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New Notoungulates (Notostylopidae and Basal Toxodontians) from the Early Oligocene Tinguiririca Fauna of the Andean Main Range, Central Chile

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ABSTRACT

Here we describe two new notoungulate taxa from early Oligocene deposits of the Abanico Formation in the eastern Tinguiririca valley of the Andes of central Chile, including a notostylopid (gen. et sp. nov.) and three basal toxodontians, cf. Homalodotheriidae, one of which is formally named a new species. The valley's eponymous fossil mammal fauna became the basis for recognizing a new South American Land Mammal "Age" intervening between the Mustersan and Deseadan of the classical SALMA sequence, the Tinguirirican. As a temporal intermediate between the bracketing SALMAs (Deseadan and Mustersan), the Tinguirirican is characterized by a unique cooccurrence of taxa otherwise known either from demonstrably younger or more ancient deposits, as well as some taxa with temporal ranges restricted to this SALMA. In this regard, two of the notoungulates described here make their last known stratigraphic appearances in the Tinguiririca Fauna, *Chilestylops davidsoni* (gen. et sp. nov.), the youngest notostylopid known, and *Periphragnis vicentei* (sp. nov.), an early diverging toxodontian, the youngest representative of the genus. A second species of *Periphragnis* from the Tinguiririca valley is provisionally described as *Periphragnis,* sp. nov., but is not formally named due to its currently poor representation. A specimen referred to *Trigonolophodon* sp. cf. *T. elegans* also is described. This taxon is noteworthy for also being reported from Santiago Roth's long perplexing fauna from Cañadón Blanco, now considered Tinguirirican in age. A phylogenetic analysis of notostylopids identifies *Chilestylops* as closely related to *Boreastylops lumbrerensis* from northern Argentina.

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INTRODUCTION

Prior to its connection with North America via the Panamanian land bridge approximately 2.8 million years ago (Woodburne, 2010), South America was an island continent during its Cenozoic and latest Cretaceous history. Apart from limited North American faunal exchange in the Late Cretaceous and possibly the earliest Cenozoic (Pascual, 2006), some connectivity to Antarctica until the mid-Paleogene, and the Eocene-Oligocene arrival of rodents and primates via sweepstakes dispersal from Africa, little terrestrial mammalian exchange occurred between South America and other continents during this period of isolation, resulting in the evolution of a highly unusual and endemic mammalian fauna (Simpson, 1940, 1948, 1967, 1980; Patterson and Pascual, 1968; Vucetich, 1980; Houle, 1998). Approximately 20 South American Land Mammal "Ages" (SALMAs) are currently recognized, the most recently proposed of which, the Tinguirirican (Flynn et al., 2003), occurs near the Eocene-Oligocene transition (~31.5 Ma) (Wyss et al., 1994).

The Tinguirirican SALMA, best known from deposits near the town of Termas del Flaco in the Tinguiririca River valley of the Andean Main Range in east-central Chile, documents an important interval of South American mammalian history. Tinguirirican mammals are also known from the enigmatic Cañadón Blanco locality in Chubut, Argentina (Roth 1901, 1903; Wyss et al., 1994; Bond et al., 1996), the Gran Barranca (Madden et al., 2010), the Cachapoal River valley of central Chile (Flynn and Wyss, 2004; Hitz et al., 2006), and from an unpublished site in the Chilean Andes at roughly the latitude of Santiago (Croft et al., 2008a). The stratotype sequence for the Tinguirirican SALMA (near Termas del Flaco) has produced a rich fauna (Flynn et al., 2003), including sparse remains of marsupials: *Klohnia charrieri* (a groeberiid sensu Flynn and Wyss, 1999, or an argyrolagoid of uncertain affinities sensu Goin et al., 2010), *Kramadolops (= Polydolops) abanicoi* (Flynn and Wyss, 1999; Goin et al., 2010), and a form of disputed higher-level affinities, *Hondonadia* (= *Pascualdelphys*) *fierroensis* (Flynn and Wyss, 1999; Goin et al., 2010). Eutherians include an indaleciine (?litoptern); *Pseudoglyptodon chilensis*, a close sloth ally (McKenna et al., 2006); and multiple dasypodids (Carlini et al., 2009). Notoungulates (a diverse, long-ranging group of extinct herbivores; Roth, 1903), however, dominate the fauna from Termas del Flaco, both in terms of species diversity and abundance. Perhaps the most peculiar aspect of this notoungulate fauna is the plenitude and unprecedented diversity of archaeohyracids (Croft et al., 2003; Reguero et al., 2003), a group generally poorly represented elsewhere, except at Salla, Bolivia (Billet et al., 2009). Although archaic in some respects, most Tinguirirican archaeohyracids are remarkably high crowned, although a few low-crowned taxa are also represented (Croft et al., 2008a). Interatheriids (Hitz et al., 2000, 2006) and notohippids also are quite common. The objectives of this report are to describe and name two previously incompletely studied components of the notoungulate fauna from the Tinguiririca, its notostylopid and homoladotheriid toxodontians.

To avoid possible confusion, we note that although the Tinguiririca Fauna was the first fossil mammal assemblage discovered in the Tinguiririca valley (see below), other faunas are currently known from the immediate vicinity. Several sets of localities producing various mammalian faunas have been identified along reaches of the Tinguiririca River between ~10–30 km west of Termas del Flaco (Flynn et al., 2005), as well as along some of its major tributaries (from east to west), the

Río Azufre, Estero Los Helados, and the Río Claro. These other locations have not produced mammals of Tinguiririca age, however, leading to the inconvenient truth that not all fossil mammals from the Tinguiririca valley and surrounding region pertain to the Tinguirirican SALMA.

ABBREVIATIONS

AMNH	American Museum of Natural History
MACN	Museo Argentino de Ciencias Naturales
MLP	Museo de La Plata
SALMA	South American Land Mammal "Age"
SGOPV	Museo Nacional de Historia Natural, Santiago, vertebrate paleontology collections

Dental abbreviations: I/i (upper/lower incisors), C/c (upper/lower canine), P/p (upper/lower premolar), M/m (upper/lower molar)

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Eutheria Huxley, 1880

Notoungulata Roth, 1903

Notostylopidae Ameghino, 1897

We define Notostylopidae phylogenetically as all notoungulates more closely related to *Notostylops* than to any other notoungulate family recognized by Simpson (1967).

DIAGNOSIS: Simpson (1948: 170) diagnosed (in a procedure Simpson referred to as "Definition," a term that has a significantly different meaning in current usage) Notostylopidae as follows: Dental formula I/i: 3-2, C/c: 1-0, P/p: 4-3, M/m: 3. "I3/i3, C1/c1, and P1/p1 styliform and reduced, often absent, tending to leave a diastema anterior to the cheek dentition. I1/i2 enlarged but rooted. Cheek teeth brachyodont. Upper premolars triangular to subquadrate, P4 often, and P3 occasionally, with a vertical interval sulcus on the inner lobe, M1–M2 quadrate, wider than long, with hypocone and larger protocone, united nearly to their apices but readily distinguishable and separated on inner face by one or more sharp vertical sulci. Protoloph simple, not completely confluent with ectoloph. Metaloph more confluent with ectoloph, giving off a long crochet (denticulate when unworn), which runs straight forward and ends freely near the protoloph. No cristae."

AMENDATION TO DIAGNOSIS: We note that the denticulation of the long crochet in notostylopids noted in Simpson's (1948) diagnosis does not appear to characterize the clade ancestrally. A denticulate region between the crochet and ectoloph is well developed in the upper molars of *Otronia* (e.g., MLP 66-V-3-3), although the specimens of this taxon that we have examined are too worn to establish whether the denticles arise from the lateral face of the crochet or the medial face of the ectoloph (being embedded within the broad wear surface between these features). Of the notostylopid taxa available to Simpson, however, our comparisons indicate that this denticulate region occurs exclusively in *Otronia.* A similar condition was subsequently identified in *Boreastylops* (Vucetich, 1980), and also occurs in the new notostylopid taxon described below. The specimen upon which this new taxon is based, SGOPV 2906, is sufficiently little worn that the bases of the denticles can be clearly seen to originate from the medial wall of the ectoloph, rather than the crochet. Consequently, although this denticulate region is potentially diagnostic of Notostylopidae (with a reversal in those forms in which it is absent), based on the phylogenetic results presented below, the distribution of this feature is more parsimoniously interpreted as reflecting an origin in the ancestor of a less inclusive grouping. We also note that the notostylopid protoloph, at least as judged from the unworn dentition of SGOPV 2906, is not demonstrably less complete than in notoungulates generally.

***Chilestylops davidsoni*, gen. et sp. nov.**

Figure 1; table 1

Holotype: SGOPV 2906, partial palate preserving little worn left P3–M1, partial M2, and lingual portions of right P2–M1.

Referred Specimens: Known only from the holotype.

Etymology: After the country of origin of the holotype, and in honor of John Davidson for his important geological mapping and stratigraphic analysis of the Chilean/Argentine border region at the latitude of the Tinguiririca valley and neighboring regions (Davidson and Vicente, 1973).

Type Locality: Upper reaches of the Tinguiririca River valley, Termas del Flaco (34° 57′ S, 70° 27′ W), east central Chile (Wyss et al., 1993); "Locality A" of figures 6–8 in Charrier et al., 1996, which is equivalent to Locality Set 1 of Flynn et al., 2003. This series of localities occurs within an ~85 m thick stratigraphic interval that is well exposed along nearly 1 km of strike immediately north and south of El Fierro Pass, the crest of which lies approximately 3 km SSE of Termas del Flaco—and roughly an equal distance south of the Tinguiririca River. Localities south of the river are far more productive than those occurring 1 to 2 km NNE of Termas del Flaco, the latter of which produced two recently described caviomorph rodents (Bertrand et al., 2012).

Stratigraphic Occurrence: Poorly bedded, purplish volcaniclastic sediments occurring near the local base of the Abanico (= Coya-Machalí) Formation, a few hundred meters west of the stratigraphic contact with underlying Mesozoic units. These volcaniclastic deposits, along with several hundred meters of overlying sedimentary and igneous deposits stretching some 4 km to the west, were long attributed the Mesozoic Colimapu Formation (e.g., Klohn, 1960, and many subsequent studies) until the initial finds of Cenozoic mammals in the region (Novacek et al., 1989). These fossils, as well as the results of isotopic dating and stratigraphic studies prompted by their discovery, have made it nearly inarguable that the mammal-bearing deposits in the Termas del Flaco region pertain to the Abanico Formation, and that the Colimapu Formation does not occur at these latitudes (Charrier et al., 1996). Recent detailed geologic mapping of the Termas del Flaco region has resulted in recognition of five members within the Abanico Formation (Mosolf, 2013). Fossils reported here derive exclusively from the La Gloria member, as do all fossils of Tinguirirican age recovered from the Tinguiririca valley. (Older fossil mammals occur fairly abundantly in some of the lower members of the Abanico Formation in more western portions of the Tinguiririca drainage.)

Age: ?Late Eocene–early Oligocene, Tinguirirican SALMA. Whole-rock ^{40}K-^{40}Ar dates ranging in mean age from 31.4 to 35.6 Ma have been obtained from the same sequence that produced the fossils reported here, namely those south of the Tinguiririca River (Wyss et al., 1990; Flynn et al., 2003). The older of these dates are from horizons several tens of meters below the fossiliferous unit. Two high-precision ^{40}Ar/^{39}Ar dates from directly within the fossiliferous sequence yielded mean ages near 31.5 Ma (Flynn et al., 2003). Mosolf (2013) reports additional radiometric dates from this sequence.

Diagnosis of Chilestylops: Sharply defined parastyle and paracone columns, and deep, well-developed anterior cingulae (these cingulae are uniquely pronounced in *Chilestylops* compared with other notostyopids); anterior cingulum on P3 (unique to *Chilestylops*) distinctive crenulated/papillate enamel in the basal cingular region of the upper cheek teeth (also seen in P4 of *Otronia*, though less developed); papillae on the lingual face of the ectoloph (as in *Boreastylops* and *Otronia);* quadrate premolars (as in *Boreastylops*).

DESCRIPTION AND COMPARISON

The sole known specimen of *Chilestylops,* SGOPV 2906, consists of a partial palate preserving fragmentary but little-worn portions of both tooth rows. The left tooth row, P3–M2, measures ~4.3 cm in length; M2 is damaged posteriorly, making this length approximate. The palate measures 1.7 cm between the lingual faces of the P3s, and 2.4 cm between the M1s, reflecting the mild posterior divergence of the upper cheek tooth rows. Additional mensural information is provided in table 1.

Second Upper Premolar: Only a triangular posterolingual portion of P2 is preserved on the right side, and an inconsequential posterior sliver on the left. Nevertheless, these pieces indicate that P2 is decidedly smaller than P3, and that a well-developed basal cingulum borders the tooth posteriorly. This structure wraps onto the lingual face and climbs to meet the protocone near the midpoint of this face. Despite the tooth's fragmentary nature, a rugose region may be discerned at the lingual base of the protocone.

Although *Boreastylops* possesses a well-developed anterior cingulum on P2, this structure is weaker than in *Chilestylops* and fails to wrap onto the lingual portion of the tooth as in *Chilestylops*. The degree to which the P2 cingulum is developed in *Chilestylops* does not occur in other notostylopids.

Third Upper Premolar: P3 is slightly smaller than P4, particularly anteroposteriorly, and is subquadrate in outline, being slightly longer than wide. The labial wall of the tooth is high (measuring ~8 mm along the metacone column), compared to its lingual face (protocone height, ~5 mm). A salient ectoloph is the tooth's most prominent feature. Its labial face displays a remarkable degree of relief, particularly the apically tapering paracone column, which is set off from the remainder of the labial surface posteriorly by a shallow vertical cleft. Although broken apically, a small parastyle projects anteriorly. The anterior crest cuts diagonally anterolabially; basal to it, the anterior cingulum meets the steep lingual slope of the ectoloph near

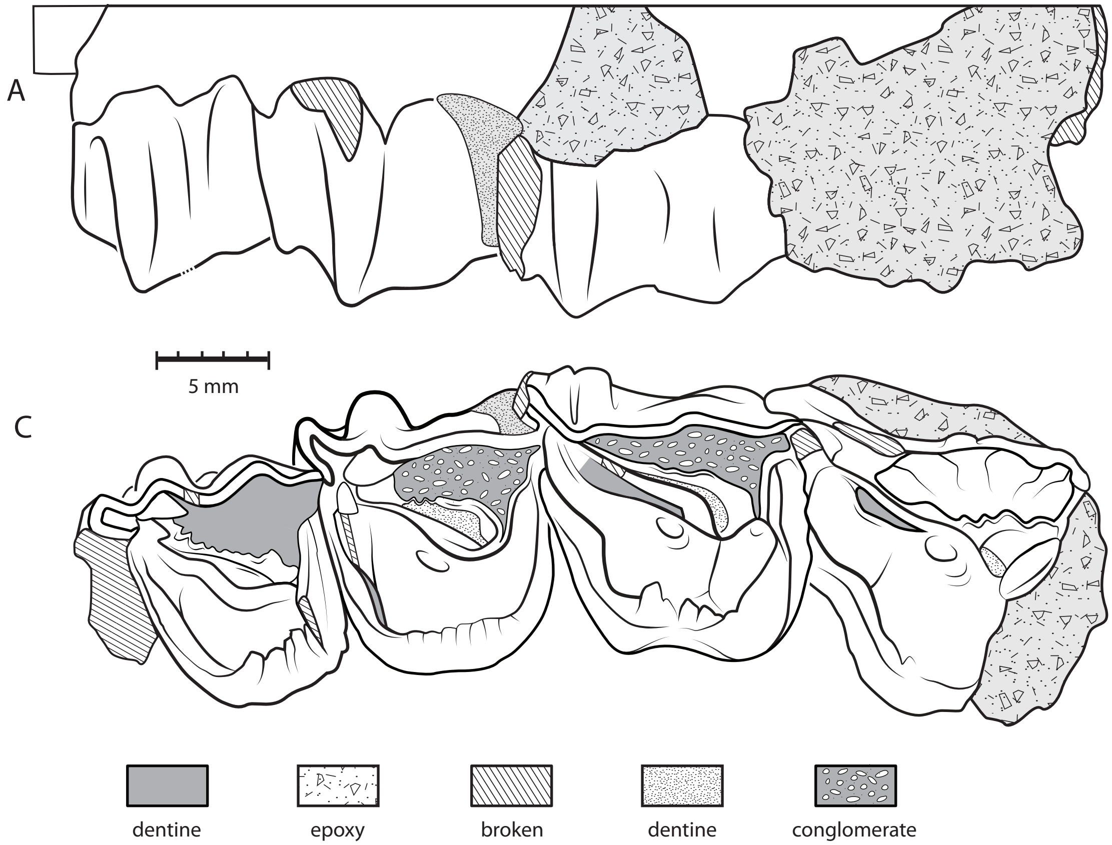
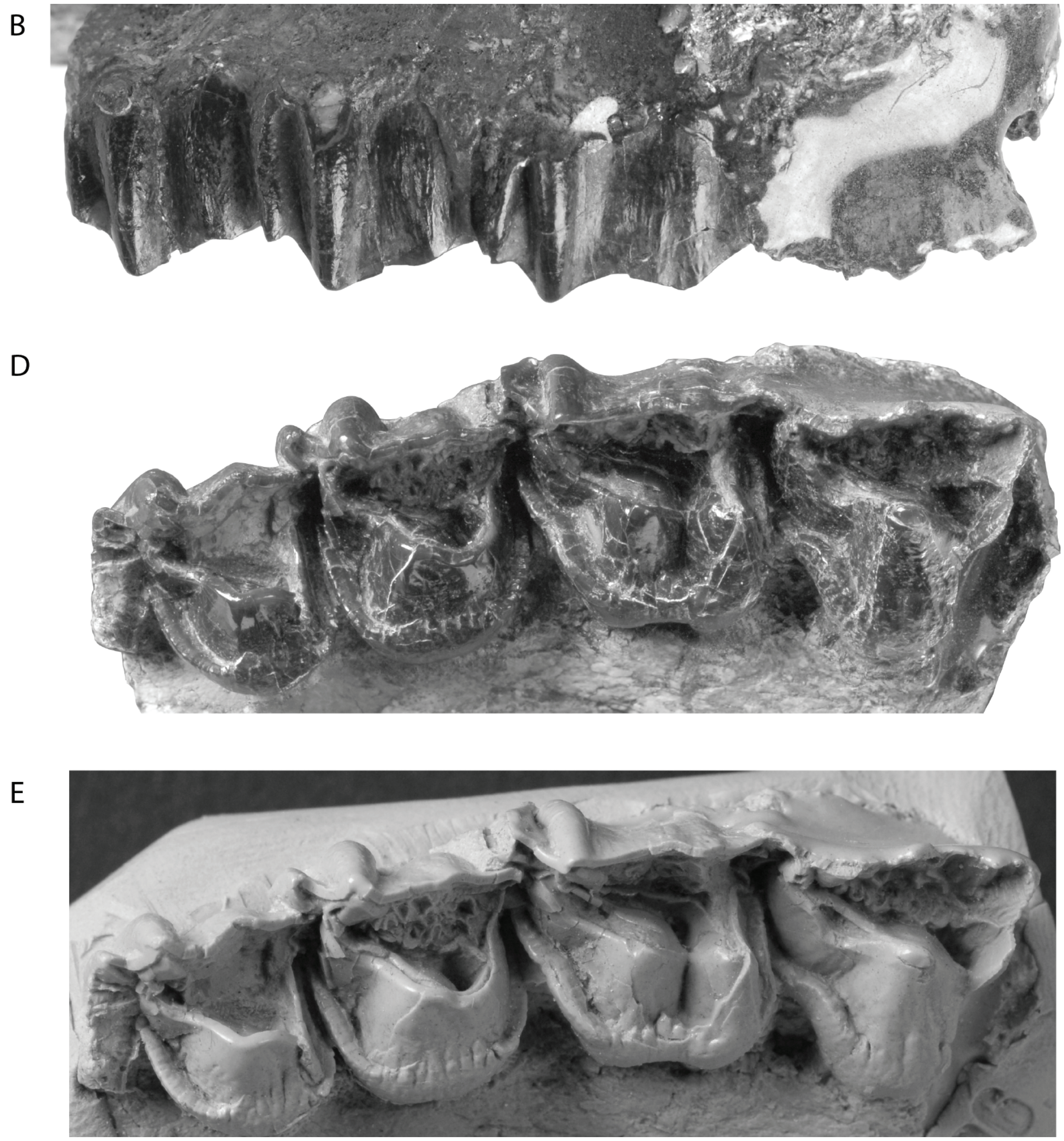


FIGURE 1. Holotype of *Chilestylops davidsoni* (SGOPV 2906) showing left P3–anterior portion of M2 (**A**) line drawing (*above*) of the buccal view, (**B**) photograph (*opposite page*) of the buccal view of the actual specimen, (**C**) line drawing (*above*) of the occlusal view, (**D**) photograph (*opposite page*) of the occlusal view of the actual specimen, (**E**) photograph of the occlusal view from a cast of the actual specimen. Anterior is to the left. Only the better-preserved left side of the specimen is shown.

the juncture of the paracone and parastyle, but far above the apex of the former. The posterior crest, forming the posterior border of the tooth, is more transverse than the anterior crest and ends lingually at the base of the internal face of the posterior end of the ectoloph. As on the succeeding teeth, considerable wear would have been required before the anterior and posterior crests merged with the functional edge of the ectoloph. The posterior half of the tooth's labial face is bowed outward, forming what could be described as a broad metacone column. The metacone column is far more subdued than the paracone column, but is nonetheless stronger than its counterparts on P4 and M1 (the only other teeth in which this region is preserved). A strong anterior cingulum begins at the base of the parastyle and curves to meet the base of the protocone lingually. The enamel at the base of the posterolingual slope of the protocone is crenulated and slightly papillate, forming four to five vertical sulci that increase in prominence posteriorly. The anterior cingulum terminates lingually at the anterior edge of this furrowed region of enamel. Similarly, a lengthy posterior cingulum, originating near the posterolabial corner of the tooth, ends at the posterior end of this roughened region of the protocone base. This cingulum is roughly half as wide anterioposteriorly as its anterior counterpart, and is not



“lipped” like the anterior one. Two sharp, unworn crests project from the protocone, one labially and the other posteriorly, forming a 90° angle with the protocone at the apex.

The P3 of *Chilestylops* is slightly wider (labiolingually) than long (anteroposteriorly), as in *Boreastylops, Notostylops, Otronia,* and *Homalostylops.* The labial face of this tooth is deeply sculpted in *Chilestylops,* including a labially projecting paracone/paracone column, a pronounced cleft posterior to the paracone column, and a less pronounced cleft between the parastyle and paracone column, resulting in a strongly undulatory labial face. This surface is also undulatory in *Boreastylops* and *Homalostylops* (the metacone column is particularly pronounced in the former), but not to the degree seen in *Chilestylops*. Relief of the labial tooth face is much more subdued in *Otronia* and *Notostylops* than in these other taxa.

TABLE 1. Mensural Data. Mensural data for specimens described in the text: *Chilestylops davidsoni* (SGOPV2906, taken from left side of specimen), *Periphragnis vicentei* (SGOPV 3107, taken from left side except P2), and *Periphragnis* unnamed species (SGOPV 2798, 2911, 2797).

Specimen	P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
Chilestylops davidsoni (SGOPV2906)	n/a	n/a	9.0	11.2	11.1	11.8	12.6	13.1	13.8	~13	n/a	n/a
Periphragnis vicentei (SGOPV 3107)	~27	~27	27.0	27.0	27.0	32.0	30.0	40.0	31.0	37.0	n/a	n/a
Periphragnis unnamed speices (SGOPV 2798)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	30.0	27.0
Periphragnis unnamed species (SGOPV 2911)	n/a	n/a	n/a	n/a	n/a	n/a	25.5	?	28.7	?	?	?
Periphragnis unnamed species (SGOPV 2797)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	~27	~34	~31	~29

In *Chilestylops* enamel at the lingual base of the protocone is marked by a series of vertical furrows that increase in prominence posteriorly. This crenulated region of enamel also occurs in *Otronia*, but only posteriorly. Moreover, the vertical sulci are similar to one another in height in *Otronia* and shorter than those of *Chilestylops*. Enamel is smooth on the lingual face of P3 in *Homalostylops, Boreastylops,* and *Notostylops*. The strong anterior cingulum of P3 in *Chilestylops* is unique among notostylopids, whereas the posterior cingulum of this tooth resembles that of *Otronia*.

FOURTH UPPER PREMOLAR: P4 is intermediate in size between P3 and M1 and is essentially a slightly enlarged version of the P3 in form. The parastyle appears to have been slightly more salient in P4 than in P3 (but only the base of this structure is preserved on the latter). As in all succeeding teeth, the P4 parastyle imbricates the metastyle of the tooth anterior to it. The paracone is slightly larger proportionally than in P3. The metacone in P4 is less pronounced than in P3. The metaloph extends a short distance posteriorly before hooking labially to pass transversely to the metastyle. The tooth bears strong anterior and posterior cingulae of roughly the same form and proportions as in P3, the main distinction being that the former is more deeply excavated in P4. As in P3, the cingulae merge lingually into a crenulated region of enamel at the protocone base. Two crests extend from the conical protocone; the protoloph extends obliquely from the protocone, intersecting the well-developed parastyle fold. A series of papillae occur on the lingual face of the ectoloph.

In *Boreastylops* and *Chilestylops,* the anterior cingulum of P4 is stronger than the posterior one; in *Homalostylops* and *Otronia* the opposite is true, whereas in *Notostylops* these cingulae are equally developed. The paracone and parastyle columns of *Chilestylops* are more pronounced than in other notostylopids. These structures are more weakly developed in *Boreastylops* and *Homalostylops*, and are weaker still in *Otronia* and *Notostylops.* A similar degree of parastyle imbrication is seen in *Boreastylops* and a lesser degree occurs in *Homalostylops,* whereas overlap of adjoining teeth is minimal or nonexistent in *Otronia* and *Notostylops.*

First Upper Molar: The quadrate M1 is intermediate in size between P4 and M2. The parastyle, positioned nearer the base of the crown than the paracone, overlaps the metastyle of P4. The metacone column is far less pronounced than the paracone and parastyle folds, and also is more muted than in P3–4. The metaloph follows a transverse course between the base of the metacone and the apex of the hypocone. The metaloph is also worn, but to a lesser degree than the protoloph. A cingulum is present posterior to the metaloph; it spans the entire width of the tooth and is only slightly less salient than its anterior counterpart. A well-developed cingulum traverses the anterior base of the tooth, extending from the base of the parastyle column to the lingual base of the protocone. The ectoloph, by far the most prominent feature of the tooth, projects apically far beyond the protocone and hypocone, which are roughly equal in height. The crest of the protoloph, which runs between the apex of the parastyle and the center of the protocone, is moderately worn, resulting in a raised rim of enamel surrounding a swath of dentine. As on P4, a region of crenulated enamel spans the lingual ends of the anterior and posterior cingulae, crossing the base of the protocone and hypocone. As on all the other teeth preserved in this specimen, a series of papillae adorns the lingual face of the ectoloph.

The strong anterior cingulum of M1 in *Chilestylops* is lacking in *Boreastylops, Notostylops,* and *Homalostylops* (M1 is unknown in *Otronia*). The anterior cingulum of M1 is better developed than its posterior counterpart in both *Boreastylops* and *Chilestylops*; in *Homalostylops,* however, the posterior cingulum is stronger than the anterior, while in *Notostylops* they are roughly equal. The crenulate enamel that spans the bases of the protocone and hypocone in *Chilestylops* does not occur in *Boreastylops, Homalostylops,* or *Notostylops*. The papillae on the lingual face of the ectoloph in *Chilestylops* (and *Boreastylops*) are absent in *Homalostylops* and *Notostylops*. The metaloph in *Chilestylops* is straight and intersects the ectoloph perpendicularly, as in *Boreastylops* and *Notostylops*. The metaloph of *Homalostylops* is more obliquely oriented. The metacone column of *Chilestylops* is far more weakly developed than the paracone and parastyle. The metacone column in *Notostylops* is also weak, whereas in *Boreastylops* and *Homalostylops* it is moderately pronounced.

Second Upper Molar: Aside from the posterolingual corner and the lingual face of the ectoloph, much of the left M2 is preserved. Judging from its strong similarity to M1, M2 very likely was quadrate in occlusal outline. Papillae span the preserved portion of the lingual face of the ectoloph. These cuspules (seen also on P4 and M1) recall the “crochet” of some notostylopids; rather than the more definitive “crochet” as in *Notostylops*, this feature more closely resembles that of *Boreastylops*. The hypocone and labial face of the ectoloph are not preserved. Anteriorly, a well-developed cingulum extends from the lingual face of the protocone to the base of the parastyle. The base of the protocone exhibits the same furrowed enamel seen on the preceding teeth. As on M1, the original enamel crest of the protoloph of M2 has been breached by wear.

Discussion: In summary, *Chilestylops* is most easily distinguished from other notostylopids by its: crenulate enamel or papillate cingulum crossing the lingual protocone base of the upper cheek teeth (at least P3–M1); its strongly pronounced paracone and parastyle columns; and its salient, deeply excavated upper premolar cingulae. *Chilestylops*, *Otronia*, and *Boreastylops* are unique among notostylopids in having a row of papillae on the lingual face of the ectoloph and in retaining better-developed cingulae than those seen in *Notostylops* and *Homalostylops*.

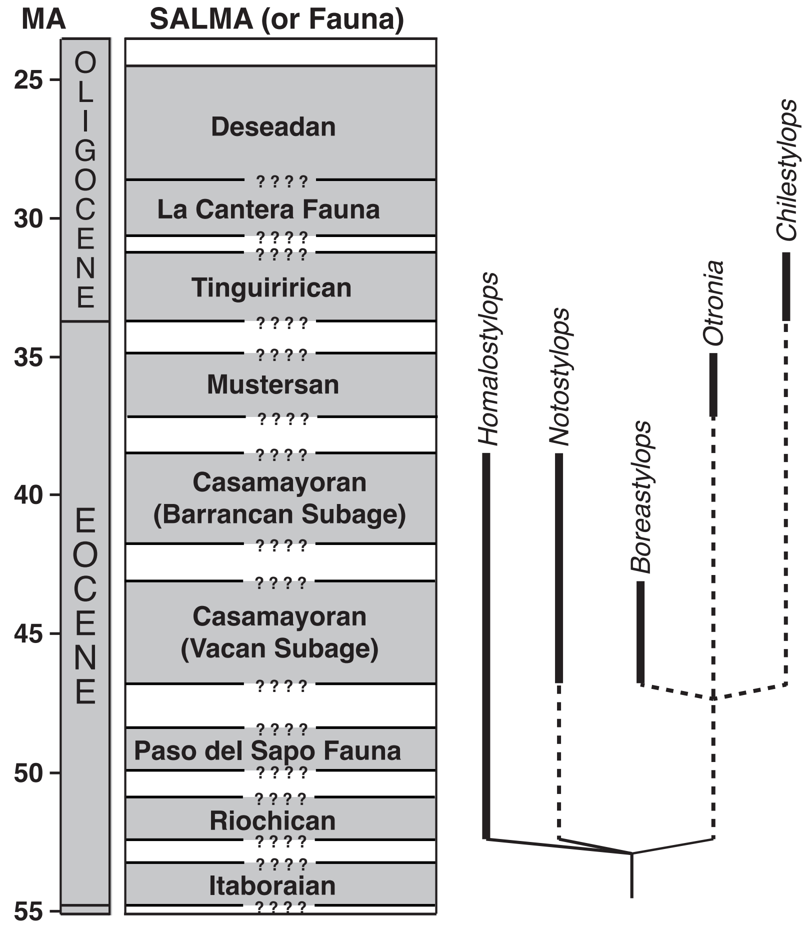


FIGURE 2. Strict consensus from three maximally parsimonious trees of notostylopid relationships, scaled to time and SALMA chronology. The minimally inclusive clade consisting of *Boreastylops*, *Chilestylops*, plus *Otronia* is diagnosed by the possession of a row of papillae on the lingual face of the ectoloph and well-developed cingula on the upper cheek teeth. SALMA sequence is based on Flynn and Swisher (1995), Gelfo et al. (2009), Tejedor et al. (2009), and Ré et al. (2010). Notostylopid occurrence data are from Vucetich (1980), Cifelli (1985), Tejedor et al. (2009), Bond and Deschamps (2010), and Powell et al. (2011). The character matrix for this phylogeny is given in the appendix.

Phylogenetic Placement of Chilestylops: The relationships of *Chilestylops, Boreastylops, Otronia, Notostylops,* and *Homalostylops* were elucidated through a parsimony analysis using PAUP (Swofford, 1991). The data matrix consisted of six characters scored across six taxa (see appendix). A branch and bound search was conducted using default settings, with *Oldfieldthomasia* specified as the outgroup. *Edvardotrouessartia* (Ameghino, 1901), known only from lower teeth, was excluded from the analysis. Three maximally parsimonious trees (eight steps in length) were identified, the strict consensus of which groups *Chilestylops, Boreastylops,* and *Otronia* in a tritomy with *Homalostylops* and *Notostylops* as unresolved outgroups to the other three taxa (fig. 2). These trees have a consistency index of 0.875, and retention index of 0.800. The bootstrap 50% majority-rule consensus tree pairs *Chilestylops* and *Boreastylops* with a 48% bootstrap support value.

Chilestylops is one of a small minority of herbivore taxa from the Tinguiririca Fauna lacking hypsodont cheek teeth. The most common herbivores in the Tinguiririca Fauna, particularly interatheriines and archaeohyracids (Croft et al., 2008b), exhibit high degrees of hypsodonty, as does one of the fauna's rodents, a chinchillid (Bertrand et al., 2012). The shift to hypsodont-dominated mammalian faunas in South America near the Eocene-Oligocene transition has been ascribed to a shift in vegetational changes associated with global climate change (e.g., Dunn et al., 2013) and, less plausibly, to an increase in volcanic grit dusting vegetation (Stromberg et al., 2013). Notostylopids are one of few notoungulate lineages that did not participate in the massively convergent acquisition of hypsodont dentitions at this time.

Toxodonta Scott, 1904
cf. Homalodotheriidae Gregory, 1910
Periphragnis Roth, 1899

Type Species*:* *Periphragnis harmeri* Roth, 1899.

Diagnosis: "Closely similar to *Thomashuxleya*, but teeth with slightly higher crowns (although still brachydont); parastyle and paracone folds of upper molars less prominent and less sharply separate; parastyle folds of upper cheek teeth strongly interlocking with preceding teeth lingual [lapsus for labial] of metastyle; p2 more complex, with well-developed posterolingual sulcus; lower premolars generally shorter and relatively broader; incisor series less anteroposterior, more transverse" (Simpson, 1967: 162).

Age: Mustersan (middle to late Eocene, fide Ré et al., 2010) of Patagonia, to Tinguirirican (late Eocene to early Oligocene) SALMAs.

Periphragnis vicentei, sp. nov.
Figure 3; table 1

Holotype: SGOPV 3107, partial palate bearing left P3–M2, partial lingual face of P2, right P2–M2, and central fossa of right M3.

Referred Specimens: Known only from the holotype.

Diagnosis: Ectoloph forms a slight prominence in the region of the metacone; well-defined parastyle and paracone columns more pronounced in the premolars than in the molars; anterior and posterior premolar cingulae forming deep gutters; molars with poorly developed anterior cingulum; central fossa V-shaped and lacking enamel islands between it and the ectoloph; row of papillae across base of the protocone in the premolars; cingulae distinctly more reduced on the molars than premolars.

Etymology: In honor of Jean-Claude Vicente and his contribution to the pioneering geological study of the Andean Main Range at the latitude of Termas del Flaco (Davidson and Vicente, 1973).

Type Locality: As for *Chilestylops*, i.e., "Locality A" of figures 6–8 in Charrier et al., 1996, which equals "Locality Set 1" of Flynn et al., 2003, except that SGOPV 3107 was collected (by Reynaldo Charrier) as a fragmented, displaced boulder, several hundred meters topographically below and north of the next most northern fossil locality south of the Tinguiririca River.

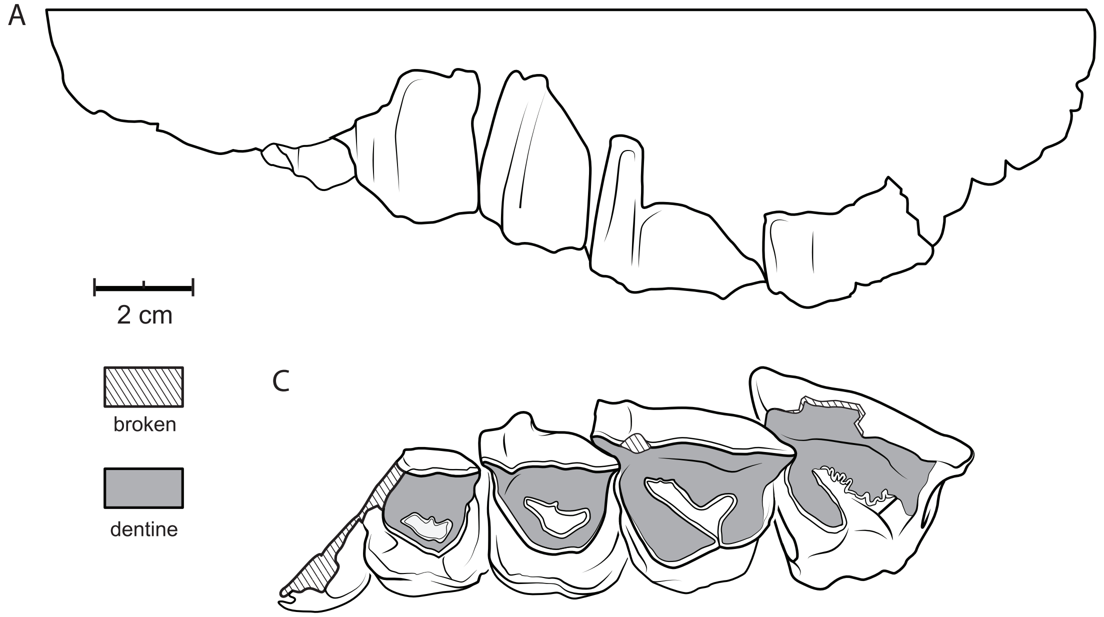
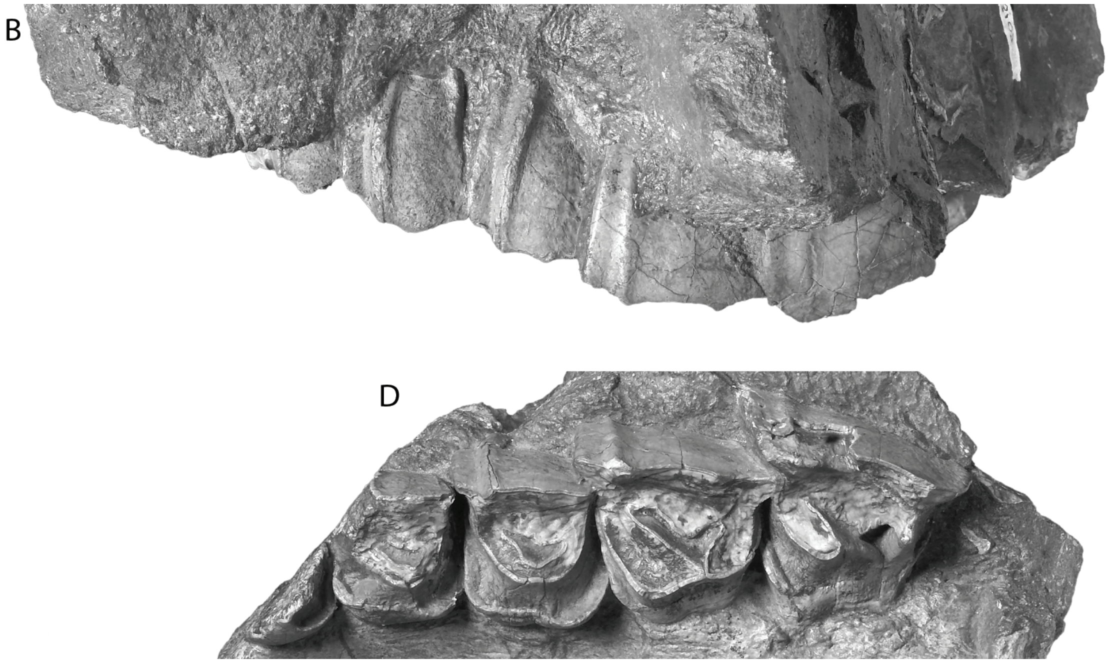


FIGURE 3. Holotype of *Periphragnis vicentei* (SGOPV 3107) showing left P3–M2 (**A**) line drawing (*above*) of the buccal view, (**B**) photograph (*opposite page*) of the buccal view of the actual specimen, (**C**) line drawing (*above*) of the occlusal view, (**D**) photograph (*opposite page*) of the occlusal view of the actual specimen, (**E**) photograph of the occlusal view from a cast of the actual specimen. Posterior is to the right. Only the left cheek teeth of the partial palate are shown as they are the better-preserved teeth in the dentition.

Stratigraphic Occurrence: As for *Chilestylops,* with the caveat that the holotype was collected from talus and may have travelled several hundred meters from its point of origin. Even so, the matrix adhering to the specimen is indistinguishable from that in which all specimens from the Tinguiririca Fauna have been recovered. No fossil mammals have been collected immediately south of Termas del Flaco that are anything other than Tinguiririican in age, which further supports referral of SGOPV 3107 to the Tinguiririca Fauna and SALMA.

Age: ?Late Eocene–early Oligocene, Tinguiririican SALMA; last known occurrence of the genus.

Description and Comparison*:* *Periphragnis vicentei* is represented by a single specimen (SGOPV 3107) consisting of a partial palate bearing left P3 through M2 and the partial lingual face of the P2. The right side preserves P2 through M2 and the central fossa of M3. The left tooth row (P3–M2) measures 12.3 cm in length, while the right side (P2–M2) measures 14.4 cm. On the right side of the specimen, a small, mesial-distal, left-lateral, strike-slip fault bisects the center of the tooth row, offsetting the labial halves of these teeth posteriorly approximately 5 mm relative to the lingual halves. More labially, these teeth are cut by one or more tensile fissures filled with a band of sediment matrix approaching 5 mm in width, and thus significantly distorting the transverse dimensions of the right P3–M2 in particular. The left dentition is not fissured or otherwise obviously deformed.



Second Upper Premolar: P2 is more completely preserved on the right side of the specimen than the left. It is irregularly quadrate in outline and considerably smaller than P3; damage in the parastyle region obscures the extent of this structure and that of the paracone column. The tooth exhibits no trace of a metacone column, but the metacone region forms the most ventrally projecting region of the ectoloph. Strong anterior and posterior cingulae meet on the lingual face of the tooth, sweeping gently ventrally toward the apex of the protocone. The lateral extent of the posterior cingulum is obscured by the encroachment of P3, but the anterior cingulum appears to span most of the width of the tooth. The anterior cingulum bears a few, minor rugosities as it curves toward, but does not meet, the protocone. The wear surface of P2 forms a roughly equilateral triangle in outline; the removal of a substantial amount (~1 cm) of crown height by wear would have been required before the cingulae merged with this surface, resulting in a more rectangular configuration.

Third Upper Premolar: This tooth is intermediate in size between P2 and P4 and bears a well-defined paracone column and parastyle (not preserved on the left side of the specimen). A fairly broad furrow separates these structures, the parastyle terminating considerably apical and medial to the paracone. A trapezoidal central fossa occupies the region between the proto- and metalophs. The posterior cingulum is wide, particularly as it rounds the posterolingual corner of the tooth. The anterior and posterior cingulae both rise lingually toward the protocone, meeting each other via a nearly horizontal row of low papillae midheight along the lingual face of the tooth. Although the anterior cingulum is well developed and forms a fairly deep gutter, it is narrower than its posterior counterpart.

Fourth Upper Premolar: The paracone and parastyle folds of P4 are the most prominent of the cheek tooth series, the latter overlapping the metastyle of P3 labially. Posterior to the paracone column, the labial face of the tooth is smoothly convex, exhibiting no trace of a metacone column. The metaloph originates from the posterior edge of the metastyle, extends transversely, curving anteriorly to merge with the protoloph, and defines the rounded lingual margin of the crescent-shaped central fossa. The anterior and posterior cingulae are prominent and deeply excavated. Both remain nearly horizontal, not rising as they approach the protocone as on P2–3. The cingulae contact one another lingually at the base of the protocone, but in this region they form a narrow row of papillae rather than a broad gutter. Approaching this papillate region, the gutter of the posterior cingulum is slightly wider and slightly more flared lingually than the anterior cingulum.

First Upper Molar: M1 is shaped very much like the capital Greek letter *pi* (Π), except that the "feet" (proto- and metaloph) converge to meet lingually. The parastyle and paracone columns are distinct, but slightly less pronounced than on the premolars. The parastyle strongly overlaps the metastyle of P4. As on the premolars, there is no trace of a metacone column on the lingual face of the molars. The roughly rectangular protoloph broadens slightly lingually and is canted posteriorly. The oblong, ovoid metaloph is more transversely oriented, meeting the posterior tip of the protoloph lingually to pinch off a V-shaped central fossa, the anterior arm of which is approximately twice the length of the posterior. In contrast to the premolars, the posterior cingulum is feebly developed, while the anterior cingulum is only slightly more pronounced. The anterior cingulum is narrow and shallow, and becomes shallower still as it extends from the anterolingual corner of the tooth toward the base of the parastyle. The lingual cingulum consists of a feeble shelf of roughened enamel running from the midpoint of the lingual face into the medial termination of the anterior cingulum.

Second Upper Molar: M2 is an exaggerated and slightly larger version of M1; the main differences include its more strongly posteriorly canted protoloph and shorter metaloph, as well as its slightly more projecting parastyle. The posterolingually projecting protoloph, short metaloph, and projecting parastyle, result in the ectoloph and lingual face of this tooth being more parallel (with the tooth's overall outline more trapezoidal) than in M1. The lingual tips of the proto- and metaloph are separated by 15 mm at the wear surface, via a large, enamel-roofed reentrant. Given the occlusal depth of this reentrant, the metaloph and protoloph would not have merged until very late in wear. Neither the poorly defined, short, posterior cingulum nor the very shallow, weak anterior cingulum extends to the lingual face of the tooth. Rather, the basal region of the lingual face of the tooth is an essentially featureless, slightly concave wall, the axis of concavity being vertical.

Third Upper Molar: M3 has obviously been displaced from life position. The tooth has been rotated posteriorly 90° along a mediolateral axis, such that its occlusal surface lies orthogonal to the occlusal surface of M2 and is exposed on the posterior face of the specimen. The original vertical axis of this tooth is now horizontal and runs anteroposteriorly, the tooth being lodged above the roots of M2 (extending perhaps to M1). The only visible portion of M3 is the posteriorly facing, triple junction–shaped central fossa. The remainder of the body of the tooth, including its outer rind of enamel, does not appear to be preserved.

TAXONOMIC ASSESSMENT OF *PERIPHRAGNIS VICENTEI*

Premolar Comparison: Four species of *Periphragnis* are currently recognized: *P. harmeri, P. palmeri, P. circunflexus* (represented only by lower teeth), and *P. exauctus*. Besides *P. vicentei,* upper premolars are known only for *P. harmeri* and *Periphragnis* sp. (MLP 69-III-24-286 and MLP 67-II-27-380, respectively). Anterior and posterior cingulae are absent on P2 of *P. vicentei*, but are present on P3–4, where they are continuous lingually via a narrow lingual rugose ridge of enamel. In MLP 67-II-27-380, on the other hand, anterior and posterior cingulae occur on P2, where they nearly meet lingually but are separated by a 2–3 mm gap, while the cingulae are smoothly (lacking the rugose connection) continuous on P3 and narrow slightly at the protocone base. The premolars bear only anterior cingulae in MLP 69-III-24-286. The premolar cingulae of *P. harmeri* generally resemble those of MLP 67-II-27-380, except that the cingulum of P2 in *P. harmeri* rises to a point extending halfway to the protocone, as in *P. vicentei*.

The central fossae of the premolars of *P. vicentei* are vaguely crescentic, with the long axis extending anteroposteriorly. Those of *P. harmeri* are slightly more ovoid, extending labiolingually, possibly becoming V-shaped in advanced wear. The shape of the premolar central fossae is generally similar in the two species, and the subtle differences just noted are likely attributable to wear, judging from their little worn condition in MLP 67-II-27-380 and more worn form in MLP 69-III-24-286 (preserved only in P3).

Molar Comparison: Upper molars of *P. vicentei* bear a small anterior cingulum and a diminutive posterior one, somewhat reminiscent of the condition in *P. exauctus* (AMNH 28651—on which all of our observations of this taxon's upper dentition are based) and *P. palmeri* (AMNH 14957), although the anterior cingulae of AMNH 28651 are wider and better developed than those of *P. vicentei*. (It merits note that AMNH 28651 and 14957 are not referred to in Simpson's monograph of 1967; hence the identifications listed above were made by him but omitted from his monograph or they were made by a subsequent worker.) The cingulae of *P. palmeri* connect seamlessly across the lingual portion of the teeth until confluently merging with the hypocone, whereas the molar cingulae of *P. vicentei* do not, and instead terminate upon reaching the protocone.

The molar central fossae exhibit a considerable range in form among species of *Periphragnis*. Those in *P. exauctus* (AMNH 28651) bear three short, closely spaced sulci extending from the central fossa toward the ectoloph (lacking in *P. vicentei*), thereby defining two short cristae. Two small, circular fossettes, occur lateral to the central fossa in *P. exauctus* but not in *P. vicentei*. Lastly, the central fossa is essentially linear in *P. exauctus* but is V-shaped in *P. vicentei* (the anterior arm of which has been lost to wear in M2). Some of these distinguishing features may reflect only differences in wear, but some likely represent true distinctions between these taxa. The central fossae in the fairly unworn molars of *P. palmeri* (AMNH 14957) are vaguely V-shaped, the V being formed by two joined circular openings, whereas the arms of the V-shaped central fossae in *P. vicentei* are more linear. With additional wear, the form of the central fossa seen in AMNH 14957 could have come to resemble that seen in *P. vicentei*.

The central fossa of *P. harmeri* is a simple elongate, oblong arm, rather than V-shaped. Although the known specimens of *P. vicentei* are more worn than most specimens referred to *P. harmeri*, the difference in the form of the central fossa in these two taxa cannot be ascribed to wear alone, as a worn specimen of *P. harmeri* (e.g. MACN 10295, in Simpson, 1967: pl. 36, fig. 2) does not resemble *P. vicentei* in this respect.

Molar paracone and parastyle columns are well developed in *P. vicentei, P. harmeri, P. exauctus*, and 67-II-27-380, but are more subdued in *P. palmeri. P. harmeri* lacks a distinctive metacone column but contains a smooth undulation in its place. *P. vicentei* and *P. palmeri* also lack metacone columns, yet the location where the metacone would be is flatter than that of *P. harmeri*.

Periphragnis unnamed species
Figure 4

Three additional highly fragmentary specimens from the Termas del Flaco area pertain to a species of *Periphragnis* other than *vicentei,* indicating the occurrence of a second potential homalodothere in the Tinguiririca Fauna. These specimens likely document a new taxon, but are too fragmentary to rule out referral to other species of *Periphragnis* (except *P. vicentei,* from which it can be excluded), and are inadequate for formally recognizing a new species in any case.

Referred Specimens: SGOPV 2798, isolated left upper molar, probably M3; SGOPV 2911, three fragmentary left upper cheek teeth, P4–M2 or M1–3; SGOPV 2797, two right upper molars with poorly preserved occlusal surfaces, probably M2–M3.

Locality: As for *Chilestylops davidsoni*.

Age: As for *Chilestylops davidsoni*.

Description of SGOPV 2798: An isolated left upper molar, likely M3 (see below), is the best preserved of the three indeterminate specimens of *Periphragnis*. It forms an irregular quadrilateral, the labial and lingual faces of which diverge anteriorly. It possesses a short, shallow anterior cingulum but lacks even a trace of a posterior one. A weak paracone column lies immediately behind a small, blunt parastyle at the anterolabial corner of the ectoloph, while a symmetric metastyle occurs posteriorly. Growth bands run transversely across the enamel of the labial face of the tooth, resembling the cross section of an open anticline. The labial face is ~2 cm high. A broad wear surface runs between the edge of the ectoloph and the slitlike central fossa. The enamel forming the lingual slope of the central fossa dips shallowly toward the ectoloph and thus is fairly broadly exposed. The central fossa is closed posteriorly by a small isthmus of dentine, joining what would be the metaloph and the posterior termination of the protoloph. (No clear metaloph exists; if it was ever present, it has been completely subsumed by the broad wear surface of the ectoloph.) The fairly heavily worn protoloph extends and broadens posterolingually from the parastyle to ultimately intersect the metaloph, and forms the anterolingual corner of the tooth.

Two lines of evidence suggest that SGOPV 2798 represents an M3. The first and second molars in *P. palmeri*, *P. harmeri,* and *P. vicentei* are more quadrate than in SGOPV 2798. The fairly triangular M3 in *P. harmeri* (e.g., MLP 12-1769), the only species of *Periphragnis* in which M3 has been definitively reported, resembles SGOPV 2798 in general outline. In addition, a gap in the enamel on the anterior face of the tooth between the parastyle and the region surrounding the anterior cingulum indicates where the anterior tooth in the series (M2) would have butted against it. Enamel across the posterior face of the tooth is continuous, suggesting that no tooth occurred posterior to it, and thus this represents the ultimate cheek tooth (M3).

Description of SGOPV 2911: This specimen consists of heavily worn portions of three left cheek teeth, including a badly damaged probable P4, and the largely intact labial halves of M1–2. Like SGOPV 2798, this specimen exhibits gently folded growth lines on the labial faces of the two posterior teeth, and very weak paracone columns. The occlusal surfaces have been highly polished by wear (best seen labial to the thin, slitlike central fossa), as is typical in homalodotheres. The anterior tooth is broken anterolabially and lingually. Its crown is preserved sufficiently to establish that the tooth was roughly rectangular in outline and transversely broad (thus likely a P4) rather than more molariform (as would be an M1) The ovoid to slitlike central fossa of all three teeth is centered and angled in the usual notoungulate fashion.

Description of SGOPV 2797: This specimen consists of the fragmented occlusal surfaces of two upper molars (probably M2–3) lodged in a small maxillary fragment. The posterior of these, smaller and better preserved, resembles SGOPV 2798 in size and outline. The form of the central fossa is highly similar in the two specimens, although in SGOPV 2797 the protoloph and "metaloph" have not yet been joined by wear. The small metastyle of SGOPV 2798 projects labially, whereas in SGOPV 2797 it projects posteriorly, a difference likely attributable to intraspecific variation. The resemblance of the posterior tooth of SGOPV 2797 to SGOPV 2798 suggests that SGOPV 2797 preserves M2–3. The more poorly preserved anterior tooth of SGOPV 2797 is larger and more rectangular than its posterior counterpart and exhibits a small portion of an anterior cingulum near the protocone.

Discussion: Collectively SGOPV 2798, 2911, and 2797 indicate the presence of a second species of *Periphragnis* in the Tinguiririca Fauna, in addition to *P. vicentei.* This material likely pertains to a new species, but given its fragmentary nature this cannot be determined definitively. (Even if demonstrably different from known species, this material is too limited to warrant formal naming of a new taxon.) Thus, we refer the second species of *Periphragnis* from Termas del Flaco to *Periphragnis* unnamed sp. indicating that this material likely represents a new taxon, but one not deserving formal recognition at this time.

Despite incomplete preservation of M3 in SGOPV 3107 (the holotype of *Periphragnis vicentei*), and slight uncertainty about which tooth positions are represented in SGOPV 2911, it is clear that SGOPV 2798, 2911, and 2797 represent a taxon 10%–30% smaller than and specifically distinct from *P. vicentei.* This is best seen in the mensural data presented in table 1. The strong development of upper molar cingulae in *P. vicentei* compared to their feeble presence in *Periphragnis* unnamed sp. (most clearly seen in SGOPV 2798) may be another distinction between the two likely homalodotheres in the Tinguiririca Fauna represented by upper teeth. To the limited extent that comparisons can be made, the cingulae of upper cheek teeth are typically equally strongly developed in the premolars and molars of *Periphragnis* (e.g., MLP 12-1769, in Simpson, 1967: pl. 35). *P. vicentei* is anomalous in this respect, having strong cingulae on the premolars and progressively weaker cingula on M1 and 2. The only specimen of *Periphragnis* unnamed sp. well-enough preserved to show the condition of the cingula, SGOPV 2798, is an M3, wherein only a small anterior cingulum is present. We presume the M3 cingula of *P. vicentei* to have been similarly reduced, based on the well-preserved M1–2. This may argue for a close relationship between *Periphragnis* unnamed sp. and P. *vicentei* (if the former is in fact distinct from other members of the genus).

In addition to their exclusion from referral to *P. vicentei,* SGOPV 2798, 2911, and 2797 very likely do not pertain to other described species of *Periphragnis*. *P. harmeri* has strongly developed molar cingula, including one spanning the entire length of M3 lingually (Simpson, 1967, plate 35), whereas SGOPV 2798 bears only an anterior cingulum and it is extremely

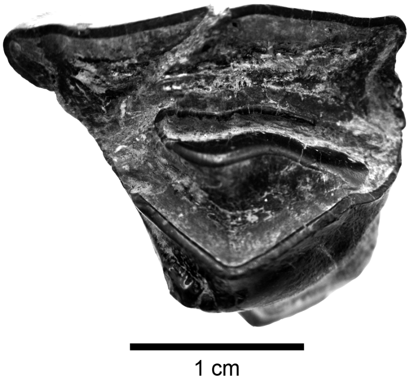


FIGURE 4. Occlusal view of SGOPV 2798, an M3, assigned to *Periphragnis* unnamed species.

small. The molar paracone columns of *P. harmeri* are far more strongly developed than in SGOPV 2798 and 2911. Moreover, SGOPV 2798 is significantly smaller than the smallest recorded M3 of *P. harmeri* (Simpson, 1967) (table 1). In *P. exauctus* and *P. palmeri* the posterior molar cingula are strong, a feature lacking entirely in SGOPV 2798. (Although M3 is not known definitively for *P. exauctus* or *P. palmeri,* these species can be assumed to have possessed a posterior cingulum on M3 based on its presence on M1–2.) It may also be mentioned that a specimen referred to *P. exauctus*, AMNH 28651, bears distinct basal cingula on the upper molars labially, no trace of which is seen on specimens from Tinguiririca.

Periphragnis unnamed sp. (SGOPV 2911, 2798, and 2797) is also excluded from assignment to “*Trigonolophodon*” *modicus* (MLP 12-2190; Simpson, 1967: pl. 41, specimen 3), an “isotemnid” from the Mustersan SALMA of Patagonia (Simpson argued that this undiagnostic specimen was equally referable to *Periphragnis,* here considered likely a homalodothere). SGOPV 2798, an M3, is more triangular in occlusal outline and lacks the shallow posterior cingulum seen in MLP 12-2190 (“perhaps M3,” fide Simpson, 1967: 178). Further, SGOPV 2798 is narrower (24.2 mm) than long (30.0 mm). The opposite is seen in MLP 12-2190, where width (34 mm) exceeds length (25.5 mm).

Trigonolophodon sp. cf. *T. elegans*

Figure 5

Referred Specimen: SGOPV 2820, posterior ends of both mandibles bearing a left m2 talonid sliver and largely complete m3, and right partial m1, and m2–3.

Locality: As for *Chilestylops davidsoni.*

Age: As for *Chilestylops davidsoni.*

Description: The sole specimen (fig. 5) of *Trigonolophodon* sp. cf. *T. elegans* from the Tinguiririca Fauna consists of the posterior ends of both mandibles bearing a left m2 talonid sliver and largely complete m3, and right partial m1, and m2–3. The molars are notably hypsodont and little worn, the hypolophid of m3 remaining essentially unabraded. Labially the crown of m3 measures at least 38 mm in height. This tooth is 44 mm long and roughly 13.2 mm wide (depending on the height at which it is measured). The molars are of canonical notoungulate form: a short paralophid persists on unworn teeth, separated posteriorly from the more robust metalophid by a wide cleft. On m3 the entoconid is a rounded bulge, the summit of which sits roughly one third of the crown height below the rim of the hypolophid. No cingulae of any kind are evident.

In general, what little is currently known of the upper dentition of *Trigonolophodon* closely resembles that of *Periphragnis,* including the upper molar of *Trigonolophodon modicus* (“*Trigonolophodon*” *modicus*, fide Simpson, 1967) from Lago Musters, illustrated by Simpson (1967: pl. 41, specimen 3), discussed below.

The recovery of additional material referable to *Trigonolophodon* and ongoing revisionary work on the species of *Periphragnis* are expected to clarify the taxonomy of these forms.

Discussion: Elements of the lower dentition of *Trigonolophodon* sp. cf. *T. elegans,* (SGOPV 2820) from the Tinguiririca Fauna (Wyss et al., 1994; fig. 5) are too large to occlude with SGOPV 2798, or with the holotype of *P. vicentei* for that matter. SGOPV 2820 is a nearly perfect match in size and morphology for MLP 12-1727, a well-preserved mandible and symphysis of *Trigonolophodon elegans* from Argentina, the two specimens having been compared firsthand. *T. elegans* was originally known from upper and lower dental remains, but only the lowers (MLP 12-1727) can currently be located. Unpublished notes by Bryan Patterson, entitled "Material from the 'Terciario inferior de Cañadon Blanco,'" lists two species of *Trigonolophodon*, *T. elegans* and *T. inflatus,* from this still enigmatic locality ("Where is it? nobody seems to know and there are no records"; Patterson, unpublished). The origin of these specimens from this locality is substantiated by the abbreviation "T.i.C.B." written in ink on the specimens.

Ironically, Roth himself (1903) indicated that MLP 12-1727 derives from Lago Musters, but this record is now considered to have been in error. As discussed elsewhere (Wyss et al., 1994), Patterson concluded that "this supposed horizon [Cañadón Blanco] is a mixture of three [faunas], the Casamayor, Musters, and Deseado," a notion he never published but which was subsequently advanced by Simpson (1967). Through unstated reasoning, Patterson allocated *Trigonolophodon inflatus* from Cañadón Blanco to the Deseadan (as the material referred to *T. elegans* was not locatable or recognizable at the time Patterson made his notes). Because of its presumed Deseadan (Oligocene) age, Simpson omitted *Trigonolophodon* from his monumental revision of Paleocene and Eocene faunas of South America (Simpson, 1948, 1967). With the discovery of the Tinguiririca Fauna, and its unexpected combination of plausibly Casamayoran, Mustersan, and Deseadan taxa, came the realization that the assemblage of fossils from Cañadón Blanco (or at least the bulk of it) constituted a unified fauna, as Roth had maintained originally. Moreover, the remarkable taxonomic congruence between the Cañadón Blanco and Tinguiririca faunas argued for their approximate temporal equivalence, both being assigned to the freshly proposed Tinguiririca SALMA typified by the more extensive, better-preserved and more intensively studied Tinguiririca Fauna (Flynn et al., 2003).

CONCLUSIONS

Discovery of the Tinguiririca Fauna (Novacek et al., 1989; Wyss et al., 1990) opened a window on an important interval of the South American mammalian succession, justifying the careful documentation of its constituents. Here we have described and illustrated a small series of specimens from the Tinguiririca Fauna, documenting two new taxa, and a possible third, as part of that effort. Three notoungulate taxa discussed here make their last known appearance in the Tinguiririca Fauna: notostylopids, in the form of *Chilestylops davidsoni* (gen. et sp. nov.), and the basal toxodontian *Periphragnis* (Roth 1899), through *P. vicentei*, and *P.* unnamed species.

A numerical cladistic analysis of notostylopids identified the following set of relationships: ((*Chilestylops, Boreastylops, Otronia*) *Homalostylops, Notostylops*).

FIGURE 5. Mandibular fragment of *Trigonolophodon* sp. cf. *T. elegans* (SGOPV 2820) bearing sliver of talonid of left m2 and largely complete m3 in occlusal (top), lingual (middle), and buccal (bottom) views.

Periphragnis—previously considered restricted to the Mustersan SALMA and regarded as an early diverging toxodontian (Billet, 2011) or “transitional” taxon between “isotemnids” (now considered paraphyletic) and homalodotheriids (Simpson, 1967)—is represented by a new species in the Tinguiririca Fauna*, P. vicentei,* and specimens referred to a distinct, but unnamed member of the genus (SGOPV 2797, 2798, and 2911). From the Tinguirirican, *P. vicentei* and *P.* unnamed sp. mark the youngest known occurrence of the genus. Since the advent of modern phylogenetic methods, fossil taxa are generally seen as mosaics of advanced and primitive features, and therefore not truly transitional in the sense of representing actual or direct ancestors of subsequent species. If *Periphragnis* is indeed closely related to homalodotheres (Simpson, 1967; Bond, personal commun.) rather than representing an earlier diverging toxodontian (Billet, 2011), the matter of whether *Periphragnis* is a homalodotheriid or instead one of its proximal outgroups is largely definitional. Since tying the name Homalodotheriidae to a particular clade of notoungulates via a phylogenetic definition falls beyond the scope of this paper, we are resigned to currently employing this name in the same ambiguous sense it has been used classically. Our qualified (“cf.”) assignment of *Periphragnis* to Homalodotheriidae above thus reflects uncertainty about former taxon’s phylogenetic placement, as well as the definition of the latter’s name.

Finally, as reflected in the limited hypodigms of the taxa discussed above, it may be mentioned that large-bodied taxa are fairly rare components of the Tinguiririca Fauna. Whether this pattern reflects the scarcity of such mammals in the fauna at the time it existed or some taphonomic filter that culled larger elements of the fauna through the volcaniclastic depositional processes involved in forming these deposits is uncertain. Of the several hundred specimens collected from the Tinguiririca Fauna to date, SGOPV 2820 and 3107 are by far the largest recovered.

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APPENDIX

Character Descriptions and Data Matrix Used for Phylogenetic Analysis

	Chilestylops	*Otronia*	*Boreastylops*	*Notostylops*	*Homalostylops*	*Oldfieldthomasia*
Upper premolar shape [0=transverse (elongated labio-lingually); 1=quadrate]	1	0	1	0	0	0
Upper molar shape [0=transverse (elongated labio-lingually); 1=quadrate]	1	1	1	1	1	0
Premolars: enamel at lingual base of protocone [0= smooth; 1= mildly rugose (on any tooth); 2= strongly rugose (on any tooth)]	2	1	0	0	0	0
Molars: enamel at lingual base of protocone [0= smooth; 1= mildly rugose (on any tooth); 2= strongly rugose (on any tooth)]	2	0	0	0	0	0
Papillae on the lingual face of the ectoloph [0= absent; 1=distinctive mass of papillae present] - on any tooth	1	1	1	0	0	0
Upper cheek tooth cingula [0= weak or absent; 1= strongly developed]	1	1	1	2	2	0

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