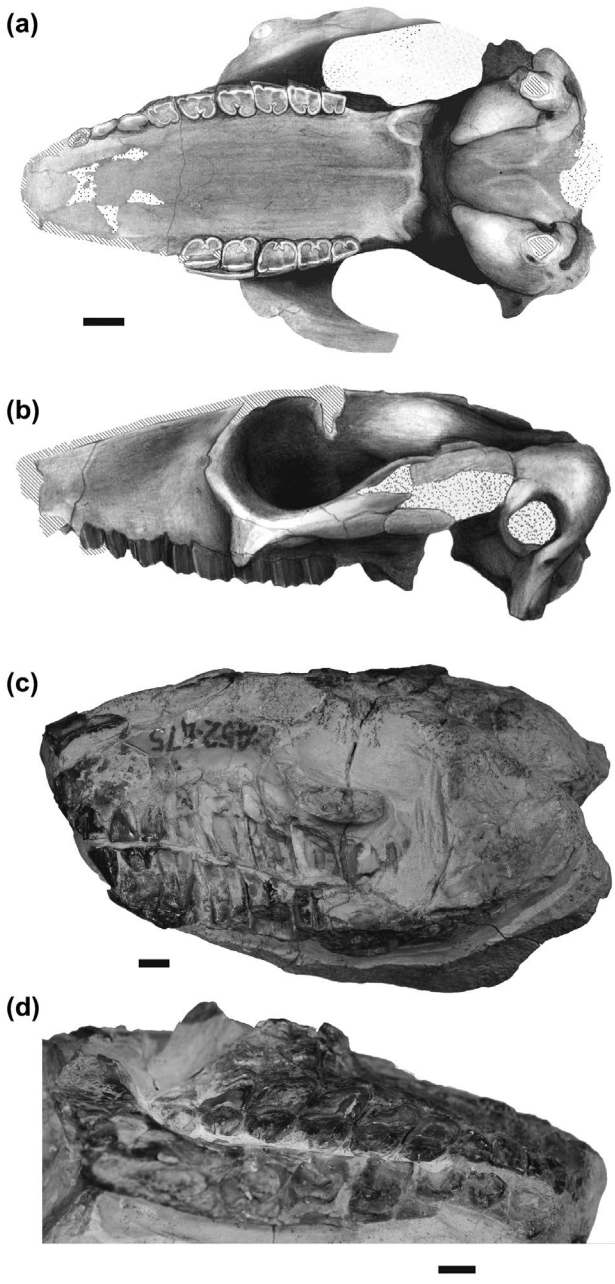

Figure 4. *Argyrohyrax proavus*: (a–b) rendering of FMNH 13415, a nearly complete skull with left C–M3 and right P3–M3, (a) ventral and (b) lateral views; (c–d) MACN A52-475, articulated skull, (c) lateral and (d) occlusal views. Scale bars are 10 mm in (a–b); 5 mm in (c–d).

cliva on the basis of a left astragalus (MACN A52-470) and the distal end of a tibia (the catalogue label MACN A52-471 refers to the distal epiphysis of a tibia, but this specimen cannot be relocated), which he suggested might pertain to the same individual. However, in 1896, Ameghino replaced the name *Clorinda* with *Plagiarthrus* because the former was preoccupied, placing the genus within Archaeohyracidae. A year later, Ameghino (1897: Fig. 21) characterised the genus *Plagiarthrus*, and the species *P. clivus*, based on two associated fragments of mandible with right p2–m3 and left p3–m2 (MACN A52-474, Figure 3(a)), without any mention of the original type specimen of this species. As a result, this mandible has been considered to be the material of reference for *P. clivus* by all subsequent authors (i.e. Loomis 1914; Simpson 1932a, 1945; Patterson 1940, 1952; Bond et al. 1998; Reguero 1999; Reguero & Prevosti 2010; Vera 2016). However, despite Ameghino's detailed description of this mandible, the type specimen of *P. clivus* is actually the astragalus MACN A52-470 (ICZN 2000, art. 73.1.2); although it has interatheriine characteristics, including bilaterally symmetrical trochlea with parallel and equally developed lateral and medial surfaces, association to the mandible MACN A52-474 cannot be assumed. Thus, a different name must be assigned to the mandible (see below), while *P. clivus* must be regarded as a *nomen dubium* (ICZN 2000, art. 75.5).

Within Archaeohyracidae, Ameghino (1897, p. 31–32; Fig. 20) described the genus *Argyrohyrax* and named three species. Of these, the type species, *A. proavus* Ameghino 1897 was based on a palate with left I1–M3 (figured by Ameghino 1897; Fig. 20) and isolated right I1–3, C, P1, P3–M3 (MACN A52-472, Figure 3(b)), the only specimen in the collection of MACN assigned to this species. Indeed, Loomis (1914, p. 83) noted 'The genus is known only by upper dentition, and while I did not find any associated lower teeth, I believe that some one of the genera known only by the lower dentition, like *Plagiarthrus*, is that lower dentition', while Simpson (1932a, p. 6) later agreed with Loomis and pointed out that 'the little that is known of the lower teeth of *Argyrohyrax* is like *Plagiarthrus*', and also 'the type species, *Argyrohyrax proavus* and *P. clivus*, appear to be of almost exactly the same'. It is probable that Simpson's comment was based on the mandible MACN A52-474 and the articulated skull MACN A52-475 (Figure 4(c) and (d)), the only specimen with associated upper and lower dentition catalogued as *P. clivus*. Consequently, Simpson proposed that *A. proavus* and *P. clivus* were probably synonymous names, *Plagiarthrus* having priority over *Argyrohyrax*.

In spite of its articulated condition, MACN A52-475 exposes the occlusal surface of the right P2–M3 (Figure 4(d)), allowing comparisons. The upper teeth are very similar in morphology and size (Table 1) to MACN A52-472 (Figure 3(b)) and the external morphology of the skull is comparable to FMNH 13415 (Figure 4(a) and (b); specimen published as *P. clivus* by Patterson [1932]). Unfortunately, the occlusal surface of the lower dentition in MACN A52-475 is completely covered, preventing direct comparisons with other lower teeth; however, the left side is labially exposed meaning that the tooth crowns can be seen. In this view, p2 has a low crown and roots, while p3–m3 have open crowns without roots (Figure 4(c)). This combination of characteristics is also observed in other adult specimens, including ACM 3142 (Figure 3(c)), AMNH 29606 (Figure 3(d)), MLP 93-XI-21-21 (Figure 3(h) and (i)), and MCNAM PV 4330. In addition, MACN A52-475 is comparable in size with MACN A52-474 and there is occlusal concordance between the latter and MACN A52-472 (the holotype of *Argyrohyrax proavus*). In this regard, we agree with Loomis (1914) and Simpson (1932a) in considering that the lower dentition assigned to *Plagiarthrus* corresponds with the upper dentition of *Argyrohyrax*. Nevertheless, establishing synonymy between *P. clivus* and *A. proavus*, as argued by Simpson (1932a), requires discussion of the fact the type specimen of *P. clivus* is an astragalus MACN A52-470, which cannot be confidently associated with the mandible MACN A52-474. Thus, on the one hand, *P. clivus* should be considered a *nomen dubium* (as proposed above; ICZN 2000, art. 75.5), including only the

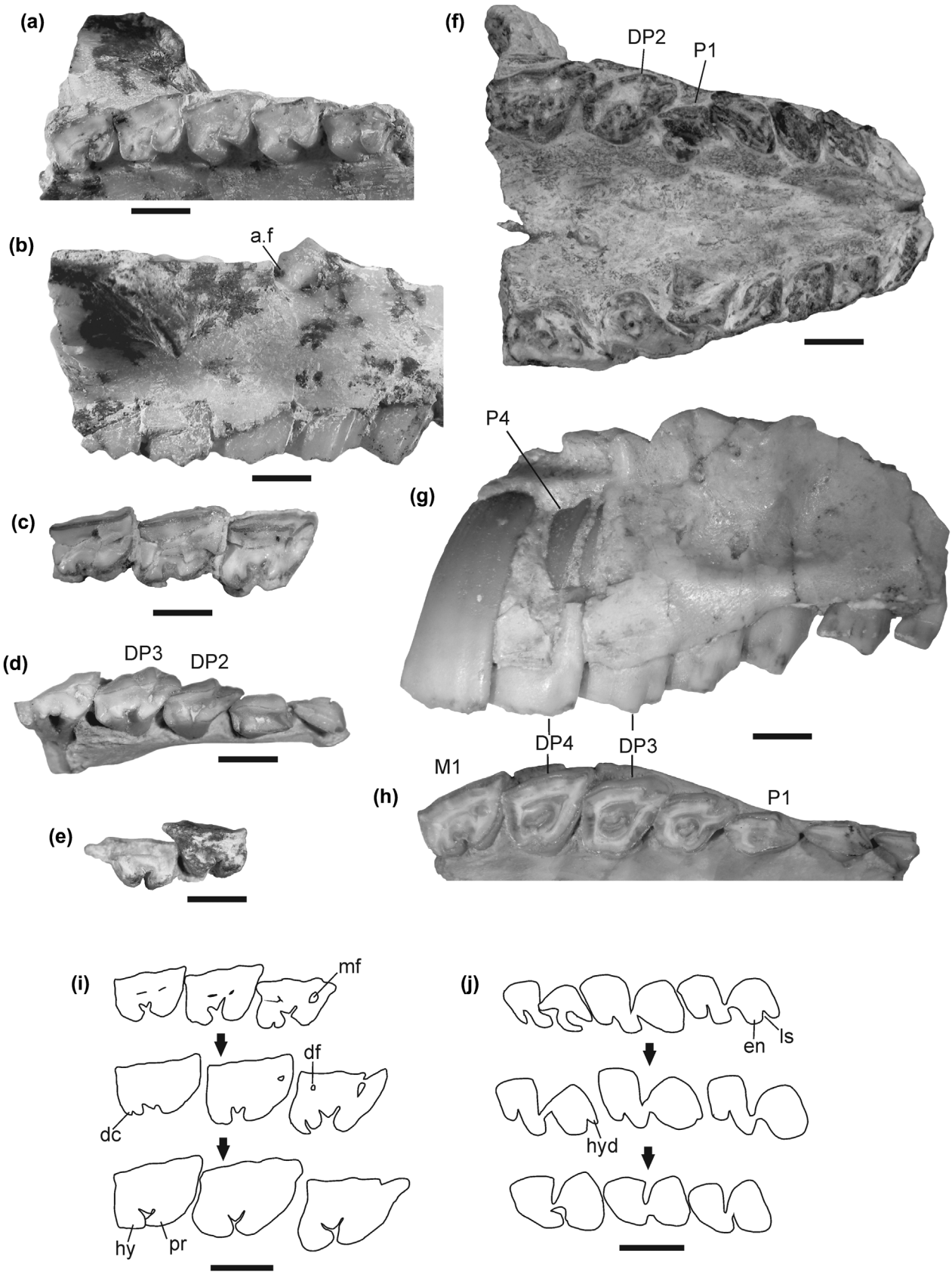

Figure 5. *Argyrohyrax proavus*: (a–b) MCNAM-PV 4233, maxilla with right P2–M2, (a) occlusal and (b) labial views; (c) MCNAM-PV 3967, right P4–M2, occlusal view; (d) MCNAM-PV 4059, maxilla with right C (broken), P1, DP2–4; (e) MCNAM-PV 4635, left DP3–4; (f) MCNAM-PV 3968, palate with left and right I1–3, C, P1, DP2–3; (g–h) MLP 79-XII-18-33, palate with right I3 (broken), C, P1, DP2–4, M1, (g) labial and (h) occlusal views; (i–j) main morphological changes through ontogeny on P4–M2 (i) and p4–m2 (j): increasing wear from top down. Scale bar is 5 mm.

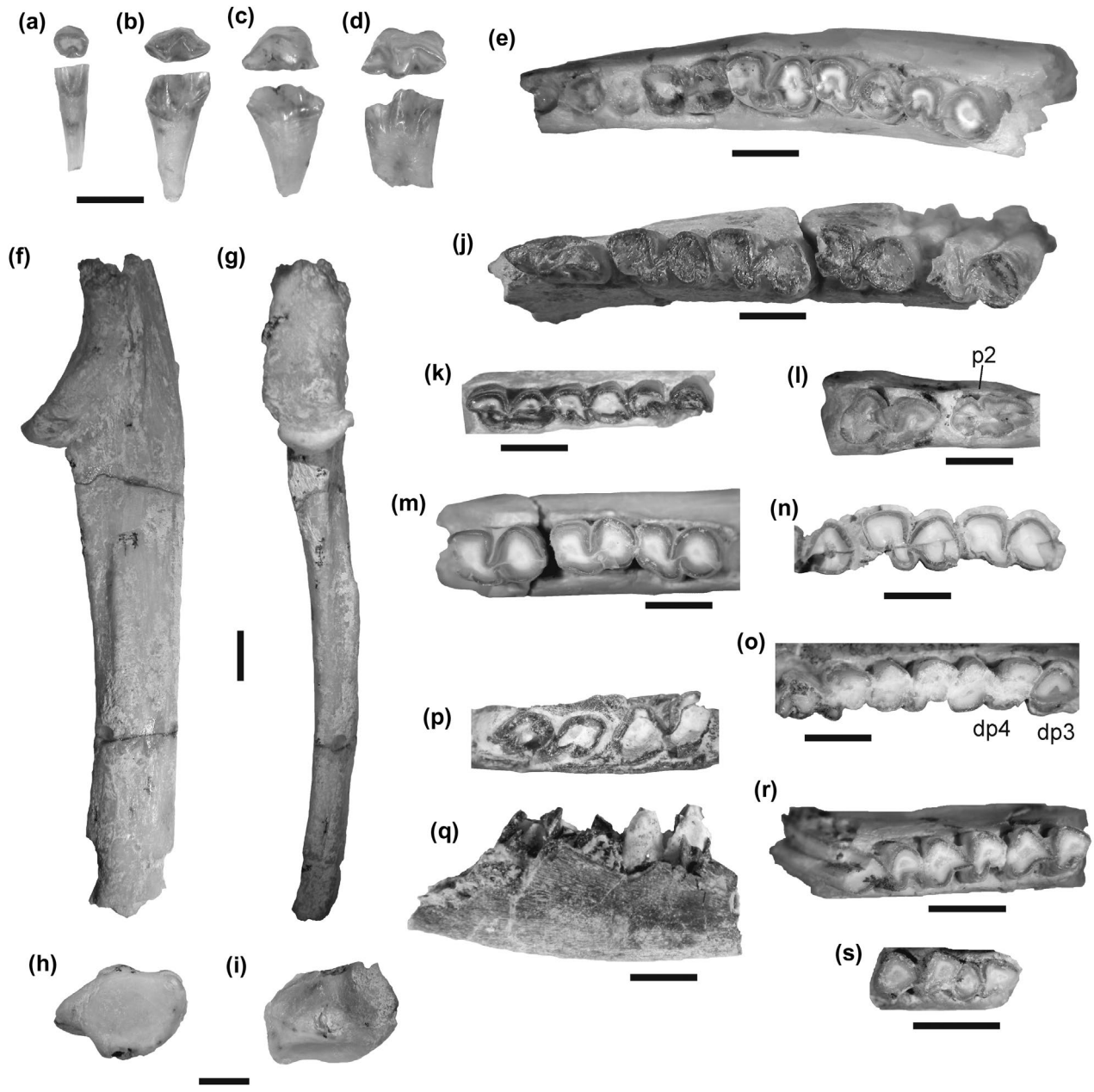

Figure 6. *Argyrohyrax proavus* (a–i): MCNAM-PV 4697, (a–c) isolated left i1, c, p1, and (d) right p1, occlusal (above) and lingual (below) views, (e) mandibular fragment with right p3 (broken)–m2, occlusal view, (f–g) left ulna, (f) lateral and (g) anterior views, (h–i) distal end of right radius, (h) distal and (i) posterior views; (j) MCNAM-PV 4330, mandible with right p2–m2, occlusal view; (k) MCNAM-PV 4055, mandible with right p4–m2; (l) MCNAM-PV 3976, mandible with left p2–3; (m) MCNAM-PV 4610, mandible with right p4–m2; (n) MCNAM-PV 3967, mandible with right p4 (talonid)–m2; (o) MCNAM-PV 4230, mandible with left dp3 (talonid)–m1–2; (p–q) MCNAM-PV 3968, mandible with left dp4–m1, (p) occlusal and (q) lingual views; *Progaleopithecus* sp.: (r) MCNAM-PV 4707, mandible with left m1–2 and trigonid of m3, occlusal view. Interatheriidae indet.: (s) MCNAM-PV 4742, mandible with left p4–m1, occlusal view. Scale bar is 5 mm.

type specimen; on the other hand, *Argyrohyrax proavus* would be the valid name to comprise both the type specimen (MACN A52-472) and the mandible MACN A52-474. The only way to resolve this issue will be a future discovery of associated dental and tarsal material that could reveal the association of both elements (astragalus and mandible) in the same taxon.

The second species of genus *Argyrohyrax*, *A. proavunculus* Ameghino 1897, is represented by just three specimens, MACN A52-478, an upper jaw with P3–M1 (Figure 3(g)); MACN A52-479, a lower jaw with left dp3–4–m1–3 (Figure 3(j) and (k)), and MACN A52-480, a very badly preserved lower jaw with m1–3, including a recently emerged m3 (Figure 3(e)). In the original description of this material, Ameghino (1897, p. 32) noted that *A. proavunculus* is a smaller species than *A. proavus*; he mentioned four upper teeth (L P3–M2 = 23 mm) and the length of seven lower teeth (L = 33 mm). However, none of these observations correspond with the specimens discussed above, meaning either that teeth have been lost from the maxilla (Patterson 1952) or that several specimens have been combined together, as was common to the work of Ameghino. Nevertheless, these three specimens are the type material (syntypes) of *A. proavunculus*. Reguero (1999, in Reguero et al. 2003) justified recognition of a second species, but in the genus *Plagiarthrus*, establishing the combination *P. proavunculus* and considering MACN A52-478 as lectotype.

Table 1. Measurements (mm) of permanent upper dentitions of Desedan interatheres.

	I1		I2		I3		C		P1		P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Argyrohyrax proavus																						
MACN A52-472	8.7	3.3	6.6	3.0	6.3	3.3	6.3	3.3	6.3	3.7	6.3	4.8	7.2	5.4	7.5	5.4	7.0	4.9	6.9	4.3	6.7	4.0
MACN A52-475											6.4	–	7.7	–	7.3	–	6.8	–	6.1	–	7.0	–
MACN A52-478															>5.5	–	6.2	4.5	5.5	–		
FMNH 13415							7.2	3.6	(5.9)	3.7	6.2	5.4	8.0	6.2	7.8	6.4	7.6	6.1	6.8	5.3	6.2	4.7
MCNAM-PV 3967													7.2	5.8	7.2	5.6	6.8	4.8	7.2	5.8		
MCNAM-PV 4059							>5.3	3.3	6.8	4.4												
MCNAM-PV 4186																			6.0	5.0		
MCNAM-PV 4233											4.9	4.0	6.5	4.2	6.5	4.3	6.1	4.4	5.9	4.0		
?Argyrohyrax proavus																						
MLP 79-XII-18-33							6.2	3.3	6.6	3.3							7.9	5.3				
Progaleopithecus tournoueri																						
AMNH 29603															5.1	–	5.3	3.9	5.4	3.7	4.9	3.3
MLP 93-XI-21-18															5.2	3.4	5.5	3.5	4.9	3.3		
MLP 93-XI-21-51																	4.5	3.9	5.3	4.2		
Archaeophylus patrius																						
MACN A52-483											3.4	2.1	3.6	2.6	3.9	2.7	4.5	2.8	4.2	2.4	3.4	1.9
MACN A52-484					3.3	1.6	3.6	1.3	3.1	1.9	3.8	2.6	3.2	3.0	4.1	3.1	3.9	3.1	3.7	2.6		

Notes: Approximate values in parentheses. Dashes represent not measured dimensions (broken tooth or alveolous).

MACN A52-478 (Figure 3(g)) is very similar to MACN A52-472 (Figure 3(b)) in having molars with a nearly straight ectoloph, as is also seen in FMNH 13415 (Figure 4(a)), although MACN A52-478 is quite smaller than both of them (Table 1), closer in size to MCNAM-PV 4233, a young individual from the Quebrada Fiera locality recognised as *Argyrohyrax proavus* (see below; Appendix 2). The lower molars of MACN A52-480 have a rounded talonid, and the m2 has a fossettid, a wide lingual sulcus on the talonid, and a labially undulated m3. The third specimen of *A. proavunculus*, MACN A52-479 (Figure 3(j) and (k)), is also similar but more worn than MACN A52-480; there is no fossettid on the talonid of m2, the lingual sulcus is shallower, and the labial sulcus of m3 is smoother. Besides, the dp3–4 of MACN A52-479 are similar to the same teeth of MCNAM-PV 4230 (Figure 6(o)) by having well-separated trigonid from talonid, although the dp4 is narrower (Table 4).

Both MACN A52-479 and MACN A52-480 differ from MACN A52-474 (Figure 3(a)) in having a thinner mandibular body and smaller size (Table 3), molars with small fossettid on trigonid and talonid, wider labial and lingual sulci, implying more separated trigonid–talonid, and a lingual sulcus on talonid of m2. These characteristics are also present in MCNAM-PV 4055 and MCNAM-PV 4230, two young specimens from the Quebrada Fiera locality. Thus, the observed differences can be explained by the younger condition of these specimens of *A. proavunculus* with respect to MACN A52-474. In consequence, the differences signalled between *Argyrohyrax proavunculus* and *A. proavus* can be related to ontogenetic variations and do not support their specific separation, implying that *A. proavunculus* could be indeed a synonymous name of *A. proavus*.

The third species of *Argyrohyrax*, ?*A. acuticostatus* Ameghino 1901, is only represented by the specimen MACN A52-626, associated right DP3–4 and M1–2, catalogued as the holotype. This fossil keeps the Ameghino's handwritten label indicating it comes from 'Golfo de San Jorge', a very imprecise location that refers to any locality or area situated in the East part of the Chubut Province; besides, the mention of 'Couches à *Pyrotherium*' indicates a Deseadan age. Ameghino's (1901, p. 361) original description of ?*A. acuticostatus* refers to the three persistent upper molars occupying a space of 21 mm, but it is not clear if they were the only teeth the author had at hand; he characterised the molars as being lingually trilobed and with a very prominent labial fold. The catalogued holotype MACN A52-626 does not match in number of teeth with the original description, because it is composed of four teeth and presents just two molars (DP3–4 and M1–2), but the latter show the mentioned characteristics. These teeth were apparently found in association, but they are not supported by the maxillary bone; DP3 and DP4 are embedded in a matrix of plaster; they are low crowned, quadrangular and worn, while M1–2, glued between them, are very high crowned and little worn. It is difficult to ascertain that this specimen is the holotype of ?*A. acuticostatus*, as we can assume that Ameghino would have commented on deciduous teeth; a possibility is that both portions were not associated and just the molars were part of the holotype, having lost the M3.

In any case, these M1–2 differ from those of *Argyrohyrax proavus* in the presence of large labial fossettes, a well-developed distal cingulum and lingual medial lobe (trilobed lingual face), narrower protoloph and metaloph, and a very convex and labially developed parastyle fold (as was mentioned by Ameghino). The length of the M1–2 falls within the range of *A. proavus*, but their width does not reach the minimum value (Appendix 2). The same differences are valid with respect to *Progaleopithecus* and *Archaeophylus*. The characteristics described for MACN A52-626 resemble those seen in the Tinguiririan taxa (pre-Deseadan/post-Mustersan, Late Eocene, Reguero et al. 2003) from Patagonia and Chile, *Santiagorothia chiliensis*, *Proargyrohyrax curanderensis* and *Eopachyrucos pliciferus* Ameghino 1901, which cannot be distinguished by their upper molars alone (Hitz et al. 2000). The fragmentary condition of MACN A52-626 prevents more conclusive comparisons, but precludes it from belonging to *Argyrohyrax* and the other two mentioned Deseadan genera, leaving open its generic ascription.

Also within the Archaeohyracidae, Ameghino 1901 described *Notohyrax conicus* from the '*Pyrotherium* beds', based on a mandible with the left p4–m2 (holotype MACN A52-473; Figure 3(l)). This specimen is a young individual very similar to *Argyrohyrax proavus* by the presence of a square trigonid with a

lingual sulcus, rounded talonid, and comparable sized teeth and mandibular ramus (Table 3). We consider that MACN A52-473 is undistinguishable from *Argyrohyrax proavus* and, in consequence, *Notohyrax conicus* is a synonymous name of *A. proavus* as suggested by Patterson (1952).

Description and comparisons

Skull

The description of the skull is based on FMNH 13415 and MACN A52-475 (Figure 4(a)–(d)), the auditory region of which was described in detail by Patterson (1932). This skull has a convex profile and a long and tall rostrum (Figure 4(b) and (c)). The orbit is large, elongate, and posteriorly open; its anterior border is at the level of the P4 and protrudes with respect to the maxilla. Ventrally, the root of the zygomatic arch is moderately expanded, differing from other interatheriines such as *Interatherium* Ameghino 1887 and *Protypotherium* Ameghino 1887, where the base of the zygomatic arch is wider. There is a prominent descending process of the maxilla above M1 (as in *Cochilius* and *Interatherium*), which is ventrally directed (Figure 5(b)). In turn, the descending process is rather developed in *Brucemacfaddenia* and absent in *Federicoanaya* (Hitz et al. 2008). The antorbital foramen is a large circular opening located between P4 and M1, as seen in MACN A52-475 (Figure 4(c)) and MCNAM-PV 4233 (Figure 5(b)). The zygomatic arches are thick laterally and increase in height posteriorly; they are laterally expanded and convex (Figure 4(a) and (b)). The postorbital apophyses are well-developed and pointed, placed at the level of the M3. Posterior to these apophyses, there is a well-marked postorbital constriction. The dorsal crest is thin and low, but barely preserved; in lateral view, it forms an arch that descends posteriorly to contact with the nuchal crest (Figure 4(b) and (c)). The palate is oval and long; its maximum width is between the M1 teeth, and its posterior border surpasses the level of the M3 (Figure 4(a)). The basicranium of this specimen is short and wide, the auditory bullae are large, inflated, and have extensive medial contact with the basioccipital.

The rostrum and palate of FMNH 13415 are roughly similar to conditions seen in the skull UF 91679, referred to *Federicoanaya sallensis* from Bolivia (Hitz et al. 2008). In both, a dorsal process on the maxilla, directly above the orbit, projects posteriorly into the frontal. However, due to poor preservation of FMNH 13415, it is not clear that an anteriorly projecting frontal sliver, excluding the maxilla from the orbit, is present, as Hitz et al. (2008) described for UF 91679.

Upper permanent dentition

In the dentition, I1 is the longest of the upper incisors (MACN A52-472; Figure 3(b); Table 1). This incisor is kidney-shaped in cross section, labially convex and lingually concave, while the I2–3 have a mesial fold on the ectoloph and a low lingual cingulum. The I2 is labially more convex and slightly longer than I3. The canine is very similar to I2–3, but having a better developed mesial fold on the ectoloph. The linguodistal sector of the I2 overlaps the labiomesial area of I3, as is the case between the I3 and C.

The P1 (MACN A52-472; Figure 3(b), and FMNH 13415; Figure 4(a)) is a simple tooth, similar to C because of the presence of a talon basin, but somewhat wider, and with limited parastyle development; P1 is overlapped by C and P2, like *Federicoanaya*, but different from *Progaleopithecus*, *Archaeophylus*, *Cochilius* and *Brucemacfaddenia*. In MCNAM-PV 3968, P1 has not completed its eruption and thus permits observation of the more convex and centred labial fold.

As is the case in P1, P2 is low-crowned and rooted in adult individuals (MACN A52-472). In FMNH 13415 P2, the protocone and hypocone are very close lingually, preserving a shallow lingual entrance, and the parastyle fold is developed, while, in contrast, in MACN A52-472 the protocone and hypocone are completely joined, isolating a small central fossette and the parastyle fold is less convex. In MCNAM-PV 4233 (Figure 5(a) and (b)), P2 lacks wear while P3–4 are worn; this indicates that P2 is the last premolar to erupt, a pattern shared with some notopithecids and other interatheriines (Vera 2016), as well as a number of other groups (e.g. hegetotheriid *Paedotherium*, Cerdeño et al. in press).

The P3–4 have a trapezoidal outline (MACN A52-472), longer and wider than P2, but as is the case in the latter, they have well-developed parastyle and paracone folds, and a parastyle sulcus (Figures 3(b) and 4(a); Table 1). In these teeth, the protoloph is transversally shorter than the metaloph, and both are separated by a lingual sulcus that bifurcates forming a small median lobe, and a small and shallow mesial fossette is also present in young individuals (MCNAM-PV 4233; Figure 5(a) and (b)). Unlike P2, P3–4 have very long and curved crowns that develop roots in very old individuals.

As is the case with the P3–4, the molars are rectangular, have a lingual sulcus and an interior median lobe, but the absence of a deep parastyle sulcus and a well-developed paracone fold give these teeth a straighter ectoloph, with the parastyle mesially directed (Figures 3(c) and 4(g)). The size and depth of the lingual sulcus decreases from M1 to M3, and the hypocone lingually protrudes with respect to the protocone (less evident than in P3–4). The M1–3 have a convex mesial face and a wide protoloph-protocone; the distal faces of these teeth are straighter, even slightly concave, and their long and curved crowns have roots in very old individuals. The cement layer is not continuous around the tooth crown, mainly concentrated on the lingual sulcus; P2–M2 have a well-developed distal cingulum, which fuses early with wear, while the mesial cingulum is absent.

The P4–M2 of MCNAM-PV 3967 (Figure 5(c)) are very similar in their size and morphology to FMNH 13415 (Table 1 and Figure 4(a) and (b)), but there is a tiny mesial fossette in P4 (not visible in molars), and a very shallow and short lingual sulcus in the hypocone (shallower in M1), the remains of the distal cingulum, perhaps because of the earlier ontogenetic stage of specimen MCNAM-PV 3967. This ephemeral sulcus is also present, but less evident, in MCNAM-PV 4233, an intermediate ontogenetic stage between MCNAM-PV 3967 and FMNH 13415 (Figure 5(i); Appendix 2). Indeed, MCNAM-PV 4233 differs from FMNH 13415 because P2–4 have a shorter protoloph than metaloph. Specimens MCNAM-PV 3967 and FMNH 13415 are similar to MACN A52-472 (Figure 3(b)), although the latter shows strong imbrication among the P3, P4 and M1, not so evident in MCNAM-PV 3967 (Figure 5(c)). Other fragmentary upper teeth (i.e. MCNAM-PV 3972, MCNAM-PV 4957 and MLP 79-XII-18-35) share the trilobed lingual face of the upper

molars as described in MCNAM-PV 3967. MCNAM-PV 4186 is an isolated upper molar (M2?) similar to MCNAM-PV 3967, but almost square and with less difference between length and width (Table 1); we opt to consider this as intraspecific variation.

Morphological variations between a very little worn specimen and a more worn individual (Figure 5(i)) are accompanied with dimensional changes that imply an increase in the general size of the teeth (Appendix 2), but the proportions between their length and width are retained (Table 1). Similar condition is observed in *Brucemacfaddenia* and *Federicoanaya* (Hitz et al. 2008; Figs. 2–3, 7; Tab. 1). Regarding these taxa, *Argyrohyrax* has wider molars and is 6% larger than *Brucemacfaddenia* (Appendix 2), and also differs from both Bolivian genera by having molarized P3–4 and less folded ectoloph on upper cheek teeth.

Deciduous upper dentition

Five specimens preserve deciduous dentition in different stages of wear. Of these, MCNAM-PV 3968 (Figure 5(f)) is the youngest, showing low-crowned, strongly overlapped incisors and canine. In this dentition, DI3 covers the mesial half of DC, DI2 covers DI3, and DI1 imbricates DI2, while DI2–DC are similar in size, labially convex, and with mesial halves that are wider than their distal portions; DI1 is narrower and longer than DI2–3 (Table 2). The incisors and canine of this specimen also have a low cingulum along the lingual face, feature that resembles the higher crowned permanent teeth of MACN A52-472 (Figure 3(b)). The DP2–4 (Figure 5(d)–(f) and Table 2) differ from the permanent premolars because they have lower crowns, are labiolingually narrower, mesiodistally enlarged, and strongly overlapped. Deciduous teeth have a more undulated ectoloph, opened mesial and central fossettes, and a shallow lingual sulcus that does not reach the base of the crown. In contrast, these teeth also have a well-developed distal cingulum and a hypocone that is more developed than the protocone of the permanent teeth (Figure 5(c)). Specimen MCNAM-PV 4635 (Figure 5(e) and Table 2) shares the strong overlapping between DP3–4 with MCNAM-PV 4059 (Figure 5(d)) because of a well-developed and mesially extended parastyle, but nevertheless also differs in having a distally extended metastyle in DP4, as well as a nearly straight ectoloph. FMNH 14688 (Appendix 1; Table 2) is considered to be a juvenile with DP2–4 that have roots and low crowns. Overall, this specimen is very similar to MCNAM-PV 4635.

In summary, the highly folded paracone on DP2–3 is a feature only seen in MCNAM-PV 4059 (Figure 4(d)), while the developed metastyle characterises MCNAM-PV 4635 (Figure 5(e)). Despite these differences, these two specimens and MCNAM-PV 3968 are considered the same taxon, comparable to FMNH 14688. Respect to *Federicoanaya* (UF 91376), the DP3–4 of *Argyrohyrax* are longer than narrow, have a well-developed distal cingulum and middle lobe, and a more prominent parastyle anteriorly projected, being comparable to the deciduous teeth of *Brucemacfaddenia* (UF 91820, UF 91822).

Specimen MLP 79-XII-18-33 (Figure 5(g) and (h)) deserves special consideration. This is because although it is a juvenile, it is very large and has the greatest length of all measured M1 teeth (Table 1). The DP2–4 (Figure 5(h)) are wider and shorter (square) than the others (Table 2), have a nearly straight ectoloph without a lingual sulcus (probably closed with wear), and equally well-developed protocone and hypocone. The P1 is similar to that of MCNAM-PV 4059, while the M1 is very similar to that of FMNH 13415. Thus, the most parsimonious interpretation of this variation is to consider all specimens in the same taxon, at two extremes (see Billet et al. 2009; Vera & Cerdeño 2014) encompassing a marked morphological and size transformation between MCNAM-PV 4059 (youngest individual) and MLP 79-XII-18-33 (much worn juvenile). This variation encompasses the longer than wide to square occlusal outline, closure of the lingual sulcus, and softening of labial folds and sulcus. In contrast, an alternative explanation could be that MLP 79-XII-18-33 represents a different taxon from *Argyrohyrax proavus*, as in addition to proportional changes there are also some morphological differences (Appendix 2). However, additional fossil material will be required to resolve these issues, and in the meantime this specimen is considered ?*Argyrohyrax proavus*.

Mandible

The height of the horizontal ramus remains approximately constant, gradually increasing posteriorly (in MACN A52–474, Hp2/p3 level = 15.0 mm; Hp4/m1 level = 17.3 mm; Hm2/m3 level = 19.4 mm). Labially, a large foramen is present below the trigonid of p4 and the ventral border of this specimen is moderately convex. Internally, this margin is concave, just above the inferior border, between m2–3, while the posterior border of the symphysis is at the p2–3 level (Figure 3(a)).

Lower permanent dentition

The enamel is discontinuous in the cheek teeth of this taxon. The specimen MCNAM-PV 4697 includes a fragment of mandible with the right p3 (broken)–m2, isolated left i1, c, p1, p2, p4, m1, m3, and a right p1 (Figure 6(a)–(e) and Table 3) associated with postcranial bones (Figure 6(f)–(i), see below). Of these teeth, the i1 (Figure 6(a)) is simple and very low, labiolingually narrow, softly convex labially, and with a lingual sulcus lending a B-shaped occlusal outline, the mesial lobe shorter than the distal. This tooth is similar to the i1 of *Cochilius* while differing from

Table 2. Measurements (mm) of deciduous upper dentitions of Deseadan interatheres.

	DI1		DI2		DI3		DC		DP2		DP3		DP4	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Argyrohyrax proavus														
FMNH 14688									(6.9)	4.5	8.4	4.7	7.9	4.7
MCNAM-PV 4059									7.2	5.0	8.1	5.9	(7.1)	–
MCNAM-PV 4635													6.8	4.6
MCNAM-PV 3968	7.8	(2.4)	6.3	2.8	6.5	3.3	6.8	3.7	8.0	(5.7)	8.9	6.0		
Argyrohyrax proavus?														
MLP 79-XII-18-33									7.1	5.7	6.9	7.1	7.4	7.0

Notes: Approximate values in parentheses. Dashes represent not measured dimensions (broken tooth or alveolous).

Table 3. Measurements (mm) of permanent lower dentitions of Desedan interatheres.

	i1		i2		i3		c		p1		p2		p3		p4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	W
Argyrohyrax proavus																						
MACN A52-474											7.1	3.4	7.2	3.8	7.3	4.1	6.2	4.0	6.2	3.6	8.2	3.6
MACN A52-479																	6.0	3.8	5.9	2.9	7.2	2.6
MACN A52-480																			5.7	2.9		
MACN A52-481			2.0	1.2	3.6	1.8	4.5	1.8			5.1	2.1										
MCNAM-PV 3957																					8.7	4.2
MCNAM-PV 3966																	5.4	3.5	5.5	3.2	6.5	2.8
MCNAM-PV 3967															6.8	4.5	6.5	4.0	6.5	4.1		
MCNAM-PV 3968																	5.2	(3.4)				
MCNAM-PV 3976											(6.5)	(3.2)	6.7	4.6								
MCNAM-PV 3977																	5.6	3.6	5.8	4.0		
MCNAM-PV 4055															6.6	(3.8)	6.6	(3.6)	6.5	(3.3)		
MCNAM-PV 4070																	6.5	4.7				
MCNAM-PV 4195															6.2	4.2	6.7	4.4	6.7	4.0	7.1	3.2
MCNAM-PV 4230																	6.3	4.0	6.7	3.5		
MCNAM-PV 4232											7.4	3.1										
MCNAM-PV 4248															7.0	3.9	6.6	4.3	8.2	(3.9)		
MCNAM-PV 4330											6.7	3.3	6.6	4.0	6.2	4.4	–	4.7				
MCNAM-PV 4610															6.6	4.4	6.4	4.3	6.5	4.3	9.0	4.0
MCNAM-PV 4697	2.5	2.0					4.7	2.4	5.7	3.1	6.8	3.0	–	–	6.3	4.4	6.4	4.2	6.6	4.2	8.1	3.3
MCNAM-PV 4709															5.8	3.7	6.8	4.2				
MCNAM-PV 4717																			6.4	4.1	9.3	3.7
MLP 73-VII-1-11																					7.0	3.2
MLP 79-XII-18-31																					8.1	3.8
MLP 79-XII-18-32																	7.1	3.2	7.0	3.0		
Argyrohyrax proavus																						
MLP 79-XII-18-40																			6.6	4.6		
MLP 79-XII-18-50																			7.0	4.5		
MLP 93-XI-21-20																			5.9	3.5	7.4	3.3
MLP 93-XI-21-21											7.5	3.5	7.0	3.7								
AMNH 29606													6.8	3.4	6.7	3.9	6.0	3.8	6.1	3.7	8.3	3.4
ACM 3055													7.3	4.8	7.0	4.8	7.1	4.7	6.4	4.8	8.4	4.2
ACM 3142	2.3	2.2	2.7	2.8	3.5	2.7	3.8	1.8	5.3	1.6	7.5	2.1	7.2	3.3	7.5	4.0						
ACM 3706																	6.9	3.8				
Progaleopithecus fissurelatus																						
MACN A52-486	–	1.3*	–	1.3*	2.2	1.3	2.7	1.4														
P. tournoueri																						
MNH DES 334	1.4	1.4	1.6	1.9	3.0	1.4	4.0	1.7	4.9	1.9	5.3	2.0										
MACN A52-479c					3.5	1.7			5.3	2.1												
MACN A52-481			2.0	1.2	3.6	1.8	4.5	1.8			5.1	2.1										
AMNH 29603	1.6	1.4	2.1	1.7	3.2	1.7	4.4	2.1	5.3	2.2	5.5	2.1	5.0	2.4	4.6	2.7	4.9	3.0	5.2	2.8	6.6	2.6
FMNH 13337													4.7	2.2	5.1	2.4	5.4	2.8	5.5	3.0		
FMNH 14687																			5.1	2.6	5.8	–
ACM 11776											4.2	1.4	3.9	1.8	4.7	2.1						
MLP 89-XI-15-6															4.9	2.4						
Progaleopithecus sp.																						
MCNAM-PV 4707																	5.1	3.5	5.1	3.6	–	3.2
Archaeophylus patrius																						
MACN A52-485													(3.3)	(1.3)	(3.3)	(1.3)	3.6	1.9	3.5	1.9	–	1.4
Interatheriidae indet.																						
MCNAM-PV 4742															4.0	2.3	4.8	2.9				

Notes: Approximate values in parentheses. Dashes represent not measured dimensions (broken tooth or alveolous).
*Values taken from Ameghino (1904).

Table 4. Measurements (mm) of deciduous lower dentition of *A. proavus*.

	dp2		dp3		dp4	
	L	W	L	W	L	W
Argyrohyrax proavus						
MACN A52-479*			6.2	2.8	5.8	2.9
MACN A52-485	4.1	1.3				
MCNAM-PV 3968					(7.2)	(4.9)
MCNAM-PV 4230					6.1	4.0
MCNAM-PV 4606			7.0	3.2	6.8	3.5
MLP 79-XII-18-32					7.5	3.7

Note: Approximate values in parentheses.
*Syntype of *Argyrohyrax proavunculus*.

Progaleopithecus, *Protypotherium* and *Federicoanaya*, whose have bifid incisors, each with two long, cylindrical columns separated from each other to the base of the crown. The canine (Figure 6(b)) is almost twice the length of the first incisor (Table 3), and in occlusal view, it forms a labially convex V with a wide lingual sulcus; the mesial ramus is concave and much shorter than the labial. This tooth is similar to, but wider and more worn than, the canine of ACM 3142 (Figure 3(c) and Table 3). The p1 of MCNAM-PV 4697 (Figure 6(c)) is in a more advanced state of wear than ACM 3142, and it has a V-shaped trigonid with two rami separated by a wide lingual sulcus, in contrast to the canine; the p1 has a very small talonid, contrary to *Brucemacfaddenia* whose p1 lacks talonid, resembling i3 (Hitz et al. 2008). The implantation of the incisors is similar to the Bolivian taxa and not as procumbent (ACM 3142) as the condition in *Cochilius*, *Protypotherium*, and *Interatherium*.

In contrast to the p1, the p2 (MACN A52-474; Figure 3(a)–(i)) has a better developed talonid, but is slightly smaller than the trigonid and has a deep labial sulcus that separates both lobes; in this tooth, the trigonid is formed by two crests divided by a deep lingual sulcus, the paralophid is very short and the protoconid is a well-convex column, while the metaconid-cristid oblique contact is lingual. These characteristics are also observed in MLP 93-XI-21-21 (Figure 3(h) and (i)), MCNAM-PV 4232, MCNAM-PV 4330 (Figure 6(j)), ACM 3142 (Figure 3(c)) and AMNH 29606 (Figure 3(d)). In a younger individual (e.g. MCNAM-PV 4055), two shallow lingual sulci delimit a wide entolophid in the talonid (Figures 5(j) and 6(k)). MCNAM-PV 3976 has a broken p2 (Figure 6(l)), but it is possible to perceive the well-developed protoconid fold as it occurs in MACN A52-474, MCNAM-PV 4232 and MCNAM-PV 4330. In *Argyrohyrax proavus*, the p1–2 are rooted, as is the case in their upper homologues.

The p3–4 are very similar to m1–2; all of them have labially quadrangular trigonids, and a talonid that is nearly circular and labially pointed. The trigonid and talonid are almost equal-sized and are separated by opposite lingual and labial sulci, as described by Ameghino (1897, p. 345). All the teeth are covered by a thick layer of cement (MACN A52-474). There is a well-developed paralophid, parallel to, and shorter than, the metalophid, and a lingual sulcus that extends between them (Figure 6(j)). In younger individuals (Figures 5(j) and 6(k)), the p3–m2 are lingually trilobed due to the presence of a sulcus separating the hypolophid from the entolophid, and a very shallow fossettid is present in the talonid. As wear increases, this linguodistal sulcus fades, the talonid becomes circular, and the fossettid closes (Figures 3(a) and 5(j)). In premolars, the cristid oblique is very short and contacts the metalophid internally; the p4 tooth has a shorter hypolophid and there is a deeper lingual sulcus present between the talonid and trigonid. In molars, the cristid oblique is short and wide; this joins with the metaconid forming a curve at a more lingual point in the m2 than in m1 (Figures 5(j) and 6(n)). In addition, variability is observed among the p3; in some specimens (Figure 3dhi), the metalophid-metaconid bends forward, which is not the case in MCNAM-PV 4330 (Figure 6(j)). With respect to *Brucemacfaddenia* and *Federicoanaya*, *Argyrohyrax* has a better developed talonid on p2 and molarized p3–4.

The m3 tooth differs from the m1–2 because of the presence of a longer and narrower talonid and a narrower trigonid. The lingual sulcus on the talonid is wide and deep in young individuals, remains open with wear, and separates into a well-developed hypolophid (Figure 3(d)). In older specimens (Figure 3(a)), the relict of the lingual sulcus is retained as a concavity on the lingual face of the talonid. Although the p3–4 and molars are high-crowned, they develop roots in very old individuals.

Differences observed among specimens in this study can be attributed to ontogenetic variation. In younger individuals, the premolars and molars have more separation between trigonid and talonid, and there is a distolingual sulcus that separates the hypolophid from the entolophid. Besides, the paralophid is short but is differentiated by a wide lingual sulcus, the metalophid is parallel to the paralophid, and there is a tiny fossettid in the talonid (Figure 3(c)–(e)). In addition, cement is often absent from these teeth (Figure 3(c)). With greater wear, both the fossettid and sulcus disappear in the talonid of m1–2, conferring a cylindrical shape (Figure 3(f)), while the sulcus is permanent in the m3 and premolars. As wear increases, the occlusal surfaces widen, the labial sulcus becomes narrower (Figure 3(a)–(f)), and the metalophid turns distolingually (Figure 6(m)). Besides, the presence of roots (ACM 3706) and a thick layer of cement on the premolars and molars (ACM 3055) characterise adult individuals (Appendix 2). On the contrary, in *Brucemacfaddenia* and *Federicoanaya* the cementum is inconsistently present, thin and patchy when it occurs (Hitz et al. 2008, p. 452).

Lower deciduous dentition

MCNAM-PV 4230 preserves the dp3 (talonid), dp4, m1–2, and an erupting m3 (Figure 6(o)), corroborating the fact that milk molars are retained after eruption of the third molar, as is the case in other interatheriines including *Federicoanaya*, *Santiagorothia*, *Protypotherium*, *Interatherium*, and *Cochilius* (Sinclair 1909; Simpson 1932b; Vera 2016). The dp3–4 are similar to the molars, even larger than the m1 (Table 4), but with lower crowns (the lingual sulcus between the trigonid and talonid in dp4 finishes before it reaches the base of the crown). In turn, *Federicoanaya* has not molarized dp4 (MNHN-Bol-V-004509), such as it happens with its p4. With respect to the permanent premolars, the dp3–4 (MCNAM-PV 4606) have trigonid well separated from talonid; the trigonid is longer and talonid is more triangular, with trace of a posterolingual groove. Specimen MCNAM-PV 3968 (Figure 6(p) and (q)) is a very badly preserved fragment of a mandible with two teeth in place that are interpreted as the left dp4–m1. The horizontal ramus of this specimen is very low (Figure 6(q)) and the m1 is similar to, but longer than, the m1 of MCNAM-PV 4055 (Figure 6(k) and Table 4). The m1 in specimens MCNAM-PV 3968 and MCNAM-PV 4230 are very similar to one another and exhibit the characteristics described above that are seen in the molars of young individuals (Figure 6(o) and (p)). Indeed, in MCNAM-PV 4055, the metalophid-cristid oblique contact is at the midpoint, while in MCNAM-PV 3968 the contact is not yet visible. Specimens MCNAM-PV 4606 and MLP 79-XII-18-32 (Table 3) are very similar to one another, but are less worn compared to MCNAM-PV 4230 (Figure 6(o)).

It is interesting to note one peculiar difference that we have observed among interatheres. In the Santacrucian representatives (i.e. *Interatherium* and *Protypotherium*), the permanent cheek teeth are high-crowned and lack roots, differing from deciduous teeth which have roots (Sinclair 1909). The available material of *Argyrohyrax* shows that P2 is easily differentiated from the

DP2 (see description) and develops two roots in worn specimens (Figures 3(a)–(i), 4(c) and 6(j)). This fact indicates that it is a permanent tooth that develops roots earlier than its counterparts, in contrast with the possibility of being a retained DP2. Analogous situation was described for highly worn specimens of *Brucemacfaddenia*, whose P2–M1 do show roots but the posterior molars and lower cheekteeth do not, considered as hypselodont teeth; in turn, the P2–M3 and p3–m3 of *Federicoanaya* are hypselodont as no roots are observed to form even in heavily worn specimens (Hitz et al. 2008).

Postcranium

MCNAM-PV 4697 comprises two vertebrae (not described), an almost complete left ulna, the proximal end of a right ulna, and the distal end of right radius (Figure 6(f)–(i); Appendix 1). The ulna (Figure 6(f) and (g)) has a diaphysis (L > 67.4 mm) that is very compressed laterally, resulting in a very narrow bone; the shaft is longitudinally smoothly curved, and the upper half of the medial face is mildly excavated, while the lateral face has a longitudinal crest anterodistally directed. The anterior and posterior borders are rounded along the entire length of this element, and the facet for the radius is concave, long and narrow, located on the internal border of the olecranon (Figure 6(f)). The articulation for the humerus is less concave and more vertically oriented with respect to the proximodistal axis (Figure 6(g)) than in *Interatherium* (YPM-VPPU 15286), *Protypotherium* (YPM-VPPU 15828), and *Cochilius volvens* Ameghino (1901) (AMNH 29686; Simpson 1932b), where the articulation is more concave and curved laterally. In turn, the ulna of *Federicoanaya* exhibits greater lateral bowing and expansion of the distal shaft, and has a more robust olecranon (MNHN-BOL-V-004500, Hitz et al. 2008).

The distal end of the radius (Figure 6(h) and (i)) has an oval and slightly concave articular surface (10.5 mm × 8.2 mm), anteriorly pointed; the dimensions of this surface are close to those of the Deseadan *Federicoanaya* (Hitz et al. 2008, p. 466). In comparison, the radius of the Santacrucian *Interatherium* (YPM-VPPU 15286) is smaller (9.1 mm × 6.8 mm), with a more circular and concave articular facet.

Genus *Progaleopithecus* Ameghino 1904

Type species. *Progaleopithecus fissurelatus* Ameghino 1904

Distribution and age. Sarmiento Formation (Santa Cruz and Chubut provinces) and base of the Agua de la Piedra Formation (Mendoza Province), Deseadan SALMA, Late Oligocene.

Diagnosis (amended). *Progaleopithecus* is characterised by P3–4 molariform, a groove on the mesial face below parastyle in M1–2, a concave labial face of the trigonid in p3–m2, a concave distal face of the talonid in m1–2, p1–2 rooted (shared with *Argyrohyrax*), and a well-expanded root of the zygomatic arch. *Progaleopithecus* differs from *Argyrohyrax* on the basis of its smaller size, the absence of a distal cingulum in P3–M2, M1–2 that are rectangular (L > W) and nearly equal in size, with a hypocone and protocone similarly developed, stronger parastyle and paracone fold, and a deeper lingual sulcus lacking a median lobe, i1–2 that are bifid (shared with *Protypotherium* and *Federicoanaya*) with procumbent implantation, p1 overlapped by c and p2, a talonid that is smaller than the trigonid in p3 (like *Archaeophylus*), triangular and equal-sized trigonid and talonid, and a concave distal face of p4–m2, m3 that is trilobed, with the third lobe smaller, and a descending process of the maxilla that is moderately developed. *Progaleopithecus* differs from *Archaeophylus* because of its larger size, M1–2 with a protocone that is similarly developed to the hypocone, a more convex parastyle and a deeper labial sulcus, m1–2 having a more quadrangular trigonid, a narrower cristid oblique, and a more triangular-shaped talonid with a concave distal face, and the fact that the cristid oblique-metalophid contact in the m3 is at the mid-point. This taxon differs from *Cochilius* because it has hypsodont teeth, a single sulcus dividing lophs on M1–2, i1–2 that are bifid, size of i3 ≥ i2, c > i, p1 that is overlapped by c and p2, lacking a well-developed protoconid in p2, a talonid < trigonid on p2 and p3, a deep hypoflexid on m3, height of the mandibular horizontal ramus approximately constant, gradually increasing forward, and a small or moderately developed descending process of the maxilla. *Progaleopithecus* differs from *Brucemacfaddenia* in lacking median lobe on upper teeth and its smaller size. In comparison with *Federicoanaya*, it is larger and has molarized P4.

Remarks. The genus *Progaleopithecus* is known from the Quebrada Fiera locality on the basis of just one specimen (see below), which unfortunately does not allow for a specific determination. Nevertheless, this isolated record, combined with the study of unpublished specimens, permits taxonomic revision and enables improvements in the diagnosis of this taxon. As result, most of the material studied here is referred to *Progaleopithecus tournoueri*.

Progaleopithecus tournoueri Ameghino 1904

Figure 2(b) and (e); Figure 7(d)–(o)

1904. *Progaleopithecus tournoueri* Ameghino, p. 173–174 (*partim*); Patterson (1940).

1897. *Argyrohyrax proavunculus* Ameghino, p. 345; Hitz et al. (2000, p. 4, based on Marshall et al. 1986).

Lectotype. MNH DES-334, a left mandibular fragment with symphysis and i1–p2.

Referred material. MACN A52-479c, MACN A52-481, MACN A52–482, ACM 11776, AMNH 29603, FMNH 14687, MLP 89-XI-15–6, MLP 93-XI-20-5, MLP 93-XI-21-18 (Appendix 1).

Distribution and age. Sarmiento Formation (Santa Cruz and Chubut provinces), Argentina, Deseadan SALMA, Late Oligocene.

Taxonomic background

The genus *Progaleopithecus* includes two species that are known on the basis of very fragmentary lower dentitions. One of the hallmark characters used by Ameghino (1904, p. 173–174) is the morphology of the incisors, which are long and divided into two columns by a notch.

The type species, *Progaleopithecus fissurelatus*, was defined on the basis of isolated teeth, originally recognised as i1, i2, i3, c, p1 and p2 (MACN A52-486, which is the only material catalogued as *P. fissurelatus* in MACN). In this study, these six teeth are interpreted as two broken bifid incisors (i1 or/and i2; Figure 7(a)), left and right i3 (probably from the same individual; Figure 7(b)), a left c (Figure 7(c)), and a right p2 (Figure 7(p)). The incisors and canine figured by Ameghino (1906, Fig. 181) are similar in appearance and probably correspond to the teeth of

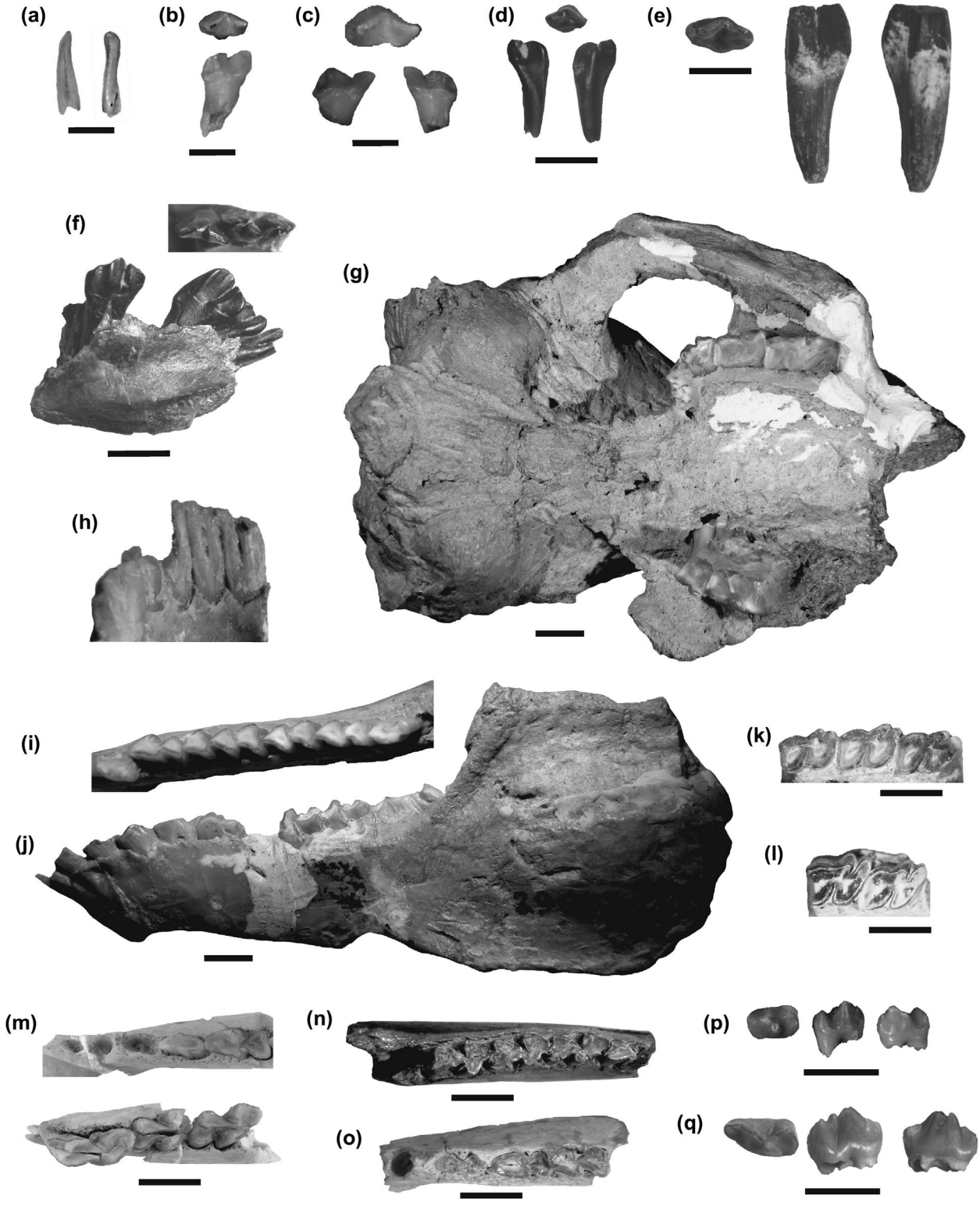

Figure 7. *Progaleopithecus fissurelatus*: (a–c) MACN A52-486, (a) fragment of i1 or i2; (b) left i3, occlusal and lingual views; (c) left c, occlusal, lingual and labial views; *P. tournoueri*: (d–e) MACN A52-479c, (d) right i3 and (e) p1?, occlusal (above), lingual and labial views; (f) MACN A52-481, left i2–c and p2, right i3 and p1, occlusal and labial views; (g–j) AMNH 29603, (g) skull with right M1–3 and left M2–3, (h) detail of left i1 and right i1–2 (not at scale), (i) lower jaw with right i1–2, dp2, p3–m3 (occlusal view) and (j) left i1–3, c, p1, dp2–p3, and m1–m3 (labial view); (k) MLP 93-XI-21-18, maxilla with right P4–M2, occlusal view; (l) MLP 93-XI-21-51, maxilla with right M1–2, occlusal view; (m) FMNH 14687, mandible with left m1–3 and right p2–3, occlusal view; (n) FMNH 13337, mandible with left p3 (broken)–m2, occlusal view; (o) MLP 89-XI-15-6, mandible with right broken p2 and p3–4; (p–q) Henricosborniidae indet.: (p) MACN A52-486, right p2, and (q) MACN A52-482, right p3, occlusal, labial and lingual views. Scale bars are 2 mm (a–d) and 5 mm (e–q).

MACN A52-486; they are comparable with, but smaller than, the homologous teeth of MACN A52-481 (*P. tournoueri*, see below). However, the premolar (p2, L = 3.5 mm, W = 2.2 mm; Figure 7(p)) present as part of specimen MACN A52-486 has a talonid that is wider than the trigonid, a characteristic that is also seen in the Henricosborniidae *Henricosbornia* Ameghino

(1901) (AMNH 28751), but not in interatheres, whose premolars have a reduced talonid that is smaller than the trigonid, as in MACN A52-481, MNH DES-334 (Patterson 1940) and AMNH 29603 (Chaffee 1952). Consequently, the p2 included in the lot MACN A52-486 is herein determined as Henricosborniidae indet. (Appendix 1).

Ameghino (1904, p. 174) described a second species, *P. tournoueri*, on the basis of a p2 and some other fragments of anterior teeth. Indeed, in the same paragraph, he also referred a fragment of left mandible (with three incisors, c, and p1–2) that was supplied by André Tournouër and figured by Ameghino (1906, Fig. 182). This specimen is actually curated in the MNHN (Paris) with the number MNH DES-334 and was re-studied by Patterson (1940, Figs. 8–9). At present, three specimens identified as *P. tournoueri* are present in the MACN collection, isolated right i3 and p1? (MACN A52-479c; Figure 7(d) and (e)), a right p3 (MACN A52-482; Figure 7(q)), and a fragment of mandible with the left i2, i3, c, p2 and the alveolus of i1 and p1 (MACN A52-481; Figure 7(f)).

Our research shows that the specimen MACN A52-482 is the premolar originally described by Ameghino (1904), and constitutes, as well as MNH DES-334, a syntype of *P. tournoueri*. However, revision of MACN A52-482 (L = 5.1 mm, W = 2.4 mm) suggests that this specimen is different from the other premolars referred to *P. tournoueri* (MACN A52-481, MNH DES-334, AMNH 29603, see below), as well as to other interatheres, such as *Argyrohyrax* (MCNAM-PV 4697, MCNAM-PV 4232, MCNAM-PV 4330) and *Progaleopithecus* (AMNH 29603, MLP 89-XI-15-6), because it has a triangular talonid that is wider than long and larger than the trigonid, a trigonid with a mesial branch that is shorter than the distal, with a well-developed metaconid separated from the mesial lophid by a notch, and the cristid oblique joined internally to the metalophid (Figure 7(q)). MACN A52-482 is similar to, but rather larger than, the p2 of *P. fissurelatus* herein recognised as Henricosborniidae indet. (see above; Figure 7(p)); indeed, the morphology and size of MACN A52-482 match the unworn p3 of specimens AMNH 28751 and AMNH 28802, referred to *Henricosbornia* by Simpson (1967). Thus, it is clear that Ameghino applied the name *P. tournoueri* to several different entities. Based on the aforementioned identification of the p3 of MACN A52-482 and in order to retain taxonomic stability, we choose the syntype MNH DES-334 as lectotype of *P. tournoueri*. This specimen displays most of the characteristics described by Ameghino (1904) for the species.

Comparatively, the lower incisors and canine of *Progaleopithecus fissurelatus* (MACN A52-486, Figure 7(b) and (c); Table 3) are similar to, but smaller than, the homologous teeth of *P. tournoueri* (MNH DES-334, AMNH 29603, Figure 7(h)). In both species, these incisors have bifid crowns and the canine is occlusaly V-shaped; therefore, size is apparently the only feature that can be used to differentiate *P. fissurelatus* from *P. tournoueri*, although establishing synonymy between them cannot be corroborated due to the incomplete and badly preserved type material of *P. fissurelatus*.

Description and comparisons

Specimen AMNH 29603 has associated upper and lower dentition (poorly preserved skull with right M1–3 and left M2–3, and lower jaw with right i1–2, p2–m3 and left i1–3, c, p1, p2–3, and m1–3; Figure 7(g)–(j); Tables 1 and 3); it was previously referred to *P. tournoueri* by Chaffee (1952), while Marshall et al. (1986) considered it to be *Argyrohyrax proavunculus*. The bifid condition of the incisors in AMNH 29603 (Figure 7(h)) is shared with the type material of both species of *Progaleopithecus*, but the incisor size (Table 3) and tooth morphology are similar to the lectotype of *P. tournoueri* (MNH DES-334). Based on these similarities, and considering the very limited material known for *P. fissurelatus*, we agree with Chaffee's (1952) determination. In addition, the nearly complete condition of AMNH 29603 permits us to associate and compare isolated upper and lower dentition curated in different institutions to the same taxon.

In general terms, the upper and lower cheek teeth of *P. tournoueri* are high-crowned with open bases and covered by cement. The enamel is discontinuous in the lower cheek teeth, similar to *Argyrohyrax*, although the sample does not allow us to corroborate the presence of roots in very old individuals, such observed in *Argyrohyrax*.

Upper dentition

The P4 and molars have one small fossette in each lobe, large, narrow and ephemeral (Figure 7(k)), while the M1–2 each has a mesial groove below the parastyle (Figure 7(l)) and a well-developed and high distal cingulum. In comparison with M1–2, the M3 is smaller, trapezoid-like and has a shallower lingual sulcus and less folded ectoloph (Figure 7(g)). Specimens MLP 93-XI-21-18 and MLP 93-XI-21-51 (Figure 7(k) and (l)) have the P4 and upper molars that are very similar in size (Table 1) and morphology to AMNH 29603, and both are here assigned to *P. tournoueri*, also including MLP 93-XI-20-5 (Appendix 1). Compared to *Argyrohyrax*, the M1–2 are rectangular (L > W) and nearly equal-sized, they have very folded ectoloph, deeper lingual sulcus and lack a middle lobe. The latter feature also distinguishes it from the Bolivian taxa. Compared to *Archaeophylus*, *Progaleopithecus* is larger (Tables 1 and 3; Appendix 2), and the M1–2 have much better developed parastyle and paracone folds, deeper labial sulcus, and nearly equal protocone and hypocone. In *Cochilius* (AMNH 29651), the M1–2 are trapezoid in shape, with almost straight, and very inclined labial faces (without a parastyle sulcus and folds), while the P3–4 are completely different from the molars, with a much folded parastyle and a deep labial sulcus. *Progaleopithecus* is smaller than *Brucemacfaddenia* (Table 1), having comparable tooth size to *Federicoanaya* (Hitz et al. 2008, Tab. 3), but differing from it in having a molarized P4 and much folded ectoloph in upper teeth (Figure 7(k) and (l)).

Lower dentition

The lower teeth of specimens MNH DES-334 and AMNH 29603 were described by Patterson (1940) and Chaffee (1952), respectively. In contrast, MACN A52-481 is a fragment of mandible with teeth (Figure 7(f)) very similar to MNH DES-334. In this specimen, the i1–2 are bifid, i3 is smaller than the canine, both i3 and canine have two rami forming a labially convex 'V' with a lingual sulcus, p2 has a V-shaped trigonid with a lingual notch, and a reduced and shorter talonid. In the series from i2 to canine, the teeth are imbricated and lingually inclined, i2–p1 each has one root, while p2 has two. The isolated right i3 MACN A52-479c is practically identical to the left i3 MACN A52-481 and probably

belongs to the same individual; instead, the p1 present in MACN A52-479c is more worn than the premolar present in MACN A52-481. As it was commented above, the p2 of MNH DES-334, MACN A52-481 and AMNH 29603 differ from the premolars MACN A52-482 and MACN A52-486 in having a reduced talonid, smaller than trigonid. Besides, the p1 and p2 of AMNH 29603 are rooted teeth, which means that the anterior premolars develop roots very early in the ontogeny (Chaffee 1952), as it also occurs in *Argyrohyrax proavus* (see above). Unfortunately, this characteristic cannot be verified in the upper premolars of *P. tournoueri*.

The p3–m2 have triangular trigonid and talonid, with concave distal face, being more evident in molars (Figure 7(i) and (m)), especially in FMNH 13337 (Figure 7(n)), differing from *Argyrohyrax* and *Brucemacfaddenia*, which share square trigonid and subcircular talonid on check teeth. In p3, the talonid is smaller than the trigonid (Figure 7(o)), while they are comparable in size in p4–m2. The mentioned distal concavity is not observed in *Argyrohyrax* or *Archaeophylus*. In *Cochilius* (AMNH 29658) the p3–m2 have triangular trigonid and subcircular talonid, which is wider than the trigonid. In turn, in *Federicoanaya*, the p3–4 have a larger trigonid than talonid, being rather different from molars.

The m3 differs from the m1–2 in having a shorter triangular trigonid and a longer and bilobed talonid due to a strong labial sulcus (Figure 7(i) and (m)). This sulcus is absent in *Cochilius*, *Brucemacfaddenia* and *Federicoanaya*, variable and smoothly marked in *Argyrohyrax* and unknown in *Archaeophylus*.

Progaleopithecus sp.

Figure 6(r)

Referred material. MCNAM-PV 4707, a fragment of mandible with the left m1–2 and the trigonid of the m3 (Table 3; Appendix 1).

Distribution and age. Base of the Agua de la Piedra Formation (Mendoza Province), Argentina, Deseadan SALMA, Late Oligocene.

Description and comparisons

The second interatheriid morphotype recognised within the Quebrada Fiera sample is represented by MCNAM-PV 4707 (Figure 6(r) and Table 3). All teeth are covered by a thick layer of cement, the enamel is interrupted on the mesial face, the m1–2 have quadrangular trigonid and triangular talonid separated by wide and deep labial and lingual sulci, the protolophid is lingually inclined, the metalophid is straight, the cristid oblique is wide and joins the metalophid below its middle point, the lingual face of the talonid is concave, the trigonid of the m3 is shorter than in the m1–2, and labially convex, differing from the straight labial face in the m1–2. In contrast, in *Argyrohyrax*, the molars have quadrangular trigonid and subcircular talonid, which are closer to each other, the protolophid is parallel (Figure 6(m)), the metalophid curves linguodistally in older individuals (Figure 3(a) and (f)) and the lingual face of talonid lacks concavity. The length of the m1 of MCNAM-PV 4707 is smaller than in *Argyrohyrax* (Table 3), falling into the range of *P. tournoueri* (AMNH 29603 and FMNH 13337, Appendix 2).

Specimen MCNAM-PV 4707 is (Figure 6(r)) rather similar to, but differs from AMNH 29603 (*P. tournoueri*; Figure 7(i)) because the molars (Table 3) have the trigonid and talonid closer between them, longer paralophid, and the longest axis of the talonid is nearly labiolingually oriented. In contrast, the longest axis of the talonid forms an acute angle in AMNH 29603. One of the diagnostic features of *P. tournoueri* is the trilobed m3, which cannot be corroborated in MCNAM-PV 4707 due to the incomplete condition of this tooth. However, the narrow trigonid of the m3 of AMNH 29603 is also seen in the m3 of MCNAM-PV 4707.

Specimen MCNAM-PV 4707 is smaller than *Brucemacfaddenia* and has comparable dimensions to *Federicoanaya* (Hitz et al. 2008), but differs from them in having a thick layer of cementum covering the teeth, a shorter, more triangular and lingually concave talonid, and a labially inclined trigonid.

In summary, MCNAM-PV 4707 can be considered in the genus *Progaleopithecus* by its general aspect and dimensions, but the noted differences with respect to *P. tournoueri* and the impossibility of checking diagnostic features and making comparisons with *P. fissurelatus* prevent us from providing a specific determination, regarding it as *Progaleopithecus* sp. until new remains can improve our comparisons.

Interatheriinae indet.

Figure 6(s)

Referred material. MCNAM-PV 4742, a mandible with two teeth interpreted as the left p4–m1.

Distribution and age. Base of the Agua de la Piedra Formation (Mendoza Province), Argentina, Deseadan SALMA, Late Oligocene.

Description and comparisons

The teeth of MCNAM-PV 4742 (Figure 6(s)) have cement that is mainly concentrated on the lingual sulcus. The m1 has a nearly circular talonid with barely concave lingual face, and a pointed metaconid. In contrast, the m1 of MCNAM-PV 4707 (*Progaleopithecus* sp.) is larger, has a more concave and triangular talonid, and a wider and rounded metaconid (Figure 6(r)). However, both m1 teeth share the well-separated trigonid and talonid by the presence of wide labial and lingual sulci. Compared with *P. tournoueri* (AMNH 29603), MCNAM-PV 4742 is similar in size (Table 3), but the m1 has a more rounded talonid and a shorter cristid oblique, and the p4 has the trigonid and talonid closer to each other. The latter feature closes MCNAM-PV 4742 to *Argyrohyrax*, but differs from this taxon because the talonid of p4 is smaller than the trigonid, the lingual face of the talonid of m1 is smoothly concave, and has smaller dimensions (Table 3; Appendix 2). On the other hand, some characteristics present in MCNAM-PV 4742 resemble the genus *Cochilius*, as the triangular and pointed metalophid-metaconid on the p4–m1 is also seen in AMNH 29654, referred by Simpson (1932b) to *Cochilius volvens*. In turn, the mesial face of the trigonid on m1 that covers the distal face of the talonid on p4 is also seen in AMNH 29552, which is ascribed to *Cochilius fumensis* (Simpson 1932a). This peculiar combination of features described for MCNAM-PV 4742, as well as the high degree of wear of their teeth, prevents us to precise its taxonomic determination.

Phylogenetic analysis

Two different searches were performed, modifying some terminal taxa from the original matrix (Appendix 4). In the first analysis, using all taxa, we obtained 18 parsimonious trees, each 109 steps long, with the consistency index (CI) of 0.53 and the retention index (RI) of 0.65. The polytomies observed in the 50% majority-rule consensus (Appendix 5, Figure a) are because of the shifting position of MCNAM-PV 4707 and MCNAM-PV 4742, two very incomplete fragments of mandibles (Appendix 1). From a total of 46 characters, only seven could be coded for MCNAM-PV 4707 and nine for MCNAM-PV 4742. It is interesting to note that MCNAM-PV 4742 appears in a more derived position than MCNAM-PV 4707 and closer to *Protypotherium australe*, forming a polytomy with the clade including *Interatherium robustum* and *Cochilius volvens*. This result agrees with the fact that MCNAM-PV 4742 exhibits a particular combination of features, some of which resemble *Cochilius*. Although MCNAM-PV 4707 is attributed to *Progaleopithecus* sp., it does not form a clade with *P. tournoueri*.

The second search was performed excluding MCNAM-PV 4707 and MCNAM-PV 4742 from the matrix, in order to reduce the instability of the analyses. As result, nine most parsimonious trees (108 steps long, CI = 0.54, RI = 0.66) were obtained. The synapomorphies common to the nine trees are shown in the 50% majority-rule consensus tree (Appendix 5, Figure b). The well-supported node A corresponds to the Interatheriinae *sensu stricto*, including *Eopachyrucos pliciferus*, and is characterised by five synapomorphies: hypsodont cheek teeth [1^1], mesial cingulum absent on the M1–3 [14^1], M1–2 with rectangular (DLL < DMD) or trapezoid shape [19^1], bifid lingual sulcus on the M1–2 [21^1], and the ectoflexid on m1–2 extends to the base of the crown [37^1]. Within node A (Appendix 5, Figure b), *Santiagorothia chiliensis* appears as sister taxon of a more inclusive clade, node B, which is a polytomy including *Argyrohyrax proavus*, *Eopachyrucos pliciferus*, *Brucemacfaddenia boliviensis*, *Federicoanaya sallaensis* and the node C. The polytomies are mainly due to the shifting position of *Eopachyrucos pliciferus*, a poorly known interathere regarded as the basal-most member of the interatheriines (Hitz et al. 2000; Reguero et al. 2003; Reguero & Prevosti 2010). Hitz et al. (2006) in fact stated that this taxon could not be considered a member of Interatheriinae, based on the phylogenetic definition for Interatheriinae proposed by Hitz et al. (2000). Evaluating the behaviour of *Argyrohyrax proavus* among the nine trees, it is interesting to note that in four of the nine topologies, *A. proavus* forms a clade with *Eopachyrucos pliciferus* (node A, Appendix 5, Figure c). This group is supported on the basis of a single synapomorphy, p1 not overlapped [28^0], and constitutes the sister group of a more inclusive clade, node B ((*Archaeophylus patrius*, *P. tournoueri*), ((*Protypotherium australe*, (*Interatherium robustum*, *Cochilius volvens*))). In this particular topology (Appendix 5, Figure c), one synapomorphy links *Archaeophylus patrius* with *P. tournoueri* (node C): triangular talonid on the m1–2 [36^1]. At the same time, this clade is the sister group of the most derived interatheres (Santacrucian and Colhuehuapian taxa), an assemblage that is charecterized by two synapomorphies (node D): hypselodont cheek teeth [1^2] and height of the mandibular horizontal ramus at the level of m2 is at least twice as high as at the incisor level [42^1].

Discussion

The present study of interatheres has led to important novelties from both taxonomic and paleobiogeographic points of view. On the one hand, the revision of a great amount of specimens from Mendoza and Patagonia allows us to establish different synonymies and, consequently, better assess the diversity of interatheres during Deseadan times. With the recognition of *P. clivus* as a *nomen dubium*, we regard four Patagonian genera as valid: *Argyrohyrax*, *Progaleopithecus*, *Archaeophylus* and *Cochilius*. The material from Quebrada Fiera permits the recognition of three taxa: *Argyrohyrax proavus*, *Progaleopithecus* sp. and an undetermined interathere, which is closer to Patagonian than Bolivian taxa. The record of *Argyrohyrax* and *Progaleopithecus* in Mendoza implies a broader geographic distribution for these taxa, notably for the latter that was previously known only from high latitudes in Patagonian localities. *Argyrohyrax* was previously documented from localities within southern latitudes as well as northeast Argentina, and is now extended to the central-west. Based on present data, *Argyrohyrax* and *Progaleopithecus* appear together in Mendoza (Quebrada Fiera), Chubut (Cabeza Blanca, Las Cascadas and Scarritt Pocket) and Santa Cruz (La Flecha) provinces, while *Archaeophylus* appears only in Chubut Province (Cabeza Blanca). *Progaleopithecus* is also recorded at Bajada del Diablo (Chubut Province) whereas *Argyrohyrax* is also present at El Pajarito and Rinconada de los López (Chubut Province), and Arroyo María Grande (Corrientes Province), making it the most widely distributed genus.

A comment is needed here about the presence of *Cochilius* in Deseadan levels. Ameghino (1901) described this genus with three species from the Colhuehuapian SALMA (Early Miocene) of Patagonia, *C. volvens* being the best known species (Simpson 1932b). Subsequently, Simpson (1932a; Figs. 2–4) described *C. fumensis* from apparently older levels of Deseadan age at west side of Cerro del Humo (Chubut Province) and mentioned only two specimens, AMNH 29551 (holotype, articulated and badly preserved skull) and AMNH 29552 (right lower jaw with p4–m3). The author recognised their close resemblances with *C. volvens* but also voiced his doubts about the stratigraphic provenance of these specimens. There are also some specimens in the MLP labelled as *Cochilius* sp. from the El Pajarito locality (Chubut Province), indicating 'Deseadan age' (Appendix 1), and are very similar to *C. volvens*. Further, *Cochilius* could be also present at Quebrada Fiera based on the shared features of the specimen MCNAM-PV 4742 with this genus, but this cannot be ascertained with the available material. A thorough systematic revision of *Cochilius* is pending.

Considering only dentition and identified specimens at family level, the interatheriids represent approximately 17% of all Notoungulata from Quebrada Fiera, hegetotheriids 25% and archaeohyracids 19%. As a faunal assemblage, Quebrada Fiera is a mix of endemic (at generic level: one notohippid, one leontiniid and one basal carnivorous metatheria) and more cosmopolitan taxa. Common genera with Patagonia are among hegetotheriids (*Prohegetotherium* and *Propachyrucos*), homalodotheriids (*Asmodeus*), interatheriids (*Argyrohyrax* and *Progaleopithecus*), pyrotheriids (*Pyrotherium*) and borhyaenids (*Proborhyaena* and *Pharsophorus*). The interatheriid *Argyrohyrax* is also shared with the north-eastern of Argentina, and the archaeohyracids are

represented at Quebrada Fiera by the same species as that from Salla, *Archaeohyrax suniensis* (see Cerdeño [2011] for a summary on faunal assemblage; Seoane and Cerdeño [2014]; Cerdeño and Reguero [2015]).

Examining both consensus trees obtained through the two phylogenetic analyses (Appendix 5, Figure ab), a moderate correspondence exists between the branching sequence and the stratigraphic record. That means, older taxa such as the Eocene *Notostylops*, *Notopithecus* and *Oldfieldthomasia* are placed closer to the basal node, while the Miocene members of interatheres, such as *Protypotherium*, *Interatherium* and *Cochilius*, occupy a more derived position in the topologies.

Conclusions

The entire studied sample (see 'Materials and methods' section) allows us to clarify the taxonomic status of some species of Deseadan interatheres and amend their diagnosis.

The type specimen of *Plagiarthrus clivus* is the astragalus MACN A52-470 and not the mandible MACN A52-474 described by Ameghino as the same species. MACN A52-474 has been incorrectly used as reference of *P. clivus* in innumerable publications. The comparison of MACN A52-474 with other specimens permits inferring its correspondence with the upper dentition of *Argyrohyrax proavus*. As the co-specificity between the astragalus MACN A52-470 and the mandible MACN A52-474 cannot be presently assured, *P. clivus* is herein regarded as *nomen dubium*, and MACN A52-474 is included in *A. proavus*. The new specimens of *Argyrohyrax proavus* comprise the anterior teeth, upper and lower deciduous dentition and postcranial bones, which have permitted expanding the diagnosis of this taxon.

Regarding *Argyrohyrax proavunculus*, we conclude that the evidence is not strong enough to support a different species from *A. proavus*, and propose the former as a junior name. Based on the only specimen referred to ?*A. acuticostatus*, we remove this species from the genus *Argyrohyrax* and other Deseadan interatheres, leaving open its generic ascription. Concerning *Notohyrax conicus*, we agree with Patterson's (1952) proposal about that it is a synonymous name of *Argyrohyrax proavus*.

In the case of *Progaleopithecus fissurelatus*, the incisors and the canine present in the type material (MACN A52-486) represent the characteristics described by Ameghino (1904) for the species. Instead, the p2 included in the lot MACN A52-486 is not recognised as an interathere, resembling Henricosborniidae; consequently, this p2 is removed from the syntype of *Progaleopithecus fissurelatus*.

Among the material assigned to *P. tournoueri*, both MNH DES-334 and the p3 MACN A52-482 are recognised as the original elements described by Ameghino. As in the previous case, the premolar MACN A52-482 resembles Henricosborniidae and it is therefore removed from *P. tournoueri*; consequently, MNH DES-334 is selected as the lectotype of this species.

The detailed study of the Interatheriidae from Quebrada Fiera allows the recognition of three Interatheriinae identified as *Argyrohyrax proavus*, *Progaleopithecus* sp. and Interatheriinae indet. The specimen MCNAM-PV 4707 identified as *Progaleopithecus* sp. shares some characteristics with *P. tournoueri*, but its incompleteness prevents an accurate specific determination. In turn, MCNAM PV 4742, determined as Interatheriinae indet., shows a peculiar combination of features, differing in some respects from *Argyrohyrax* and *Progaleopithecus*, while sharing some features with *Cochilius*. Based on this, the presence of *Cochilius* in Quebrada Fiera remains a possibility, but cannot be definitively determined at this time.

The cladistic analysis yielded consistent results; MCNAM-PV 4707 appears at a basal position with respect to MCNAM PV 4742, which in turn groups closer to *Protypotherium* and the most derived interatheres. Notably, *Argyrohyrax proavus* does not gather into any group, but it appears at a basal position in relation to other Deseadan interatheres, such as *Progaleopithecus* and *Archaeophylus*. The Interatheriinae *sensu stricto*, including *Eopachyrucos pliciferus*, is supported by 10 unambiguous synapomorphies.

The record of *Argyrohyrax* and *Progaleopithecus* from Mendoza extends the known geographic distribution for both Deseadan interatheres into the middle latitudes of central-west Argentina. Interatheres add to the list of other mammal groups from Quebrada Fiera that show closer affinities with the high latitude (Patagonia) than to middle (Fray Bentos) or lower (Salla) latitude faunas, and contribute significantly to the knowledge of the Late Oligocene Deseadan SALMA and the paleobiogeography of southern South America.

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The authors state that there is no potential conflict of interest derived from the present research.

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