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New Basal Interatheriidae (Tyrpotheria, Notoungulata, Mammalia) from the Paleogene of Central Chile

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ABSTRACT

Two new basal interatheriids (“notopithecines”) are described from central Chile. Specimens of a new taxon, *Johnbell hatcheri*, derive from Abanico Formation deposits near Termas del Flaco, in the valley of the Río Tinguiririca, forming a distinctive element of the Tinguiririca Fauna. The Tinguiririca Fauna, which forms the basis of the recently defined Tinguirirican SALMA, documents the co-occurrence of species of archaic, dentally primitive herbivores and basal members of later diverging groups of more advanced hypsodont forms, and other transitional aspects of mammal evolution near the Eocene/Oligocene boundary. A specimen recovered from the Abanico Formation in the drainage of the Río Cachapoal (~100 km north of Termas del Flaco), SGOPV 3451 is referred to *Johnbell hatcheri*. This is the first time a specimen from elsewhere in the central Chilean Main Range has been assigned to a species represented in the stratotype sequence of the Tinguiririca Fauna (upper Río Tinguiririca Valley). *Ignigena minisculus*, the other new basal interatheriid recognized herein, is known only from older strata of the Abanico Formation, from the Tapado Fauna within the Río Tinguiririca Valley, estimated to be Casamayoran in age. Phylogenetic analysis shows these two new basal interatheriids to be outgroups to the Interatheriinae. Both new taxa are smaller than all other interatheriids known, except *Punapithecus*. Small body size may reflect geographic provincialism, as these diminutive forms are restricted to more northern latitudes compared to larger basal interatheriids, which derive from Patagonia.

SGOPV 3604, from the Abanico Formation along the Río Azufre, several kilometers north of the Río Tinguiririca drainage, is referred to the early interatheriid *Antepithecus brachystephanus*, a taxon otherwise known only from Casamayoran (“late” Barrancan subage) SALMA deposits in Patagonia.

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A phylogenetic definition for the name Interatheriidae is proposed on the strength of the resolution achieved in the phylogenetic analysis. This analysis also shows clearly that “Notopithecinae” represents a paraphyletic assemblage. We suggest that taxa formerly termed “notopithecines” are more appropriately referred to as “basal interatheriids”.

INTRODUCTION

The Tinguiririca Fauna, the first indications of which were uncovered in 1988 (Novacek et al., 1989), was the first in a long series of new mammalian assemblages being discovered in the Abanico Formation (and equivalents) in the central Andean Main Range of Chile (Wyss et al., 1990, 1992, 1993, 1994; Charrier et al., 1990, 1996; Flynn et al., 1991, 1995, 2003; Hitz et al., 2000; Croft et al., 2003; Reguero et al., 2003a; Flynn and Wyss, 2004). This formation and its lateral correlatives strike parallel to the Main Range (i.e., north-south) and have yielded mammalian faunas across a >400 km long band, between approximately 33°45'S (directly east of Santiago in the Río Colorado and Cajón del Maipo regions) and ~37° 20'S (Laguna del Laja) (fig. 1). These faunas represent many distinct temporal horizons, ranging in age from the Casamayoran (probably late Eocene, Kay et al., 1998) through the Colhuehuapian (early Miocene, Flynn and Swisher, 1995) or younger SALMAS; radioisotopic data indicate that deposition of the Abanico Formation extended until at least middle Miocene time (Charrier et al., 2002). Mammal faunas are preserved in volcanoclastic intervals of the infilling of long-lived extensional basin(s); these accumulations, approaching 5 km in stratigraphic thickness, were uplifted and deformed by compressional tectonics beginning in the middle-late Miocene (Charrier et al., 2002, 2005). Deposition of the unit may have begun prior to the Casamayoran, but the precise timing of initiation of sedimentation in the basin is currently uncertain, given stratigraphic complexity arising from strong compressive deformation and often limited applicability of radioisotopic dating owing to low-temperature metamorphic alteration.

This paper extends description and phylogenetic analysis of new taxa from the Abanico Formation, both from the Tinguiririca valley (in the original Tinguiririca Fauna and the older Tapado Fauna), and others more recently discovered elsewhere. Two of the speci-

mens described below fall in the latter category, coming from the Cachapoal Fauna (Río Cachapoal) discovered in 1996 and the Azufre Locality (Río Azufre) discovered in 1997. Complementing our earlier work on Tinguiririca interatheriids (Hitz et al., 2000) we here describe two new early diverging members of this group of small- to medium-sized notoungulates, and present a phylogenetic analysis of the Interatheriidae (Typotheria). Interatheriids, including both brachydont (presumably browsing) and hypsodont (presumably grazing) forms, are generally well represented in South American early-middle Cenozoic land mammal faunas. Interatheriids first appear in the Paleocene Riochican South

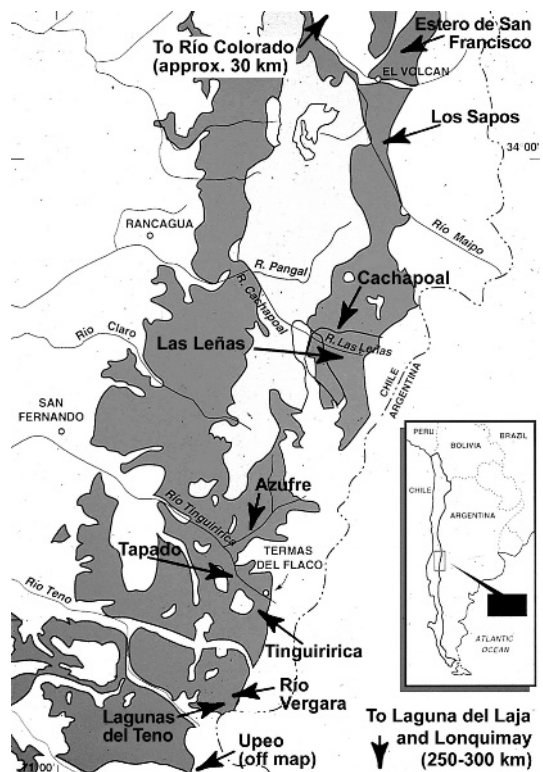


Fig. 1. Map of the central Chilean Andes, illustrating the broad swath of Abanico Formation and equivalent deposits (shaded) and localities/faunas referred to in the text.

American Land Mammal "Age" (SALMA) (Marshall et al., 1983) and persist into the Huayquerian SALMA (Late Miocene), exhibiting a radiation of hypsodont forms during late Oligocene time (Cifelli, 1985; Marshall and Cifelli, 1990). Interatheriids are traditionally divided into two groups (Simpson, 1945; McKenna and Bell, 1997), the Notopithecinae (early Paleogene, low-crowned forms) and the Interatheriinae (late Paleogene and Neogene, hypsodont and hypselodont forms). Phylogenetic studies (Cifelli, 1993; Hitz, 1997; Hitz et al., 2000; Reguero et al., 2003b; this paper) have corroborated the monophyly of the Interatheriinae, whereas the taxa generally referred to the Notopithecinae form a paraphyletic assemblage. As detailed below, owing to the paraphyly of "Notopithecinae" we favor referring to these forms collectively as "basal interatheriids", reflecting their lack of membership in the Interatheriinae. Lastly, the new Chilean basal interatheriids illustrate an interesting biogeographic-morphologic pattern—an assemblage of unusually small-bodied forms having an extra-Patagonian distribution. The two new Chilean taxa, and *Punapithecus*, a recently described basal interatheriid from Catamarca and Salta Provinces, Argentina (López and Bond, 1995; Alonso et al., 1988) are significantly smaller than previously known interatheriids, and all three taxa are known exclusively from localities far removed from Patagonia.

Hitz et al. (2000) described two interatheriines, *Santiagorothia chiliensis*, from the Tinguiririca Fauna and several Patagonian localities, and *Proargyrohyrax*, known only from Patagonia. Emended descriptions and diagnoses for the Patagonian interatheriines *Argyrohyrax acuticostatus* and *Eopachyruchos plicifera* were provided as well. *Santiagorothia chiliensis* and *Proargyrohyrax* are the earliest (Tinguirirican SALMA; Flynn et al., 2003) known interatheriines (sensu Hitz et al., 2000: 3). Notably, specimens from various Argentine Patagonian localities ("Astraponotéen plus supérieure level", Chubut [Bond et al., 1996, 1997a]; Lomas Blancas, Chubut [Hitz et al., 2000]; Rocas Bayas, Rio Negro [Pascual et al., 1984; Bond et al., 1997b]; Laguna de la Bombilla, Chubut [Pascual, 1965]) have been referred to *Santiagorothia chiliensis* (the holo-

type of which is from Chile; Hitz et al., 2000) thereby highlighting the biostratigraphic utility of interatheriid taxa from the Tinguiririca Fauna. The correlations offered in Hitz et al. (2000), and the occurrence of a conspecific outside the Tinguiririca valley reported below, add to a growing body of evidence indicating that strata referable to the Tinguirirican SALMA (Flynn et al., 2003) occur beyond central Chile (see also Croft et al., 2003; Reguero et al., 2003a, 2003b).

Specimens examined in this study for systematic comparison and character assessment in the phylogenetic analysis are housed in the American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Florida Museum of Natural History (FLMNH); Servicio Geológico de Bolivia (GEOBOL); Los Angeles County Museum (LACM); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo de La Plata (MLP); Museo Nacional de Historia Natural, Bolivia (MNHN); Museo Nacional de Historia Natural, Santiago (SGOPV); University of California Museum of Paleontology (UCMP); and Yale Peabody Museum (YPM). Other abbreviations include: R (Right), L (Left), i/I (lower/upper incisor), c/C (lower/upper canine), p/P (lower/upper premolar), m/M (lower/upper molar), dp/dP (deciduous lower/upper premolar), HI (hypsodonty index), SALMA (South American Land Mammal "Age").

SYSTEMATIC PALEONTOLOGY

NOTOUNGULATA ROTH, 1903

TYPOTHERIA ZITTEL, 1893

INTERATHERIIDAE AMEGHINO, 1887

Johnbell hatcheri, new taxon

Figures 2–5

HOLOTYPE: SGOPV 3106: left maxilla, L13-M3.

PARATYPE: SGOPV 2950: mandibles preserving symphysis, Ri2-3, Li1-m3.

REFERRED SPECIMENS: SGOPV 2910: Rp4-m2. SGOPV 2902: Rp1-m3. SGOPV 5001: a palate and mandibles, partially prepared,

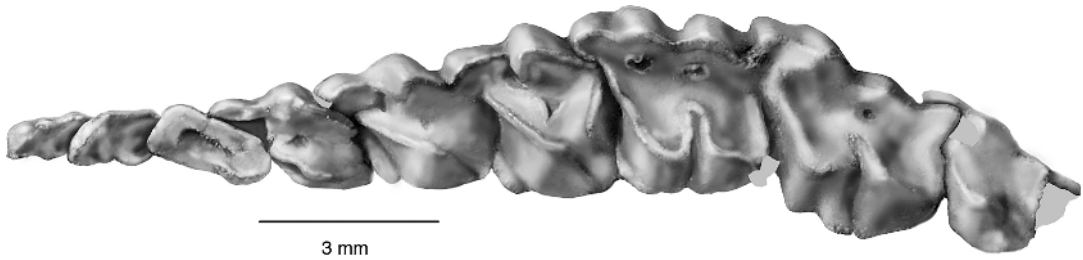


Fig. 2. *Johnbell hatcheri*, new taxon, SGOPV 3106 (holotype), left maxilla, LI3-M3, occlusal view. Tinguiririca Fauna.

LP2-M3 and Lp3-m3 exposed. SGOPV 3451: RP2-M2.

ETYMOLOGY: For John Bell Hatcher, a coal miner turned vertebrate paleontologist, known for his prodigious collecting and pioneering fieldwork in remote regions of Patagonia, where he secured valuable Miocene fossil mammal collections including many interatheriid specimens.

DIAGNOSIS: *Johnbell hatcheri* is a small tyotheres possessing upper molars that are longer than wide and have fossettes that disappear rapidly with wear, leaving a featureless crown save for a persistent lingual sulcus. Among tyotheres, this combination of features is found only in one subgroup of interatheriids (unnamed clade, node 2 in fig. 6, this paper). The following distinctions exclude *Johnbell hatcheri* from other groups of small-bodied tyotheres: archaeopithecids have upper molars that are equidimensional or wider than long, with long-lived fossettes, and

archaeohyracids and hegetotheriids are much larger tyotheres lacking a persistent lingual sulcus on upper molars. Assignment to the Mesotheriidae is ruled out by their larger size and pronounced trilobed (only trilobed early in wear in trachytheriines, persistently trilobed in mesotheriines), hypsodont upper molars.

Johnbell hatcheri is an early diverging member of the least inclusive clade (unnamed) including Interatheriinae (sensu Hitz et al., 2000, see fig. 6, node 4 this paper), *Eopachyrucos*, and *Ignigena minisculus* (new taxon, below). This clade (clade 2, fig. 6) is characterized ancestrally, and distinguished from all other interatheriids, by the following derived features: smooth posterior ectoloph on the upper premolars, and upper molars longer than wide. Interatheriids excluded from this unnamed clade (*Notopithecus*, *Transpithecus*, *Guiliemoscottia*, *Punapithecus*, *Antepithecus*) lack these features, readily distinguishing them from *Johnbell hatcheri*.

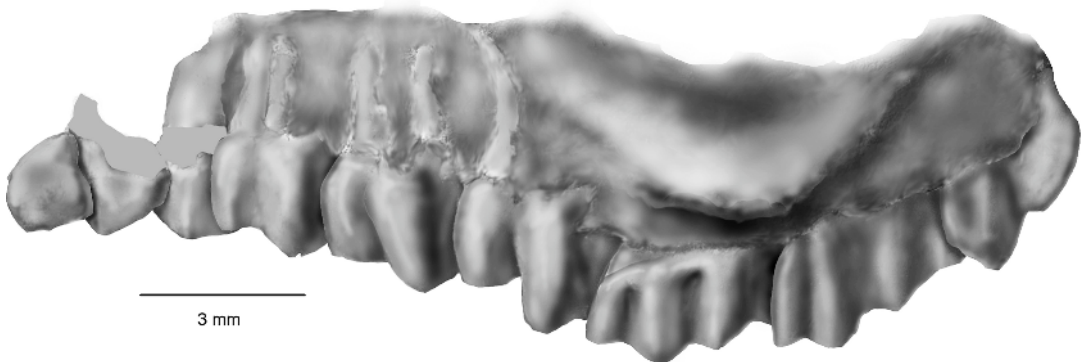


Fig. 3. *Johnbell hatcheri*, new taxon, SGOPV 3106 (holotype), left maxilla, LI3-M3, buccal view. Tinguiririca Fauna.

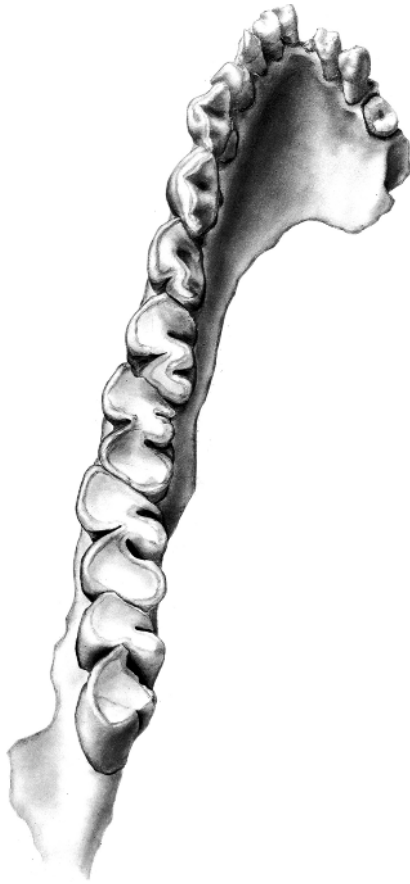


Fig. 4. *Johnbell hatcheri*, new taxon, SGOPV 2950 (paratype), mandibular symphysis, Ri2-3, Li1-m3, occlusal view. Tinguiririca Fauna.

Conversely, *Johnbell hatcheri* is excluded from clade 3 of figure 6 (i.e., Interatheriinae—sensu Hitz et al., 2000—plus *Eopachyrucos*), in lacking many of the synapomorphic dental features diagnosing that clade (see phylogenetic analysis, below): a low or flat ectoloph on M1-3, and hypsodont or hypseledont cheek teeth (HI for *Johnbell hatcheri* SGOPV 3106 is 0.86 as measured on the M2). *Johnbell hatcheri* is one of the smallest interatheriids known (rivalled only by *Ignigena minisculus* and *Punapithecus*). Its strikingly narrow premolars (in the transverse direction) and anteroposteriorly narrow internal sulcus on the upper molars nevertheless clearly differentiate it from these two other diminutive taxa. In addition, *Johnbell hatcheri* lacks the anterior cingulae on the upper cheekteeth present in *Punapithecus*.

TYPE LOCALITY: The holotype derives from Locality Set 3 (Flynn et al., 2003) in the Abanico (= Coya Machalí) Formation, Río Tinguiririca valley, central Chile. Locality Set 3 (= “Locality C” of Charrier et al., 1996: figs. 6–8) occurs in purplish volcanoclastic sediments north of the Río Tinguiririca, less than 5 km north of the other two main localities (Locality Sets 1 and 2, Flynn et al., 2003) yielding the Tinguiririca Fauna at Termas del Flaco (see Wyss et al., 1994; Charrier et al., 1996; Flynn et al., 2003).

KNOWN DISTRIBUTION: Tinguirirican SALMA (Flynn et al., 2003; = Tinguiririca faunal interval or “Tinguirirican” of Flynn and Swisher, 1995). Known from the Tinguiririca Fauna type locality (Locality Set 1; SGOPV 2902, 2910, and 5001) and Locality Set 3 (the holotype and paratype, SGOPV

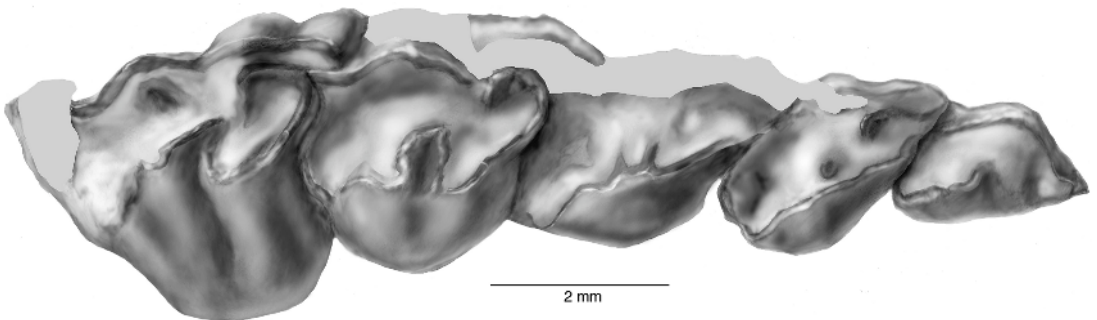


Fig. 5. *Johnbell hatcheri*, new taxon, SGOPV 3451 (referred specimen), partial maxillary with RP2-M2, occlusal view. Cachapoal Fauna.

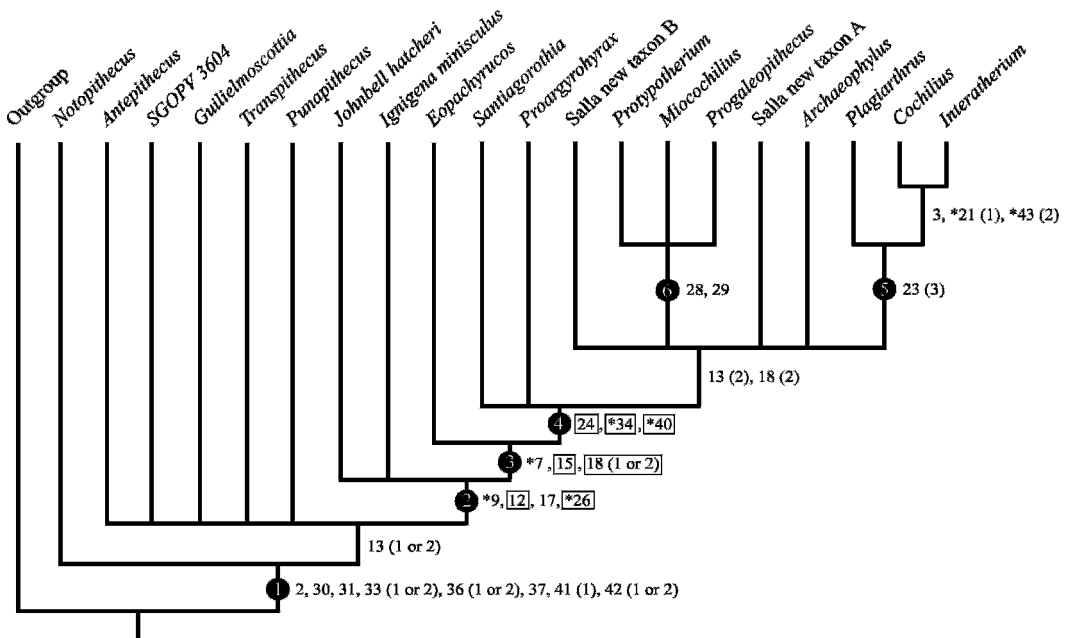


Fig. 6. Consensus of 623 equally parsimonious trees of 70 steps (branch and bound search, all characters unordered, equally weighted; for individual trees: CI = 0.74, RI = 0.86). Labeled nodes are referenced from the text. Character states supporting nodes are listed adjacent to the node (if no number is given, it is the single derived state for the character, coded as “1”). Character states with an asterisk indicate an equivocal condition in which either the most basal member of the clade in question is missing data for that character or the outgroup to that clade is missing the data for that character. Boxed character states represent conditions identified as diagnostic of Interatheriinae sensu Hitz et al., (2000) but are shown in this study to have a broader distribution.

3106 and 2950) of Flynn et al. (2003) (Localities “A” and “C” of Charrier et al., 1996, figs. 6–8), respectively lying 2 km south and 3 km northwest of the town of Termas del Flaco and the Río Tinguiririca. The occurrence of *Johnbell hatcheri* at both Locality Sets 1 and 3 is important in correlating between the discontinuously exposed fossil-bearing horizons of the Abanico Formation from the north side of the Tinguiririca valley to strata south of the river. Additionally, a single specimen (SGOPV 3451) is known from a locality (Cachapoal Locality and Fauna) within the Abanico Formation in the Río Cachapoal drainage, some 100 km north of Termas del Flaco (Charrier et al., 1996; Flynn and Wyss, 2004). More detailed locality information is on file at the American Museum of Natural History. Radioisotopic determinations from Tinguiririca bracket the age of the fauna there between approximately 37.5–31.5 Ma, with

the fossiliferous horizons themselves directly dated at ~ 31.5 Ma (Wyss et al., 1994; Flynn et al., 2003) and the Tinguirirican SALMA likely spanning at least 31–33 Ma (Flynn et al., 2003).

REMARKS: In a preliminary description of these specimens (Hitz, 1997), SGOPV 2950, a mandible, was designated as the principal specimen representing this new taxon, and SGOPV 3106, a nearly complete maxilla, was designated as the equivalent of the paratype, although it was not formally named in that dissertation. Upon further consideration, we formally designate SGOPV 3106 the holotype and SGPOV 2950 the paratype, as maxillae tend to be more abundant in the notoungulate fossil record and preserve a greater number of diagnostic characters. Supporting the latter claim is the fact that in the phylogenetic analysis of Interatheriidae presented below, we recognize eighteen distinct characters for the upper dentition but only ten for the lower.

TABLE 1
Dental Measurements (in mm) for Upper and Lower Jaws of *Johnbell hatcheri*

Jaw	SGOPV 2950	SGOPV 3106	SGOPV 2910	SGOPV 5001	SGOPV 5001	SGOPV 3451
	lower	upper	lower	lower	upper	upper
AP I1	0.56	—	—	—	—	—
TR I1	0.43	—	—	—	—	—
AP I2	0.63	—	—	—	—	—
TR I2	0.48	—	—	—	—	—
AP I3	0.88	1.59	—	—	—	—
TR I3	0.62	0.86	—	—	—	—
AP C	1.16	1.79	—	—	—	—
TR C	0.92	0.86	—	—	—	—
AP P1	1.95	2.01	—	—	3.08	—
TR P1	1.14	1.44	—	—	—	—
AP P2	2.35	2.91	—	—	—	2.30
TR P2	1.37	1.87	—	—	—	1.40
AP P3	2.60	2.95	—	—	—	2.80
TR P3	1.71	2.45	—	—	—	2.10
AP P4	2.81	3.12	2.95	—	—	2.90
TR P4	1.97	2.97	1.59	—	—	2.60
AP M1	3.22	3.90	3.41	3.53	3.40	3.50
TR M1	2.05	3.01	1.95	—	—	3.30
AP M2	3.47	4.08	—	3.81	3.83	3.70
TR M2	2.29	2.72	—	—	—	—
AP M3	3.98	—	—	5.01	—	—
TR M3	2.09	—	—	—	—	—

In addition to the dental features noted above, interatheriines (sensu Hitz et al., 2000) are diagnosed by two derived cranial features, an anteriorly projecting sliwer of the frontal on the superoanterior orbit rim, and a posterior portion of the auditory bulla that laps onto the paraoccipital process. Given the scarcity of known cranial material, these features cannot be scored for most early interatheriids, including *Eopachyrucos* and *Johnbell hatcheri*. Nevertheless, the known distribution of these features argues that they diagnose a clade at least as inclusive as Interatheriinae, but less inclusive than Interatheriidae.

DESCRIPTION

Johnbell hatcheri is known from nearly complete maxillary and mandibular dentitions (figs. 2–5). Only SGOPV 5001 shows an articulated upper and lower dentition, but the teeth of this specimen are tightly clenched and embedded within an extremely hard and brittle volcanoclastic matrix, making the crowns of the lower dentition inaccessible to

preparation (without risking destruction of the teeth). The remaining suite of upper and lower dentitions is allocated to the same taxon based on similarities of the labial faces of the cheekteeth (visible in 5001), common morphological features of the occlusal surfaces among those specimens with crowns prepared, similarity in size, and the presence of features identifying all specimens as basal interatheriids. Mensural information is presented in table 1.

UPPER DENTITION

The description of the upper dentition is based principally on the holotype SGOPV 3106, the specimen with the best preserved and most completely exposed upper dentition.

Only I3 is preserved among the upper incisors. It is incisiform; a shallow, vertically oriented groove divides the tooth into anterior and posterior portions labially, a division that is less apparent lingually. The upper canine is incisiform and similar in size to I3. The anteroexternal swelling (anterior portion of

tooth) is better developed on the canine than on I3.

The first upper premolar bears a distinct anterolabial swelling on the "ectoloph" and a posterolingual shelf heel, the latter of which probably represents a diminutive protocone. Otherwise the tooth is relatively narrow.

The succeeding premolars are progressively larger but otherwise share the same distinctive morphology seen in the premolars of other interatheriids. A distinct parastyle and prominent paracone occur on P2-4, producing a fold or groove between the two (although it does not penetrate the crown deeply). A small protocone occupies a position near the metacone. The lingual premolar margins are smooth and straight, being oriented nearly anteroposteriorly. There is no hypocone, thereby making the three posterior upper premolars rather narrow. Anterior cingulae are lacking (but a small emargination may be present on P3-4). A high posterior cingulum may have occurred on P3-4, as one is present on P2, but it has since merged with the remainder of the crown through wear. A strong undulation on the ectoloph corresponds to the parastyle and paracone, but the remainder of the ectoloph is nearly straight posteriorly.

The first two upper molars are very similar in morphology, the most significant difference being the greater length of M2. These teeth are expanded anteroexternally, lending this portion of the teeth a wedge shape. A small parastyle is present, as is a shallow parastyle/paracone inflection. The ectoloph shows mild undulations; the parastyle, paracone, and metacone have approximately an equal amount of relief on M1, but on M2 the metacone shows decidedly less relief compared to the parastyle and paracone. The protoloph extends posterolingually from the parastyle; it does not bear a cingulum (or if it did, this feature coalesced with the remainder of the crown early in wear). The protocone and hypocone are separated by a deep sulcus, which extends nearly to the roots. The posterior border is oriented transversely and is marked by a high cingulum, which appears to merge with the remainder of the crown early in wear. Anterior and posterior fossettes are seen on M1, but wear has nearly erased

them. A posterior fossette is visible on M2, but also is nearly obliterated by wear. A small irregular feature is visible on the anteroexternal quadrant of the crown, which may be the remnant of an anterior fossette, but this structure is faint and we refrain from identifying it conclusively as a fossette. Given the faintness of the fossettes in SGOPV 3106 (the holotype, which exhibits an early wear stage), we conclude that even modest wear in this taxon would likely have rendered the molar occlusal surfaces featureless. The lingual sulcus on both molars is deep and probably persisted until wear neared the roots.

The third upper molar is a smaller version of M1-2. The main morphological contrast between it and the two preceding teeth is in the posterior margin. The hypocone is less prominent on M3, making the posterior margin angle anterointernally from the posterior margin of the ectoloph, rather than transversely as in M1-2. Fossettes are not visible on M3, and were probably absent entirely, given the early wear stage of this tooth on SGOPV 3106. The lingual sulcus appears to be deep and probably persisted into late wear stages.

Teeth of the upper dentition are rooted and may be described as brachydont, but the crowns of the cheekteeth are heightened somewhat. The hypsodonty index (HI; greatest ectoloph height divided by greatest ectoloph length) for M2 on *Johnbell hatcheri* (SGOPV 3106) is 0.85. For comparison, HI values of the M2 of other small basal interatheriids are: *Notopithecus adapinus* (specimen not identified), 0.81 (Simpson, 1967); *Antepithecus adapinus* (specimen not identified), 0.72 (Simpson, 1967); SGOPV 3168 (new taxon, *Ignigena minisculus*, below), 0.79; *Punapithecus minor* (MLP-V-10-1), 0.61; *Antepithecus brachystephanus* (SGOPV 3604, below), 0.45. All values were calculated based on teeth with trace to slight wear.

LOWER DENTITION

This description is based on the paratype (SGOPV 2950), SGOPV 2910, and SGOPV 5001, all of which possess well-preserved lower teeth.

The first two lower incisors are both small, each having a faint, vertically oriented groove

lingually. The i3, which is slightly larger than i1-2, bears a similar groove. The lower canine is very poorly preserved and provides little information.

The p1 is transversely narrow; a deep, vertically oriented groove opens lingually, giving the crown a V-shaped appearance. The posterior arm of the V is slightly larger than the anterior arm and bears a small posterior heel set off from the remainder of the crown by a shallow vertical groove labially.

The p2 closely resembles p1, except that the posterior heel is larger and more distinct. This heel is accentuated by a shallow groove on the labial face of the posterior crest, as well as a vertical groove lingually.

The p3 consists of a distinct trigonid and talonid. The trigonid is dominated by a gently convex protolophid (opening lingually) and a small metalophid. This convexity produces a shallow internal vertical trough between the metaconid and the anterior portion of the protolophid. A small talonid attaches directly to the metaconid and is demarcated from the trigonid by a strong labial vertical groove and a mild lingual one.

The p4 is larger than the p3 and bears a strongly curved protolophid. The anterior margin of the protolophid is oriented transversely and, given its size, may be termed a paralophid. The metalophid is also oriented transversely; a deep vertical groove lies between it and the paralophid. A small talonid arises from the metaconid and is separated from the trigonid by a deep labial groove and a shallower, more posterior lingual groove.

The trigonids of m1-3 are similar, consisting of a diagonal paralophid (the lingual margin of which is posteriorly positioned relative to the labial margin), a longitudinal protolophid, and a diagonal metalophid (parallel to the paralophid) displaying a prominent metaconid. The vertical groove between the paralophid and the metalophid is very shallow, reaching midway down the crown toward the roots. The molar talonids are demarcated from the trigonids by deep labial and lingual vertical grooves, the former being slightly more posteriorly situated than the latter. These grooves extend nearly to the base of the crown. No hypoconulid is seen on m1 or

m2 and the talonids are essentially ovate in crown view, with the long axis oriented transversely. The m1 talonid attaches to the trigonid just labial to the metaconid. The m2-3 talonids attach more labially, nearer the center of the metalophid. The m3 talonid is larger than those of the preceding two molars and displays a prominent hypoconulid, which produces a slight groove on the tooth's lingual surface.

MANDIBLE

SGOPV 5001, the paratype SGOPV 2950, and SGOPV 2910 preserve partial mandibles. SGOPV 2910 displays a mental foramen near the ventral margin of the horizontal ramus, positioned directly below p4. The other two specimens do not clearly preserve mental foramina, although a possible trace of one is present below p4 on SGOPV 5001. The mandible is 7.47 mm and 7.90 mm deep below m2 on SGOPV 5001 and SGOPV 2910 respectively.

DISCUSSION

SGOPV 3451, consisting of a portion of a right maxilla containing P2-M2 (fig. 5), is remarkably similar to specimens of *Johnbell hatcheri* from the Río Tinguiririca valley (type area of the Tinguiririca Fauna) in size and morphology, and the anatomical description provided above applies to this specimen as closely as it does to specimens from the Tinguiririca region. SGOPV 3451 derives from an as yet little studied locality (yielding the Cachapoal Fauna; Charrier et al., 1996; Flynn and Wyss, 2004) in the Río Cachapoal drainage, about 5 km NW of the Río Las Leñas fossiliferous sites (Flynn et al., 1995) and ~100 km N of the fossiliferous strata cropping out near Termas del Flaco that bear the Tinguiririca and Tapado faunas.

The Cachapoal specimen, SGOPV 3451, shares a key diagnostic feature with *Johnbell hatcheri* (transversely narrow upper premolars), and the specimen otherwise displays no taxonomically significant features or size differences differentiating it from all other specimens here referred to *Johnbell hatcheri*, substantiating inclusion of this specimen in the

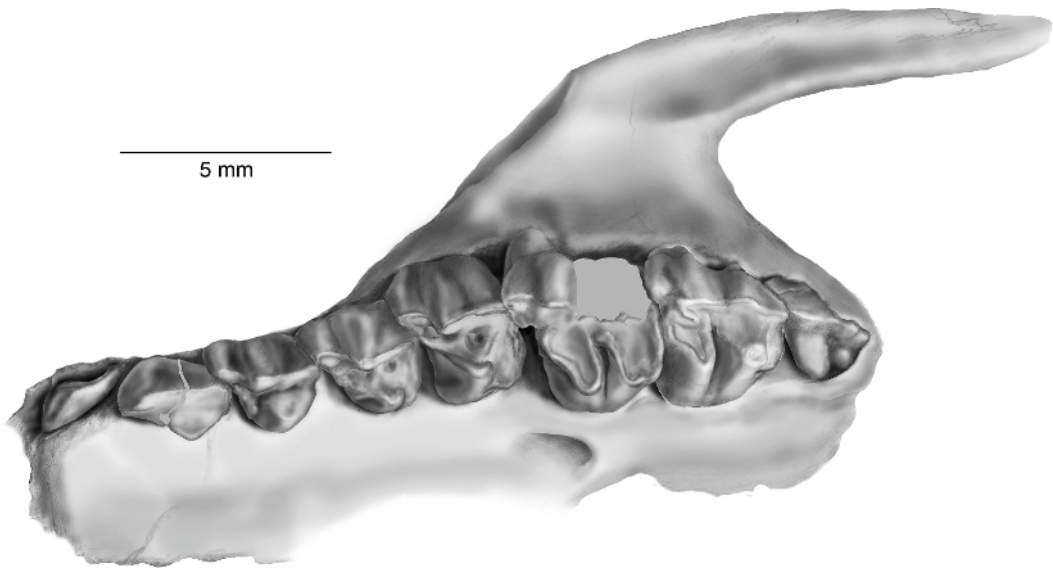


Fig. 7. *Ignigena minisculus*, new taxon, SGOPV 3168 (holotype), left maxillary fragment, partial zygoma, C-M3, occlusal view. Tapado Fauna.

hypodigm. This is the first Andean specimen from outside the stratotype sequence of the Tinguiririca Fauna (upper Río Tinguiririca valley) referable to a species from that fauna, demonstrating, among other things, the utility of *Johnbell hatcheri* for long distance biochronologic correlation.

SGOPV 3451 is in an earlier ontogenetic wear state than is the holotype of *Johnbell hatcheri* (SGOPV 3106). The posterior cingulum on the M2 of SGOPV 3451, for example, has not yet completely merged with the crown, as it has on SGOPV 3106. The M1 and M2 of SGOPV 3451 both appear to display a faint anterior fossette, and the M2 also has a posterior fossette. The lack of a posterior fossette on M1 in SGOPV 3451 is in contrast to the condition in SGOPV 3106, which still retains a posterior fossette on this tooth despite greater wear. This variation seems taxonomically inconsequential, likely reflecting only the extremely ephemeral nature of the molar fossettes in this taxon.

Ignigena minisculus, new taxon

Figures 7–10

HOLOTYPE: SGOPV 3168: left maxilla, including partial zygoma and C-M3.

REFERRED: SPECIMENS SGOPV 3167: left mandible with p1-p3, m1.

ETYMOLOGY: *Ignigena*, meaning “born of fire”, in reference to the volcanoclastic deposits from which the specimens derive; and *minisculus*, meaning “small”, in reference to the diminutive size of the specimens.

DIAGNOSIS: The same criteria listed in the previous section marking *Johnbell hatcheri* as a basal interatheriid, and distinguishing it from all known interatheriines, apply to this taxon as well. Fundamental differences in tooth characters differentiate *Ignigena minisculus* from other groups of small bodied typotheres: archaeopithecids have equidimensional upper molars with long-lived fossettes, and molars wider than long; archaeohyracids and hegetotheriids are much larger typotheres, and lack a persistent lingual sulcus on upper molars; even small mesotheriids are clearly larger and have pronounced trilobed (except for late wear stages in trachytheriines, where these teeth become bilobed) hypsodont upper molars.

Ignigena minisculus belongs to the least inclusive clade (unnamed) containing Interatheriinae (sensu Hitz et al., 2000, see fig. 6, node 4 this paper) plus *Eopachyrucos* and *Johnbell hatcheri*, characterized ancestrally,

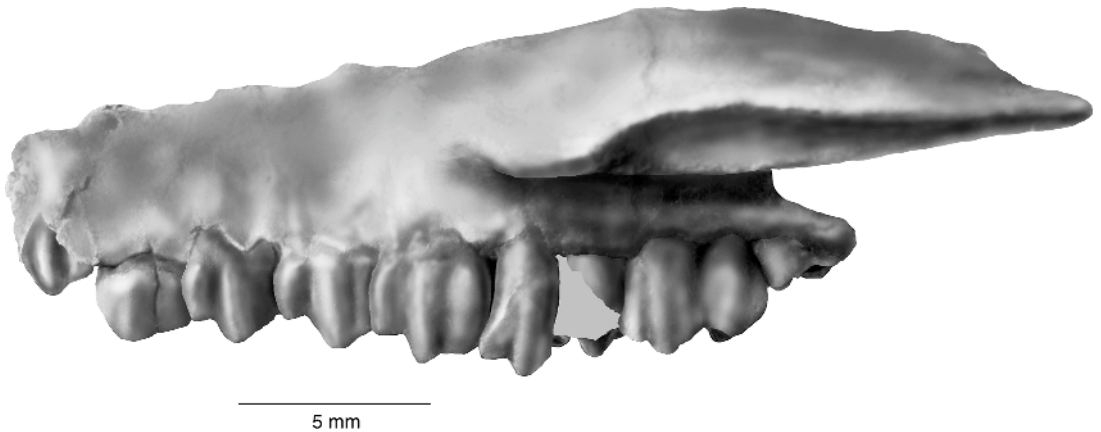


Fig. 8. *Ignigena minisculus*, new taxon, SGOPV 3168 (holotype), left maxillary fragment, partial zygoma, C-M3, left buccal view. Tapado Fauna.

and distinguished from all other interatheriids, by the following derived features: smooth posterior ectoloph on the upper premolars and upper molars longer than wide.

Ignigena minisculus lacks the suite of synapomorphic dental features that diagnose the clade of Interatheriinae (sensu Hitz et al., 2000) plus *Eopachyrucos*: a low or flat ectoloph on M1-3; hypsodont or hypseledont cheekteeth (HI for *Ignigena minisculus* is 0.81, as measured on the M2).

Ignigena minisculus differs from *Johnbell hatcheri* in having upper premolars with stouter protocones, resulting in broader teeth (most apparent on P3-4). The lingual sulcus on M1-2 also is wider than on *Johnbell hatcheri*. *Ignigena minisculus* is distinguished from *Punapithecus* (besides *Johnbell hatcheri*, the only other diminutive basal interatheriid known) by the former's larger size, lack of anterior cingulae on the upper premolars and molars, and upper molars that are longer than wide.

TYPE LOCALITY: Tapado ("Main") Locality, Abanico Formation, Río Tinguiririca valley, east central Chile (Wyss et al., 1994). The Tapado ("Main") Locality is located 14 km northwest of the Tinguiririca Fauna localities (see above; Wyss et al., 1994; Charrier et al., 1996; Flynn et al., 2003). Although fossils potentially referable to the Tapado Fauna have been recovered from exposures on both the north and south sides of the Tinguiririca River (over a N-S distance of more than 3 km), most specimens have been recovered from sites south of the river. Casual observation, and even previous mapping (e.g., Klohn, 1957, map cross-section B) of the nearly continuous exposures of the Abanico Formation in the Tinguiririca valley give the impression that the western horizons producing the Tapado Fauna are substantially higher stratigraphically (many hundreds of meters) than the eastern deposits bearing the Tinguiririca Fauna. Nevertheless, the Tapado Fauna is undoubtedly older (probably Casa-



Fig. 9. *Ignigena minisculus*, new taxon, SGOPV 3167 (referred specimen), left mandible, p1-p3, m1, occlusal view. Tapado Fauna.

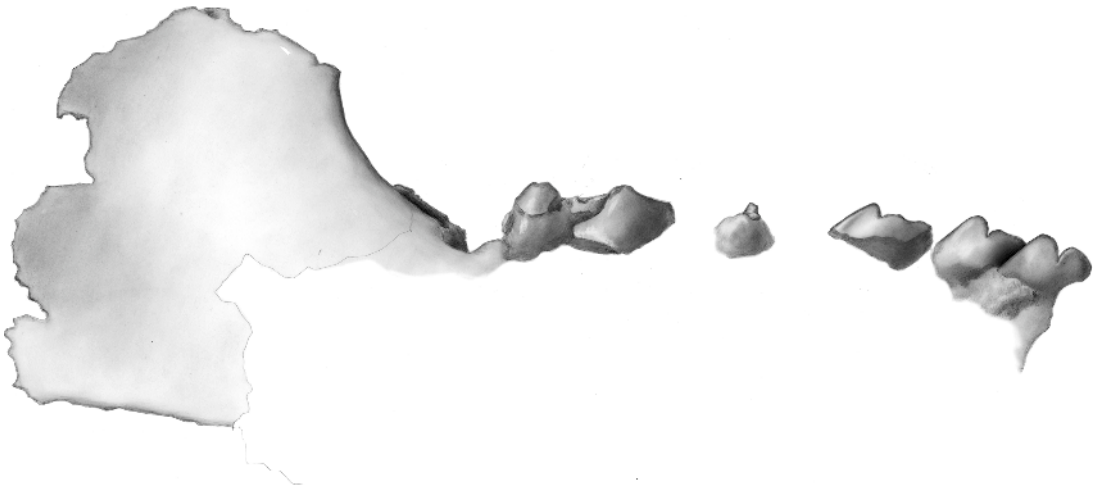


Fig. 10. *Ignigena minisculus*, new taxon, SGOPV 3167 (referred specimen), left mandible, p1–p3, m1, left buccal view. Tapado Fauna.

mayoran SALMA) than the Tinguiririca Fauna, demonstrating that low-angle faulting has thrust (albeit cryptically) older strata over younger within the Tinguiririca valley. Evidence suggesting a Casamayoran age for the Tapado Fauna includes the didolodontid *Ernestokokenia*, *Notostylops*, and possibly *Eohyrax isotemnoides* (Wyss et al., 1996; Flynn et al., 2005). A more definitive age assignment awaits ongoing taxonomic and radioisotopic work.

KNOWN DISTRIBUTION: Known only from the Tapado Fauna, from the Tapado (“Main”)

TABLE 2
Dental Measurements (in mm) for Upper and Lower Jaws of *Ignigena minisculus*

Jaw	SGOPV 3167	SGOPV 3168
	lower	upper
AP P1	1.73	2.35
TR P1	0.83	1.73
AP P2	1.96	2.45
TR P2	—	2.22
AP P3	—	3.14
TR P3	—	2.69
AP P4	—	3.32
TR P4	—	3.20
AP M1	—	3.69
TR M1	—	3.45
AP M2	—	3.95
TR M2	—	3.72

Locality, south of the Río Tinguiririca; likely Casamayoran in age.

DESCRIPTION

Mensural information for the two interatheriid specimens currently known from the Tapado Fauna is presented in table 2.

UPPER DENTITION

The interatheriid occurring in the Tapado Fauna compares closely with *Johnbell hatcheri* from the Tinguiririca Fauna, and the morphological features of the dentition presented above for *Johnbell hatcheri* also pertain to *Ignigena minisculus*, except where noted below. The two forms differ significantly only in the points noted in the diagnosis of *Ignigena minisculus*. Also in contrast to *Johnbell hatcheri*, the P4 of *Ignigena minisculus* shows a minor posterior cingulum high on the crown. A similar but more distinct cingulum occurs on M1 and M2. (However, the holotype of *Johnbell hatcheri* [SGOPV 3106] shows greater wear than specimens of *Ignigena minisculus*; thus, the difference in posterior cingulum expression may reflect wear rather than discrete, taxonomically informative character differences.) The third upper molar in SGOPV 3168 is in the process of erupting, with only the tips of the paracone and protocone having emerged from the tooth crypt.

CRANIAL MATERIAL

The anterior root of the zygoma extends from the posterior half of M2 to the middle of P4 and is thus is not remarkably broad. The zygoma is marked by a small descending process. The palatine/maxillary suture of the palate is curved (concave posteriorly); its anterior end is even with P4.

LOWER DENTITION

Reference of lower dental material (SGPOV 3167) to *Ignigena minisculus* is based on size (relative to the holotype SGPOV 3168) and similar suites of upper and lower dental features (as present in other basal interatheriids).

SGOPV 3167 preserves fragments of an unworn lower dentition, the anterior premolar portion of which displays some unusual morphology for an interatheriid. The first two premolars are unworn. The occlusal outline of each of these teeth, which are narrow, forms a broad “V”, opening lingually. In lateral view, the two wings of the “V”, each of which is somewhat rounded, are separated by a cleft at their juncture, giving the teeth the appearance of “Mickey Mouse ears”. This shape is more emphasized on p1 than on p2. The “V”-shaped p1–2 seem to resemble the morphology of these teeth in *Notopithecus* and *Johnbell hatcheri*, but the latter two taxa are not known from unworn specimens, complicating direct comparison with SGOPV 3167.

Only the tip of the crown of p3 is preserved, but this tooth appears to have formed a thin crescent, convex labially. Other morphological details of this tooth are obscured by breakage.

The m1 is partly exposed labially, showing a convex (labially) protolophid, a transversely oriented metalophid, and a deep labial sulcus between the trigonid and talonid. The talonid is ovate in outline with a flattened posterior margin. The well-defined labial sulcus on m1 is similar to that observed in other basal interatheriids, such as *Notopithecus* and *Johnbell hatcheri* (although some other small non-interatheriid tyotheres also have this feature).

Antepithecus Ameghino, 1901*Antepithecus brachystephanus* Ameghino, 1901
Figures 11–12

REFERRED SPECIMEN: SGOPV 3604: partial cranium, with palate bearing right and left dP1–dP4, and right and left M1, and an erupting right M2, as well as portions of the right zygoma and rostrum.

LOCALITY AND DISTRIBUTION: Azufre Locality, Río Azufre valley, Abanico Formation, Chile. SGOPV 3604 represents part of a small suite of dental and postcranial material recovered in 1997 during helicopter access and reconnaissance prospecting of remote western exposures of the Abanico Formation along the Río Azufre, due north of the Río Tinguiririca drainage and west of Volcán Tinguiririca. Its taxonomic assignment indicates a Casamayoran age (likely “late” Barrancan subage, of Cifelli, 1985). Extremely steep cliff exposures along the west side of the north-south trending Río Azufre precluded access to most of the thick, nearly horizontal stratigraphic sequence exposed in the area during this brief exploratory trip. All of the specimens recovered from the area were collected in a large quebrada from float blocks of uncertain provenance.

BACKGROUND: We refer SGOPV 3604 from the Azufre Locality to *Antepithecus* (Ameghino, 1901). *Antepithecus* (1901) is a basal interatheriid from the Casamayoran SALMA; its dentition is nearly identical to *Notopithecus*. Simpson (1967) provided a thorough treatment and revision of *Antepithecus*, noting that its similarities with *Notopithecus* caused him to vacillate before ultimately concurring with Ameghino (1901) that *Antepithecus* indeed represents a distinct taxon. Simpson (1967) noted, in his diagnosis for *Antepithecus*, the following distinctions of *Antepithecus* (relative to *Notopithecus*): “slightly more brachydont, protocone and hypocone less united, cheek teeth more elongate, horizontal mandibular ramus shallower” (Simpson, 1967: 96). With respect to the greater elongation of the teeth in *Antepithecus*, Simpson stated elsewhere in his discussion (pp. 77–78) that the “p3, p4, m1, and m2 are significantly longer” and for the upper cheek teeth, “*A. brachystephanus*

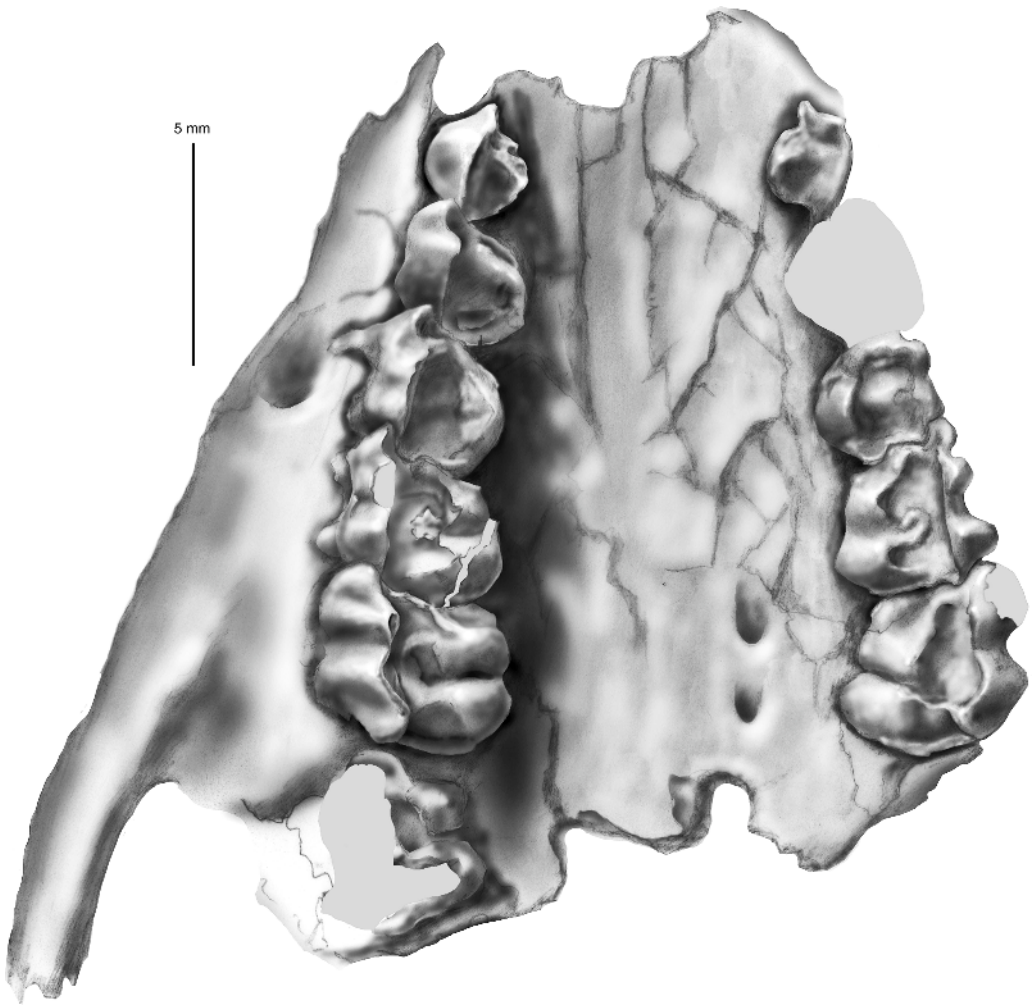


Fig. 11. *Antepithecus brachystephanus*, SGOPV 3604 (referred specimen), palate, right and left dP1-dP4, right and left M1, erupting right M2, portions of the right zygoma and rostrum, occlusal view. Azufre Locality.

averages longer than *N. adapius*." Simpson provided t-test support for this size distinction for some of the teeth in the lower dentition, but due to small sample size did not apply the statistical test to the upper dentitions.

Other than these highlights, Simpson provided a single detailed description of a dentition that served to characterize both *Antepithecus* and *Notopithecus*. *Antepithecus* is not yet known from cranial material. Following is a description of SGOPV 3604, and a discussion of its diagnostic resemblances

to *Antepithecus* and differences from *Notopithecus* and other basal interatheriids. Mensural information is presented in table 3.

DESCRIPTION: The specimen consists of the right and left sides of a heavily worn dP1-dP4 series, recently erupted and unworn M1s, and a RM2 in the process of erupting. Also exposed are the palate, a portion of the right zygoma, and a portion of the right rostrum (maxilla and premaxilla). Additional portions of the rostrum may be preserved within the matrix of the sample, but have yet to be prepared.

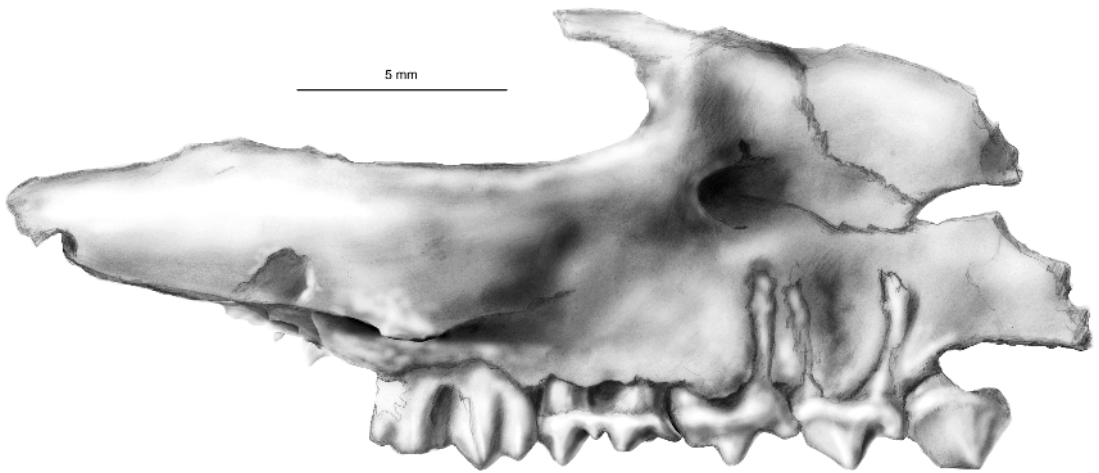


Fig. 12. *Antepithecus brachystephanus*, SGOPV 3604 (referred specimen), right dP1-dP4, right M1, erupting right M2, portions of the right zygoma and rostrum, right buccal view. Azufre Locality.

The primary criterion for identifying the dentition as consisting of dP1-dP4, and M1-2, is the relative wear on each tooth. The anterior tooth is less worn than the succeeding three, while the two posterior teeth show almost no wear (the last one is only partly erupted). This is the expected pattern of wear for a dP1-4, M1-2 series in notoungulates, where the eruption sequence for upper cheekteeth is dP2, dP3, dP4, dP1, M1, M2, M3, P2, P3, P4 (M. Bond, personal commun.). Evidently, this specimen is a juvenile in which the permanent premolars had yet to erupt.

The dP1 is worn, but still shows a prominent paracone and small parastyle. An ill-defined

anterior emargination occurs low on the tooth. Wear has carved a basin between the paracone and protocone. Enamel is visible on all sides of the tooth but is completely absent on the worn occlusal surface.

The dP2 is a larger version of dP1, but with a definite low anterior cingulum and a more distinct parastyle.

The dP3 is likewise similar to the preceding two teeth, save for the presence of a small metacone.

The paracone and metacone of dP4 are of equal height (this tooth is less worn than the first three); an anterior cingulum occurs high (dorsally) on the crown, while the protocone and hypocone remain separate until the dorsal edge of the crown is reached (producing a lingual sulcus). A small cusp is present on the ectoloph between the paracone and metacone. The presence of this cusp defines a tiny basin on the ectoloph.

The nearly unworn M1 has a distinct paracone and parastyle with an inflection between these two structures labially. The paracone connects lingually with a less elevated protocone. The tooth's anterior margin bears a distinct cingulum low on the crown. The height of the metacone matches that of the paracone; strong undulation of the ectoloph reflects the large size of these two cusps and the inflection between them. The metacone connects lingually to the hypocone, the

TABLE 3
Dental Measurements (in mm) for Upper Jaw of
SGOPV 3604 (*Antepithecus brachystephanus*)

Jaw	SGOPV 3604	
	upper	
AP P1	3.0	
TR P1	2.6	
AP P2	3.0	
TR P2	3.5	
AP P3	3.4	
TR P3	3.6	
AP P4	3.8	
TR P4	4.3	
AP M1	4.5	
TR M1	4.8	

latter of which equals the protocone in height (the two lingual cusps being lower than the labial ones). The protocone and hypocone are deeply divided; likely they would have merged only after heavy wear. A posterior cingulum sits low on the tooth. Enamel covers the entire crown.

The only observable morphology on the erupting M2 is the emerging tip of the protocone, and a portion of the loph connecting the protocone to the paracone, the latter of which remains unerupted. Except for the complete lack of wear, the protocone and loph are identical to those seen on M1.

The palatine-maxilla suture is arcuate, reaching anteriorly to the middle of dP4. The maxilla is excavated anteriorly of the orbit, the infraorbital foramen being located above dP3. The zygoma bears a small descending process on its anteroventral border. In addition, it displays what we interpret as the suture between the maxilla and jugal. The latter element is reduced and excluded from the orbit, a hallmark interatheriid synapomorphy (Riggs and Patterson, 1935).

DISCUSSION

With the modest amount of morphology available for study, especially with most of the preserved teeth being deciduous and with minimal occlusal wear on the only fully erupted permanent teeth (L & R M1), the precise taxonomic assignment of this specimen is tentative. SGOPV 3604 is clearly a basal interatheriid (see next paragraph) and in comparison to early interatheriids, a number of conditions distinguish this specimen from *Notopithecus* and support its referral to *Antepithecus*, including brachydonty, well-separated hypocone and protocone, and size. In morphology and size SGOPV 3604 is extremely similar to *Antepithecus brachystephanus*, to which we assign the new material from the Azufre Locality, Chile. Simpson (1967) provisionally recognized a second species of *Antepithecus*, *A. innexus*, distinguishing it solely by its wider molars (a primitive feature, see below), but noted that it may represent an extreme variant of *Antepithecus brachystephanus*; if *A. innexus* is a valid species, SGOPV 3604 differs from it in its

narrower molars (and possibly the deciduous premolar features noted directly below). SGOPV 3604 does differ from specimens of *Antepithecus brachystephanus*, one of only two early interatheriid taxa preserving deciduous premolars (the other being *Punapithecus minor*), in having a more pronounced protocone on dP1-4, resulting in teeth with longer lingual margins, and thus less triangular in outline, than in *A. brachystephanus* (although the proportions of the M1 are very similar to that of *Antepithecus*). We decline to name the material of *Antepithecus* from the Azufre Locality as a new species at this time, because it would be diagnosed solely on differences in deciduous premolars; these are only rarely preserved, and their within-species variability is unknown. Recovery of additional specimens of the Chilean form (showing diagnostic differences in the permanent upper premolars or upper or lower teeth not represented in SGOPV 3604), or the recovery of comparable deciduous teeth of other taxa, may ultimately warrant recognition of a new species of *Antepithecus*, one most closely related to *A. brachystephanus* among known species of interatheriids.

Following the phylogenetic analyses of typother relationships by Hitz (1995, 1997; see also Hitz et al., 2000), early diverging members of the minimally inclusive clade that includes *Colbertia*, *Maxschlosseria*, *Brachystephanus*, *Tsamnichoria*, *Oldfieldthomasia*, and *Acropithecus* are characterized by permanent upper molars that are significantly wider than long. In *Oldfieldthomasia debilitata*, for example, the upper molars are 30% wider than long. These dimensions impart an occlusal pattern that is likewise wider than long (following the very initial wear stage). In other typotheres (interatheriids, hegetotheriids, mesotheriids, and archaeohyracids) the paracone/parastyle region expands anteriorly, producing upper molars that are equidimensional (or even longer than wide). SGOPV 3604 has nearly equidimensional deciduous premolars and M1 (the only permanent cheek-tooth erupted in the specimen). SGOPV 3604 differs from mesotheriids, archaeohyracids, and hegetotheriids in being much smaller and very low crowned. The latter condition also distinguishes it from archaeopithecids.

General dental morphology thus indicates that SGOPV 3604 represents a basal interatheriid (given its brachydont condition and lack of synapomorphies of later diverging interatheriid clades). The tentative recognition that the jugal is excluded from the orbit substantiates assignment to the Interatheriidae rather than any other tytothere subgroup. The presence of an anterior cingulum on M1 of SGOPV 3604 is shared by only three interatheriid taxa: *Notopithecus*, *Antepithecus*, and *Punapithecus*. The extremely small size of *Punapithecus* argues against referring the new Chilean material to this taxon. Additionally, the M1 of *Punapithecus* has a parastyle that projects more anteriorly, giving the tooth a different aspect than SGOPV 3604, and the ectoloph of the M1 of *Punapithecus* is considerably smoother. Although the M1 in SGOPV 3604 is nearly the same size as that of *Notopithecus*, the brachydont nature of this tooth (hypso-donty index or HI = 0.45), plus the well-separated protocone and hypocone, compare more favorably to *Antepithecus*. Recognizing the limited available diagnostic morphology, and the lack of recent taxonomic revisions or comparisons of *Notopithecus* and *Antepithecus*, the balance of evidence suggests that *Antepithecus* is the most reasonable assignment currently possible. AMNH 28701, *Antepithecus brachystephanus*, a juvenile specimen figured in Simpson (1967: 97) provides a useful comparison. The M1 of AMNH 28701 closely resembles that of SGOPV 3604, as do the deciduous premolars. The most notable distinction between AMNH 28701 and SGOPV 3604 is the more robust protocone on dP1-4 of the Chilean specimen, resulting in teeth with longer lingual (and hence less triangular) margins, than in *A. brachystephanus*. Although this difference might indicate a species-level distinction, lacking other diagnostic differences (particularly in the adult morphology or permanent dentition), and given the paucity of deciduous dentitions known for other basal interatheriids and poor understanding of within-species variability in deciduous premolar morphology, we choose not to recognize the Azufre Locality specimen as a new species.

SGOPV 3604 would thus seem to indicate a Casamayoran age (possibly the "late"

Barrancan subage, Cifelli, 1985) for the strata in which it occurs along Río Azufre. Should the discovery of additional specimens (preserving M3, permanent upper premolars or other anterior teeth, or lower dentitions) tilt the taxonomic assignment of the Azufre material toward *Notopithecus* (unlikely, given their many morphological differences) rather than *Antepithecus*, the biochronologic implications remain the same, as both *Antepithecus* and *Notopithecus* occur throughout approximately the same temporal interval. With a few (likely erroneous) exceptions, both *Notopithecus* and *Antepithecus* are restricted to the Casamayoran SALMA. Simpson (1967) listed *Notopithecus* as occurring within the Riochican, but Cifelli (1985) questioned this assignment, identifying the suspect specimens as *Notopithecinae* indet. Although Simpson (1967) and Marshall et al. (1983) both listed ?*Notopithecus* as occurring in the Mustersan SALMA, these authors obviously were not convinced of this allocation. Thus, the range of specimens securely identifiable as *Notopithecus* and *Antepithecus* is restricted to the Casamayoran. Moreover, both taxa are limited to the Barrancan subage of the Casamayoran, the younger of the two subages identified by Cifelli (1985) on the basis of exposures at two classic localities, the Gran Barranca and Cañadón Vaca. Cifelli (1985) further divided the Barrancan subage into "early" and "late" intervals. With one exception (see below), *Notopithecus* appears only in the "early" Barrancan and *Antepithecus* in the "late" Barrancan. In the uppermost portion of Section 2 from Cañadón Vaca, Cifelli (1985) reported the isolated occurrence of *Notopithecus*, indicating that the range of this taxon extends very slightly into the preceding Vacan subage. Kay et al. (1999) used new radioisotopic data to correlate the Barrancan subage of the Casamayoran SALMA to two possible paleomagnetic chrons, giving an age range of 35.34–37.60 Ma for this section, and an entirely late Eocene age for the Casamayoran (as opposed to its traditional conception as early Eocene, see Flynn and Swisher, 1995). Kay et al. (1999) did not directly address the age of the Vacan in the Cañadón Vaca section.

INTERATHERIID PHYLOGENY AND
THE RELATIONSHIPS OF THE
CHILEAN BASAL INTERATHERIIDS

Several cladistic studies of the Interatheriidae have been completed in recent years (Cifelli, 1993; Hitz, 1997; Reguero, 1999; Reguero et al., 1996, 2003b), with varying levels of success with respect to resolution of interathere phylogenetic relationships. Cifelli's work, based almost exclusively on dental characters, identified epidemic homoplasy in the group; the single resolved node stemming from his study was one demarcating the Interatheriinae from *Notopithecus*. Cifelli (1993) suggested, as in previous papers (Cifelli, 1985; MacFadden et al., 1985; Marshall et al., 1986), the probable existence of two monophyletic groups within the Interatheriinae: "*Interatherium* and allies" and "*Protypotherium* and allies". Cifelli also highlighted four provisional synapomorphies for Interatheriidae: maxilla excluding jugal from orbit (*sensu* Riggs and Patterson, 1935), I₁-C bifid, I²-P¹ transversely compressed, lower molars bilobate.

Hitz (1997; the phylogeny stemming therefrom is presented in Hitz et al., 2000) proposed a more highly resolved interatheriid phylogeny based on an analysis of 44 dental and cranial characters across 17 taxa. This more comprehensive level of sampling, and the degree of resolution achieved, motivated a phylogenetic definition (node-based) for the name Interatheriinae to accompany the list of synapomorphies diagnostic of the clade to which this name was associated (Hitz et al., 2000).

Reguero et al. (2003b) presented a phylogenetic analysis of Interatheriidae, focusing mainly on interatheriine taxa (*Notopithecus* representing the only basal interatheriid), building on the studies of Reguero et al. (1996) and Reguero (1999). Reguero et al. (2003b) achieved well-resolved relationships within Interatheriinae, although differing somewhat from those proposed by Hitz (1997), Hitz et al. (2000), and herein. Possible sources of these discrepancies are discussed below.

Here we present an analysis of interatheriids based on the data set used in Hitz (1997) augmented with the information available for

TABLE 4
Taxa Studied for Phylogenetic Analysis

<i>Archaeophylus patrius</i> Ameghino, 1897
<i>Plagiarthrus clivus</i> (= <i>Argyrohyrax proavus</i>) Ameghino, 1897
<i>Progaleopithecus tourneri</i> (= <i>Argyrohyrax proavunculus</i>) Ameghino, 1904
<i>Protypotherium australe</i> Ameghino, 1887 (see also Sinclair, 1909)
<i>Protypotherium praerutilum</i> Ameghino, 1887 (see also Sinclair, 1909)
<i>Interatherium robustum</i> Ameghino, 1887 (see also Sinclair, 1909)
<i>Interatherium extensum</i> Ameghino, 1887 (see also Sinclair, 1909)
<i>Cochilius volvens</i> Ameghino, 1902
<i>Cochilius fumensis</i> Simpson, 1932
<i>Miocochilius anamopodus</i> Stirton, 1953
<i>Punapithecus minor</i> Reguero et al., 1996
<i>Santiagorothia chiliensis</i> Hitz et al., 2000
<i>Proargyrohyrax curanderensis</i> Hitz et al., 2000
<i>Notopithecus adapinus</i> Ameghino, 1897
<i>Transpithecus obentus</i> Ameghino, 1901
<i>Guillemoscottia plicifera</i> Ameghino, 1901
<i>Colbertia magellanica</i> Price and Paula Couto, 1950
<i>Eopachyrucos plicifera</i> (Ameghino, 1901)
<i>Eopachyrucos ranchoverdensis</i> (Reguero et al., 2003b)
Salla new taxon A (informal taxon, Hitz, 1997)
Salla new taxon B (informal taxon, Hitz, 1997)

five additional taxa: 1) *Punapithecus*, a basal interatheriid from northwestern Argentina (López and Bond, 1995); 2) *Proargyrohyrax*, a recently described interatheriine (Hitz et al., 2000); 3) *Antepithecus brachystephanus*; 4) SGOPV 3604 (treated in isolation from *Antepithecus* and *Notopithecus*); and 5) *Eopachyrucos* (the diagnosis of which has been recently emended [Hitz et al., 2000], including a recently described species *E. ranchoverdensis* [Reguero et al., 2003b]) (see table 4 for a list of taxa in the analysis). *Colbertia*, an oldfieldthomasiid, served as the outgroup. The character list and data matrix (appendix 1) included 43 dental and cranial characters across 21 taxa. The analysis, using PAUP 4.0 (Swofford, 2002), yielded 623 equally parsimonious trees of 70 steps (branch and bound search, all characters unordered, equally weighted; for individual trees: CI = 0.74, RI = 0.86). All characters discussed below are numbered as in the character matrix.

Several nomenclatural issues regarding the names *Plagiathrus* Ameghino, 1896, *Argyrohyrax* Ameghino, 1897, and *Progaleopithecus* Ameghino, 1904, require clarification. All recent sources agree that the name *Argyrohyrax* is a junior synonym of *Plagiathrus* (Patterson, 1952; Marshall et al., 1986; Reguero, 1999; Reguero et al., 2003b), as suggested initially by Loomis (1914) and Simpson (1932). This synonymy was documented most concretely by Patterson's (1952) observation that *Argyrohyrax proavus* (the type species of *Argyrohyrax*) is based on an upper dentition belonging to *Plagiathrus clivus* (the type species of *Plagiathrus*). Following Hitz (1997) and Hitz et al. (2000), we use the name *Plagiathrus* to refer to specimens of *Plagiathrus clivus* as well as those previously referred to *Argyrohyrax proavus*.

Secondly, Patterson (1952; repeated by Marshall et al., 1986) suggested that the type specimen of *Progaleopithecus turneri* Ameghino, 1904, probably represents a portion of the same specimen upon which Ameghino based *Argyrohyrax proavunculus*, rendering *Progaleopithecus* a junior synonym of *Argyrohyrax*. This synonymy was accepted by Hitz (1997) and Hitz et al. (2000), wherein species previously placed in *Progaleopithecus* (sensu Ameghino) were transferred to *Argyrohyrax*.

Lastly, Reguero (1999) and Reguero et al. (2003b) further revised interatheriid nomenclature, although some of their recommendations are at odds with the points just discussed. While recognizing the general synonymy of *Argyrohyrax* and *Plagiathrus*, these authors regard *Plagiathrus* as having priority (over *Argyrohyrax*), and recognize *proavunculus* as a distinct species within *Plagiathrus*—proposing the new combination *Plagiathrus proavunculus* Reguero 1999. Although unable to examine specimens of *Argyrohyrax proavunculus* directly, we note that in Ameghino's original descriptions (1897) of *Argyrohyrax proavus* and *Argyrohyrax proavunculus* he stated that *A. proavunculus* is merely a smaller version of *A. proavus* and otherwise is very similar in morphology. Accepting *A. proavus* as a junior synonym of *Plagiathrus clivus* justifies the new combination *Plagiathrus*

proavunculus (Reguero, 1999) for "*A. proavunculus*". Reguero (1999) and Reguero et al. (2003b) also suggested, based on the presence of diagnostic characters (bicolumnar lower incisors, rounded [?]molar] trigonids; Reguero et al., 2003b), that *Progaleopithecus* should continue to be recognized as distinct, rather than as a synonym of *Argyrohyrax proavunculus* as suggested previously by Patterson (1952) and Marshall et al. (1986). Having examined specimens of *Progaleopithecus turneri* firsthand, we concur that there are sufficient diagnostic characters to justify continued recognition of this taxon. Here we use the name *Plagiathrus* to refer to *Plagiathrus clivus* (= *Argyrohyrax proavus*) and *Plagiathrus proavunculus*, while *Progaleopithecus* refers to *P. turneri*, which is distinct from *Plagiathrus proavunculus* (= *Argyrohyrax proavunculus*).

The differences between the maximally parsimonious hypothesis of relationships identified here and the results from our previous analyses (Hitz, 1997; Hitz et al., 2000) primarily center on decreased resolution of the basal part of the entire tree. Three of the taxa added to the current analysis are very fragmentary with respect to the character matrix; for example, SGOPV 3604 is only 13% complete, *Punapithecus* is 46% complete, and *Proargyrohyrax* is 50% complete. None preserves a significant amount of cranial material. Novacek (1989, 1992a, 1992b) documented that missing data contributed to tree instability insofar as greater numbers of maximally parsimonious trees resulted from the inclusion of taxa with considerable missing data. The missing data associated with SGOPV 3604, *Punapithecus*, and *Proargyrohyrax* seem to account for the decreased resolution from our earlier results. We have opted to employ the complete character matrix rather than exclude fragmentary taxa that potentially could act as "wildcards" (Nixon and Wheeler, 1992) or otherwise obscure phylogenetic relationships, for several reasons. First, the correlation between missing data and "wildcard behavior" is not well demonstrated (Kearney and Clark, 2003). Second, the results of our analysis, although more polytomous than in the analysis by Hitz (1997) still identify many well-supported

clades. Moreover, as it happens, some of the taxa we are most interested in placing phylogenetically (e.g., SGOPV 3604) are also among the most fragmentary.

An important contrast between the results of the present analysis and those presented by Hitz (1997) is that *Santiagorothia chiliensis* (as a consequence of adding new taxa to the analysis) is no longer resolved as the sole proximal outgroup to all other previously recognized interatheriines. This raises some questions with respect to the phylogenetic definition for the name Interatheriinae (sensu Hitz et al., 2000) considered below.

A strict consensus tree (fig. 6) identifies a clade (node 1 in fig. 6) that we equate with Interatheriidae. Monophyly of this clade is supported by many unambiguous synapomorphies: I²-C laterally compressed (sensu Cifelli, 1993) (character 2: character state 1), jugal excluded from orbit by maxilla (sensu Cifelli, 1993; Riggs and Patterson, 1935) (character 30: character state 1), nasofrontal suture anterior of orbit margin (character 31: character state 1), descending process on zygoma (character 33: character state 1 or 2), zygoma angled steeply at juncture with face (character 36: character state 1 or 2), narrow muzzle (character 37: character state 1), glenoid fossa deeply excavated and narrow (character 41: character state 1), postglenoid process sharp and narrow and separating fossa from meatus (character 42: character state 1 or 2). Two additional features identified by Cifelli (1993) (I₁-C bifid, lower molars bilobate) as characterizing Interatheriidae are less widely distributed and therefore are not regarded as synapomorphic for all interatheriids in this analysis.

Numerous clades within Interatheriidae are supported by unambiguous synapomorphies. (There exist additional, potential synapomorphies diagnosing the nodes in fig. 6—beyond those listed. Nevertheless, these are considered equivocal, as at least one basal taxon of the clade that the character potentially diagnoses, and the nearest outgroup of that clade, cannot be scored.) Of note is the clade (the polytomy of node 4 in fig. 6) that is roughly equivalent to—aside from including *Proargyrohyrax*—the Interatheriinae (sensu Hitz et al., 2000, p. 3, defined as: “the clade stemming from the most recent ancestor of *Santiagorothia chilien-*

sis and *Interatherium* plus all of its descendants”). Following the phylogenetic definition of Hitz et al. (2000), *Proargyrohyrax* is thus presently considered a member of the Interatheriinae. Should future work resolve the polytomy and place *Proargyrohyrax* as an outgroup to the least inclusive clade containing *Santiagorothia chiliensis* and *Interatherium*, then *Proargyrohyrax* would no longer be an interatheriine, by definition (Hitz et al., 2000). Thus, new results might yield changes in the phylogenetic placement of taxa (*Proargyrohyrax* in this case), without perturbing in the least a stable definition of the widely used name Interatheriinae. Three subgroups within the above clade warrant discussion. The first (node 5 in fig. 6), including *Interatherium*, *Cochilius*, and *Plagiarthrus*, is diagnosed by talonids on p2–4 subequal or larger than the trigonids (character 23: character state 3). The second (node 6 in fig. 6) is an unresolved tritomy of *Protypotherium*, *Progaleopithecus tournoueri*, and *Miocochilius*, diagnosed by a distinct third lobe on m3 (character 28: character state 1) and a narrow anterior border on the lower premolars and molars (character 29: character state 1). These two subgroups appear to correspond to the “*Interatherium* and allies” and the “*Protypotherium* and allies” of Cifelli (1993). A clade (node 2 in fig. 6) relevant to the systematic discussions in this paper is the least inclusive one containing Interatheriinae (sensu Hitz et al., 2000) plus *Eopachyrucos*, *Johnbell hatcheri*, and *Ignigena minisculus*; it is diagnosed by two synapomorphies: M1–3 paracone/parastyle inflection is reduced or absent (character 12: character state 1), and upper molars longer than wide (character 17: character state 1).

In a second analysis, all trees ≤ 71 steps (i.e., one step more than the maximally parsimonious) were retained, and a strict consensus tree derived from them. This process yielded 12,548 equally parsimonious trees. Several clades of note persist in this consensus tree: the pairing of *Interatherium* and *Cochilius*, a clade consisting of Interatheriinae (sensu Hitz et al., 2000) plus *Proargyrohyrax* and *Eopachyrucos* (node 3, see fig. 13), and a clade consisting of *Johnbell hatcheri* and *Ignigena minisculus* plus the previous clade (node 2, see

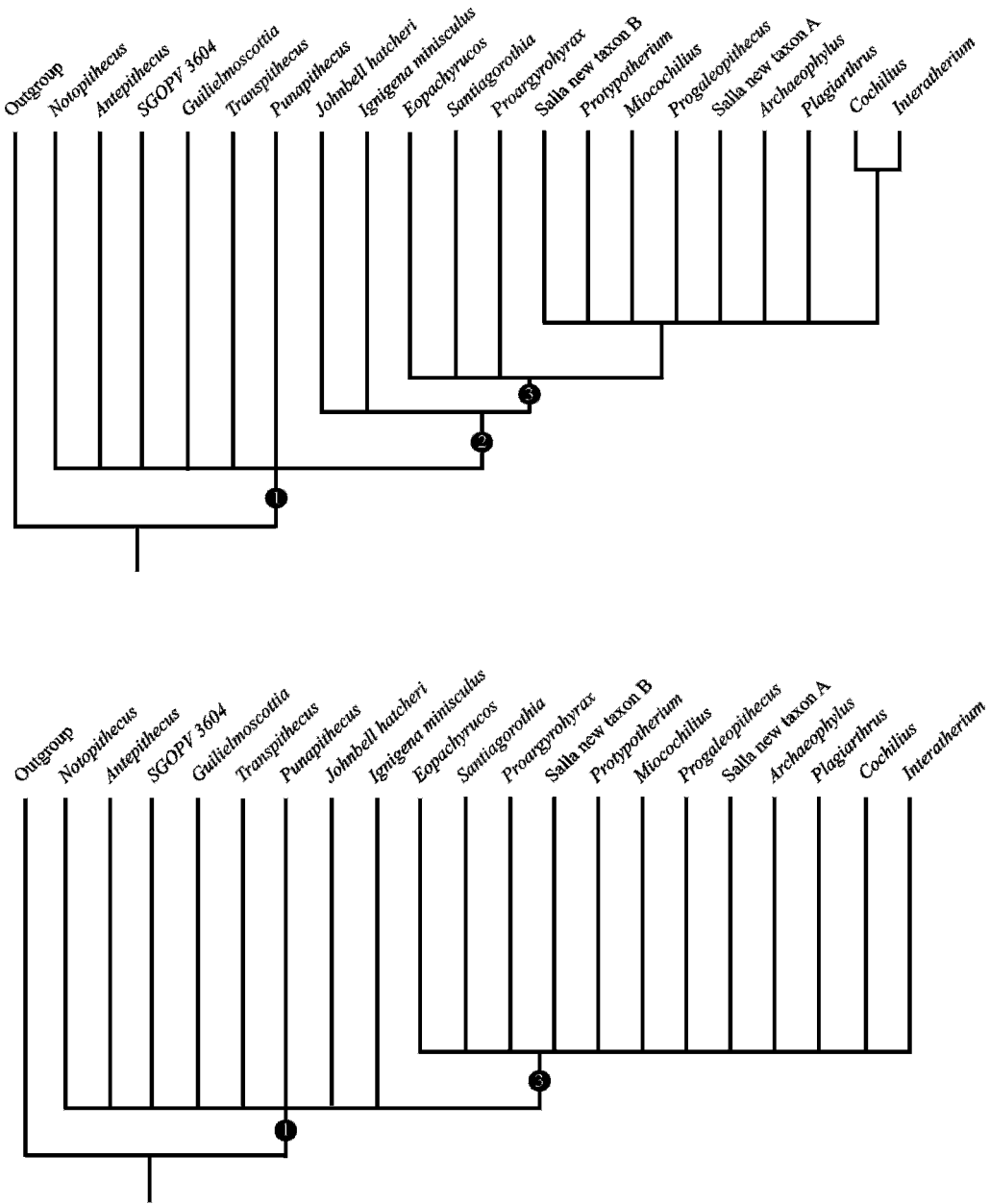


Fig. 13. Upper cladogram is a consensus of all trees 71 steps or shorter. The labeled nodes are those that persist compared to the consensus tree of 70 steps and shorter (fig. 6). The lower cladogram is a consensus of trees 72 steps and shorter, with persisting nodes labeled.

fig. 13). The former clade (node 3) is the only one to persist in a third analysis, in which all trees ≤ 72 steps were retained (126,998).

We next compare our results with those of Reguero et al. (2003b) to the extent possible given differences between the datasets (fig. 14).

Reguero et al. (2003b) used 29 characters (22 dental; seven mandibular, cranial, and post-cranial) across 12 taxa. Ten of the taxa in their analysis were interatheriines, and one was a basal interatheriid. They presented a single consensus of their most parsimonious trees, but

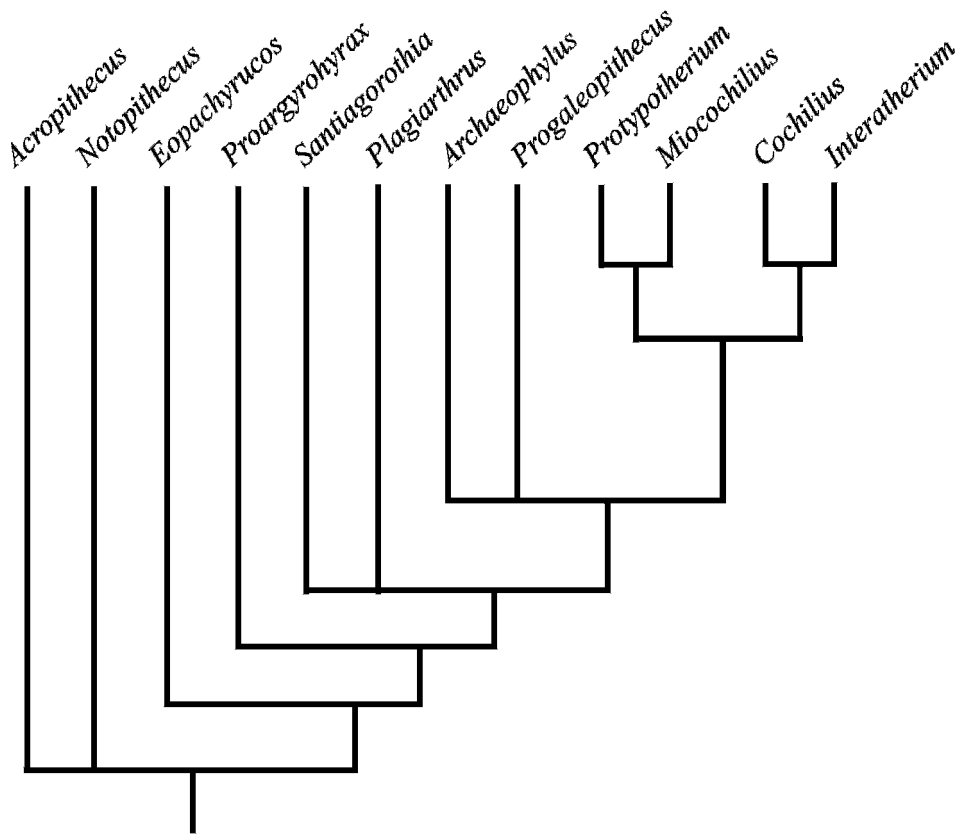


Fig. 14. Interthere phylogeny after Reguero et al. (2003b; fig. 8). Reguero et al. (2003b) presented two different phylogenies using two different analytic techniques but the topologies of the trees are identical.

they did not run additional analyses retaining trees of greater length. By contrast, we employed 43 characters (29 dental; 14 mandibular, cranial, and postcranial) across 21 taxa (11 interatheriines, 9 basal interatheriids, and 1 outgroup). Reviewing the characters in Reguero et al. (2003b), we determined 18 of them as roughly coincident with characters in our dataset, leaving 11 characters not corresponding to any of ours. Conversely, 25 characters in our dataset have no equivalents in Reguero et al. (2003b). The main difference between the consensus trees presented in Reguero et al. (2003b) and this study is the topology of the clades within the Interatheriinae (sensu Hitz et al., 2000). Reguero et al. (2003b) placed *Plagiarthrus* and *Progaleopithecus* in more basal positions within Interatheriinae than did our results.

Both studies identify *Eopachyrucos* as having diverged prior to the appearance of

the interatheriine (sensu Hitz et al., 2000) common ancestor. Reguero et al. (2003b) identified *Proargyrohyrax* as the nearest outgroup to Interatheriinae (sensu Hitz et al., 2000), whereas in the current analysis *Proargyrohyrax* falls in a basal interatheriine tritomy. Although *Eopachyrucos* was considered an interatheriine by both Hitz et al. (2000) and Reguero et al. (2003b), based on its very high-crowned cheekteeth, it cannot be considered such any more, given that it now lies as an outgroup to the clade linked to the name Interatheriinae, sensu Hitz et al. (2000). The shifting taxonomy of *Eopachyrucos* presents an opportunity to discuss the usefulness of applying phylogenetic definitions to groups the understanding of whose phylogenetic relationships is in flux, and why a phylogenetic definition is of particular utility in the case of the name Interatheriinae.

A potential criticism of the phylogenetic definition for Interatheriinae (sensu Hitz et al., 2000) is that it is now at odds with the distribution of one of the characters commonly used to diagnose interatheriines traditionally, high-crowned cheekteeth (Cifelli, 1985). We explore an alternative to our earlier phylogenetic definition (Hitz et al., 2000), one possibly better conforming to classical usage, concluding, however, that our original node-based definition is as robust as any conceivable alternative and that its continued use enhances the stability of interatheria taxonomy.

An alternative to a node-based phylogenetic definition (as that of Hitz et al., 2000) would be an apomorphy-based definition (de Queiroz and Gauthier, 1990, 1992), with hypsodonty being the logical candidate as the specifying apomorphy. A hypothetical apomorphy-based phylogenetic definition might read, “the clade stemming from the most recent common ancestor of all interatheres marked by hypsodonty”. The name would refer to a clade encompassing all interatheria taxa historically considered to be interatheriines (those that are hypsodont), plus it would be in alignment with moderately robust nodes in both the phylogenetic analyses of Reguero et al. (2003b) and this study (node 3 in fig. 6). [An extension of this example would be to use any of the diagnostic characters associated with the clade named Interatheriinae.]

We perceive two weaknesses with this alternative, the first being that hypsodonty is ultimately a gradational designation. Hypsodonty indices vary continuously from very low to very high; it does not occur in discrete states.

The second, more fundamental, problem is that with the broad sampling of interatheres in our analysis, we observe that the morphological contrast between what have traditionally been termed interatheriines and their nearest outgroups has been lessened, with the continuing recognition of successive outgroups forming a “comb” (e.g., nodes 2, 3, and 4 in fig. 6). Morphological “jumps” along this comb are small (i.e., nodes with significantly more supporting character changes than preceding and following nodes). Indeed, the

characters identified by Hitz et al. (2000) as diagnostic of Interatheriinae are now spread across nodes 2, 3, and 4 (fig. 6). *Santiagorothia chilensis*, *Proargyrohyrax*, and *Eopachyrucos*, all of which have been recently described (or emended), may be construed as morphologically intermediate between basal interatheriids and classic interatheriines such as *Interatherium* and *Protypotherium*. This is well illustrated by the consensus of trees 71 steps or shorter (fig. 13), which identifies the former three taxa as sharing a unique common ancestry with (but being placed outside of) the clade containing all other interatheriines. In this case, new discoveries clearly document that traits once thought to arise coincident with the origin of “interatheriines” (possibly as a correlated suite of adaptations to grazing or rapid environmental change) actually were acquired sequentially or in a mosaic fashion across a longer time span, and only appeared clustered because of substantial taxonomic and temporal sampling gaps. In fact, recovery of morphologically intermediate taxa is precisely the expected outcome of sampling new temporal intervals or previously poorly understood portions of the phylogeny (recent discoveries of a long series of transitional feathered dinosaurs are an appropriate analogy).

One could argue that the name Interatheriinae has been used historically to refer to taxa clumping at one end of a morphological spectrum ranging from early, small, brachydont basal interatheriids to later, larger, hypsodont or hypselodont forms, but without a clear demarcation of the taxonomic “dividing point”. The increasingly blurred “boundary” between traditional “interatheriines” and their proximal outgroups highlights the many clades available to choose from in crafting a phylogenetically defined version of that name.

In the interest of stability, and in the absence of a stronger alternative, here we opt to leave the phylogenetic definition of Interatheriinae (sensu Hitz et al., 2000) unchanged. To modify the definition to better conform with the traditional delineation between basal interatheres and interatheriines is to chase an historical ideal that, in light of

recently described “intermediate” taxa, no longer exists.

There are several consequences of this action. First, the character diagnosis of the node associated with the name Interatheriinae in Hitz et al. (2000) changes to reflect the present analysis (distinctly bilobed p3-4 with persistent labial and lingual sulci; maxilla excluded from the superior orbital border by an anteriorly projecting sliver of frontal; auditory bulla lapped posteriorly onto the paraoccipital process—the latter two characters are provisional, as proximal outgroups to the clade in question cannot be scored for these characters). Second, *Eopachyrucos*, previously considered an interatheriine (Hitz et al., 2000; see also Reguero et al., 2003b) based on the phylogeny and diagnosis of the clade accepted at that time, is currently seen as falling outside the clade to which that name is tied. Our conception of the clade’s membership has thus changed slightly since the phylogenetic definition was first proposed.

Our current phylogenetic results, and those of other studies (e.g., Cifelli, 1993; Reguero et al., 1996, 2003b; Hitz, 1997), underscore the strong support for the monophyly of Interatheriidae, regardless of the precise list of synapomorphies diagnosing it. In these phylogenies, Interatheriidae is consistently diagnosed by the apomorphic sandwiching of the jugal between the maxilla and squamosal, plus the exclusion of the jugal from the orbit, unusual features not seen in other notoungulates and that have long been used to assign taxa to the Interatheriidae. Other conditionally synapomorphic attributes are listed above and in Cifelli (1993). As the name Interatheriidae has not been defined phylogenetically, we do so here.

The unique configuration of the zygoma in interatheres offers a convenient basis for defining the name of this clade of notoungulates via an apomorphy-based phylogenetic definition. Defining the name Interatheriidae in this manner maximizes its congruence with historical usage. In apomorphy-based definitions the appearance of a particular character provides the means of stipulating the specific clade/ancestor to which a given name is linked. Interatheriidae is hereby defined as the no-

toungulate clade stemming from the ancestor displaying a splintlike jugal on the zygomatic arch, wherein this element is “sandwiched” between the maxilla and squamosal and excluded from the orbit.

All cladistic analyses of the Interatheriidae to date (e.g., Hitz, 1997; Reguero et al., 2003b; this study) highlight the paraphyletic nature of the Notopithecinae. Ameghino (1897) coined the name Notopithecidae to encompass solely *Notopithecus adapinus*, a taxon he considered ancestral to “prosimians” and other primates. More credibly, within the same paper he also recognized the close relationship of Notopithecidae to the Interatheriidae (= “Protyopotheriidae”). Although the proposed link of *Notopithecus* to Primates has long been outmoded, Riggs and Patterson (1935) persuasively confirmed the affiliation of *Notopithecus* and interatheriids by virtue of the unique configuration of the jugal mentioned previously. Attempting to highlight this anatomical finding, Simpson (1945) proposed the subfamily Notopithecinae (within Interatheriidae) to encompass *Notopithecus*, *Antepithecus*, *Transpithecus*, and *Guilielmoscottia*—to emphasize their lack of derived features such as hypsodont teeth, a taxonomic grouping that remains in wide usage to this day (e.g., McKenna and Bell, 1997).

Simpson (1967) provided a comprehensive systematic treatment of Notopithecinae. His “definition” (diagnosis—in current terminology) of the group listed a mix of cranial and dental characters, some being primitive features that also are typical of other tyotheres (such as oldfieldthomasiids and archaeopithecids), while others are more likely synapomorphic for Interatheriidae. No synapomorphies uniting “notopithecines” to the exclusion of other interatheriids have yet been identified. We propose that non-interatheriine interatheriids are more appropriately termed “basal interatheriids” as this phrasing lacks any connotation of the monophyly of those taxa. The name Notopithecinae (and all of its derivatives) may someday be useful if any interatheriid species prove to be more closely related to *Notopithecus* than to other interatheriids. In such a case, this vintage name might be linked to this newly recognized clade.

DISCUSSION

The two new taxa described here, *Johnbell hatcheri* and *Ignigena minisculus*, and the specimen referred to *Antepithecus brachystephanus*, are derived from four geographically distant faunas (Tinguiririca, Tapado, Azufre, Cachapoal), adding to the burgeoning diversity of fossil mammals known from the Abanico Formation of central Chile. This work provides new information about the systematics of basal interatheriids, and biochronological age estimates for localities outside of the original Abanico Formation fossil mammal discoveries in the Portozuelo El Fierro area near Termas del Flaco in the Río Tinguiririca valley.

As one of the youngest known basal interatheriids, *Johnbell hatcheri* underscores the transitional nature of the Tinguiririca Fauna, wherein “archaic” Paleogene taxa and later diverging clades co-occur (Wyss et al., 1994; Flynn et al., 2003). The occurrence of *Johnbell hatcheri* at the Río Cachapoal Locality (Cachapoal Fauna) indicates a tentative Tinguirirican (Flynn et al., 2003) age assignment for these deposits, consistent with preliminary evidence provided by other faunal elements (Flynn and Wyss 2004) and geological data (Charrier et al., 1996, 1997, in progress).

The age of the Tapado Fauna is somewhat less certain, but the presence of a basal interatheriid, *Ignigena minisculus*, is compatible with a Casamayoran age estimate (Wyss et al., 1994, 1996; Flynn et al., 2005) for this locality based on other taxa.

Our referral of a specimen from the Azufre Locality to *Antepithecus brachystephanus* suggests a Casamayoran age for these deposits, and is the first report of this taxon outside of Patagonia. Fieldwork in the Río Azufre specifically targeted western exposures of the Abanico Formation, the structural region from which the oldest fauna known previously (Tapado Fauna, Río Tinguiririca valley) is derived, in an attempt to uncover even older faunas, thereby better constraining the age of initiation of basin subsidence. Because this prospecting trip had an auxiliary educational objective (see acknowledgments), we chose to explore a region that had never previously yielded fossils, making an explicit prediction

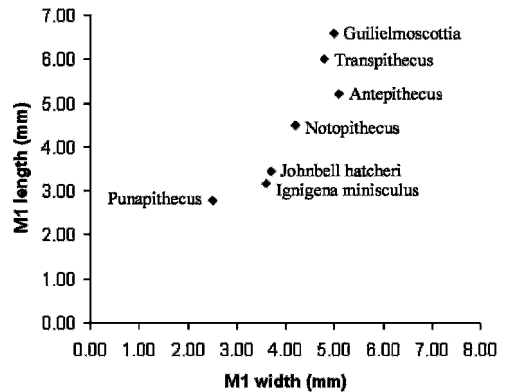


Fig. 15. Bivariate plot of basal interatheriids (excluding *Eopachyrucos*) using upper first molar dimensions.

about the age of the unit in this region. Based on our experience in the Río Tinguiririca valley, we used aerial photographs to trace large-scale lithologic units from that valley to the Río Azufre valley. This led to the prediction that the targeted strata would likely be correlative with, or somewhat older than, the Tapado Fauna (~ Casamayoran in age; and older than the youngest known faunas [Tinguirirican SALMA] cropping out at the eastern end of the Tinguiririca valley). The Casamayoran age indicated by SGOPV 3604 (*Antepithecus brachystephanus*) confirms that prediction. Radioisotopic dating and additional paleontological collecting from the Río Azufre region will help refine the geochronology of some of the oldest Abanico Formation strata currently known.

The two new basal interatheriid taxa from the Abanico Formation are substantially smaller than forms known from Patagonia (fig. 15). The diminutive nature of these Andean forms is shared uniquely with *Punapithecus minor*, the smallest interatheriid known, recently described from Mustersan age localities in the Salta and Catamarca Provinces of northern Argentina (López and Bond, 1993, 1995; Alonso et al., 1988). All three of these taxa are from latitudes well north (Tinguiririca ~35° S; *Punapithecus* = ~25–26° S) of those yielding other basal interatheriids such as *Notopithecus*, *Transpithecus*, and *Guilielmoscottia*, which are known solely from Patagonian localities

(e.g., Gran Barranca south of Lake Colhue Huapi, $\sim 46^\circ$ S). Although only three such diminutive basal interatheriids are currently known, it is tempting to posit that a provincial biogeographic pattern existed during the Paleogene, with smaller basal interatheriids to the north and larger forms to the south. A related possibility, amenable to testing with future discoveries, is the possibility of clinal variation (large to small body size; Bergman's Rule) from Patagonia to central Chile to northern Argentina. Our phylogenetic analysis of Interatheriidae does not identify a separate clade of basal interatheriids diagnosed by small size, indicating perhaps that small size appeared convergently in these geographically disjunct species, potentially in response to similar environmental pressures. Alternatively, depending on how existing polytomies are resolved, very small size might have characterized part of the main interatheriid stem lineage.

There appears to be a temporal component to the distribution of small-bodied taxa as well, given their restriction to Mustersan and Tinguirirican SALMA deposits, whereas somewhat larger basal forms are found in localities of Casamayoran through Mustersan age, and large-bodied interatheriines occur only in Tinguirirican and younger sites.

Our work here does not fully resolve uncertainty about whether *Antepithecus* and *Notopithecus* are distinct, but it does bear on the issue. The morphological differences between these two taxa are slight, with *Antepithecus* differing from *Notopithecus* in only a single character state in our character matrix (table 2: character 13: character state 1: *Antepithecus* has a lingual sulcus on the upper molars that persists longer than in *Notopithecus* [scored as "0"], due to more prominent hypocone and protocone in *Antepithecus*), placing *Antepithecus* within a clade including all interatheres except *Notopithecus*. Comparison beyond the dentition is hindered by lack of cranial material for *Antepithecus*. Based on these results, we concur with Simpson's (1967) view that these taxa, although very similar, are nonetheless distinct. SGOPV 3604 scored identically to *Antepithecus* in our data matrix and thus is positioned at the same polytomy as

Antepithecus on our consensus tree. Although this provides no positive evidence of special relationship between *Antepithecus* and SGOPV 3604 (i.e., a pairing of these taxa to the exclusion of other interatheres), it does not preclude this possibility either. Since SGOPV 3604 from the Azufre Locality cannot be distinguished from *Antepithecus brachystephanus* in any morphological attributes, we conservatively refer this specimen to that Casamayoran taxon.

The phylogenetic analysis presented here substantiates the existence of a clade encompassing *Santiagorothia chiliensis* plus all other previously recognized interatheriines (except *Eopachyrucos*), validating the phylogenetic naming of that clade (Hitz et al, 2000). Two clades roughly equating to the "*Interatherium* and allies" and "*Protypotherium* and allies" suggested by Cifelli (1985) occur in our consensus tree of 70 steps. These two clades collapse, however, in the consensus tree resulting from trees ≤ 71 steps, arguing that is it probably premature to name them formally.

CONCLUSION

The work detailed here may be summarized by these concluding points:

- Two new basal interatheriid taxa (non-interatheriine interatheriids) are recognized from the Andean Main Range of central Chile, *Johnbell hatcheri* and *Ignigena minisculus*. *Johnbell hatcheri* derives from the same horizons of the Abanico Formation as those producing the Tinguiririca Fauna (Tinguirirican SALMA), near Termas del Flaco. *Ignigena minisculus* also derives from the Abanico Formation in the Río Tinguiririca valley (Tapado Fauna, ~ 14 km W of Termas del Flaco) but from older parts of the stratigraphic section, and is estimated to pertain to the Casamayoran SALMA.
- We also refer SGOPV 3451, a maxillary fragment from the Río Cachapoal drainage ~ 100 km N of the fossiliferous strata in the Tinguiririca River valley, to *Johnbell hatcheri*. This is first time an Andean fossil mammal from from outside of the type area of the Tinguiririca Fauna (upper Río Tinguiririca valley) has been referred to as a member of

that fauna at the species level. The occurrence of *Johnbell hatcheri* at the Río Cachapoal Locality suggests a tentative Tinguirirican (Flynn et al., 2003) age for the Cachapoal Fauna and at least part of these deposits.

- We refer a specimen recovered from western exposures of the Abanico Formation along the Río Azufre (Azufre Fauna), immediately north of the Río Tinguiririca drainage and west of Volcán Tinguiririca, to the basal interatheriid *Antepithecus brachystephanus* (SGOPV 3604). *Antepithecus brachystephanus* has previously been reported only from Patagonian deposits of the “late” Barrancan subage of the Casamayoran SALMA.

- We provide the first phylogenetic definition of the name Interatheriidae, applying an apomorphy-based definition (“the notoungulate clade stemming from the ancestor displaying a splint-like jugal on the zygomatic arch, wherein this element is ‘sandwiched’ between the maxilla and squamosal and excluded from the orbit”) to best preserve historical conceptions of this major notoungulate clade. Basal interatheriids form a highly pectinate paraphyletic assemblage relative to interatheriines; hence, we eschew the name “Notopithecinae” in favor of the informal phrase “basal interatheriids”, which has the advantage of lacking phylogenetic connotations of monophyly. Both of the new taxa, *Johnbell hatcheri* and *Ignigena minisculus*, are shown to be closely related to (but are not members of) the Interatheriinae (as defined by Hitz et al., 2000), but they themselves do not appear to constitute a monophyletic group. Discovery of these two new taxa significantly increases the known diversity of basal interatheriids, and their incorporation into phylogenetic analyses enhances understanding of character transformations within this important herbivorous “ungulate” clade.

- Both new taxa are smaller than all previously known interatheres except *Punapithecus*. *Johnbell hatcheri*, *Ignigena minisculus*, and *Punapithecus* occur only in localities well north of the Patagonian deposits that have yielded all other basal interatheriids known. This pattern may reflect minor geographic provincialism or clinal variation, with smaller-bodied basal interatheriids inhabiting

more northerly latitudes than their larger-bodied relatives, until the Tinguirirican. Following the Tinguirirican, all interatheres taxa are larger-bodied.

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APPENDIX 1

DESCRIPTION OF CHARACTERS IN PHYLOGENETIC ANALYSIS AND DATA MATRIX

1. **I1 size:** larger than other anterior teeth (0); greatly enlarged (1)
2. **I2-C shape:** I2 laterally compressed, I3-C ovoid/conical (0); all laterally compressed (1)
3. **C size:** large (0); reduced (1)
4. **I2-3 size:** subequal (0); reduced, with I3 smaller than I2 (1)
5. **I2-C exterior face:** convex or vague anterior swelling (0); distinct vertical anteroexternal ridge (1)
6. **P1 vertical anteroexternal ridge:** no ridge (0); ridge present (1)
7. **P2-4 parastyle/paracone inflection:** shallow (0); deep (1)
8. **P3-4 fossettes and internal sulcus:** anterior, posterior, and lingual fossette moderately to strongly persistent (0); lingual remains open as a sulcus, others disappear rapidly with wear (1)
9. **P2-4 metacone ectoloph:** moderate to strong metacone ectoloph column (0); metacone ectoloph very low or almost flat (1)
10. **P3-4 dimensions:** $W > L$ or with mild anteroexternal expansion (0); $L > W$, rectangular shape (1)
11. **P2-4 cingulum:** anterior cingulum low on crown, posterior about midway up crown (0); anterior cingulum absent, posterior high on crown, merging early in wear (1)
12. **M1-3 paracone/parastyle inflection:** distinct but shallow (0); absent or reduced (1)
13. **M1-2 lingual sulcus and fossettes:** anteroexternal, posteroexternal and lingual fossettes present (0); moderately persistent lingual sulcus, other fossettes of varying longevity (1); completely persistent lingual sulcus, fossettes absent or very rapidly disappear with wear (2)
14. **M3 hypocone:** absent or diminutive (0); developed (1)
15. **M1-3 metacone ectoloph:** distinct (0); very low or flat (1)
16. **M1-3 anterior cingulum:** present and low on crown (0); absent (1)
17. **M1-3 dimensions:** $W > L$ or about equidimensional (0); $L > W$, rectangular shape (1)
18. **Crown height in posterior Ps and Ms:** brachydont (0); hypsodont (1); hypseledont (2)
19. **i3 size:** $i3 > i2$ (0); reduced (1)
20. **i1-3 shape:** two shallow lingual grooves (0); i1-2 bifid labial and lingually (1)
21. **c size:** larger than i1-3 (0); subequal to i1-3 (1); smaller than i1-2 or missing (2)
22. **c-p1 diastema:** absent (0); present (1)
23. **p2-4 talonid development and relative size:** p2 no talonid, p3 very small, p4 present but smaller than trigonid (0); p2-3 distinct talonids but small, p4 smaller or subequal to trigonid (1); p2-4 display reduced talonids (2); p2 subequal to larger, p3-4 larger talonids (3)
24. **p3-4 crown morphology:** narrow labial sulcus, more posteriorly oriented lingual sulcus (0); two lobes, well defined labial and lingual sulci opposite one another (1)
25. **Relative size of m1-3 trigonid and talonid:** m1 talonid subequal to or slightly smaller than trigonid, m2 talonid subequal to or slightly larger to trigonid, m3 talonid larger than trigonid (0); all talonids larger than trigonids (1)
26. **m1-3 crown morphology:** not bilobed, lingual sulcus broad and extends posteriorly (0); bilobed, persistent labial and lingual sulci directly opposite one another (1)
27. **p3-4 molarization:** p4 approaching molariform, p3 considerably smaller than the molars (0); p4 molariform, p3 enlarged but smaller than molars (1)
28. **m1-3 trigonid shape:** anterior margin broad (0); anterior margin short, producing a triangular appearing lobe (1)
29. **m3 third lobe:** small (0); larger with a distinct labial groove (1)

