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Paleontología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico-CONICET-Mendoza, Avenida Ruiz Leal s/n, 5500 Mendoza, Argentina

The present paper deals with the leontiniid remains recovered from the Late Oligocene (Deseadan) levels of Quebrada Fiera, Mendoza Province, central-western Argentina. The material consists of an almost complete skull associated with 11 vertebrae, as well as some maxillary and mandibular fragments and postcranial elements of different individuals, enabling a life reconstruction. The comparative study allows morphological differences with respect to other Deseadan taxa to be established, such as *Scarrittia*, *Leontinia*, *Ancylocoelus*, *Anayatherium* and *Elmerriggsia*, leading to the proposal of the new taxon *Gualta cuyana* gen. et sp. nov. The new genus and species is close to *Scarrittia canquelensis* in having upper I1 more developed than I2–3, mainly by its greater crown-height, and the canine overlapping the P1; it differs from this species by the longer, narrower nasals, longer rostrum, I2 not reduced, P3–4 with shallow lingual sulcus, shorter cervical vertebrae, and shorter calcaneum, lacking navicular facet. The complete dentition and/or the larger I1 differentiate *Gualta cuyana* from *Leontinia*, *Ancylocoelus* and *Anayatherium ekecoa*, as well as from the Miocene *Colpodon*. The lingual sulcus on P3–4 is much shallower than in *Scarrittia barranquensis*, *Leontinia*, *Anayatherium* and *Elmerriggsia*. The phylogenetic analysis shows poorly resolved relationships among leontiniids; when using equal weights, the analysis shows that *Gualta cuyana* is more related to the species of *Anayatherium* and *Scarrittia canquelensis*, whereas under implied weights, the new taxon is basal to other Palaeogene taxa. *Gualta cuyana* adds to other endemic taxa of the peculiar Deseadan assemblage from Quebrada Fiera. The new leontiniid constitutes a low percentage of fossil mammals within the Quebrada Fiera fauna, as is also true for this family in Salla (Bolivia), but in contrast with some Patagonian localities or the Brazilian Tremembé Formation where leontiniids are the best-represented mammal group.

http://zoobank.org/urn:lsid:zoobank.org:pub:17749C84-4028-4FC8-A140-E1A6FE02466D

Keywords: leontiniids; systematics; new taxon; Deseadan; Cuyo region

Introduction

The Late Oligocene Argentinean locality of Quebrada Fiera (36°33′13.3″S, 69°42′3.5″W, 1406 m asl) is located in the Malargüe Department, south of Mendoza Province (Fig. 1). It was discovered in the 1970s during geological prospecting. The fossil-bearing levels of Quebrada Fiera consist of white-greyish tuffs and tuffaceous palaeosols currently considered to represent the base of the Agua de la Piedra Formation (Gorroño *et al*. 1979; Combina & Nullo 2008, 2011). Initial studies assigned the recovered fossils to the Deseadan South American Land Mammal Age (SALMA), mainly based on the presence of *Pyrotherium* Ameghino, 1888 and *Proborhyaena gigantea* Ameghino, 1897 (Gorroño *et al*. 1979; Bond & Pascual 1983), two classic representatives from the Deseadan of Patagonia. Aside from some additions to the faunal list

(Pascual & de la Fuente 1993), no other detailed taxonomic studies were carried out until recent years.

Since 2006, new field projects have revealed a much more complete faunal association than was known before, with endemic elements and others that make the Quebrada Fiera fauna similar to that from Salla (Bolivia) or to Patagonian assemblages (see Cerdeño 2011 for a summary). Notohippids (Cerdeño & Vera 2010, 2014), archaeohyracids (Cerdeño *et al*. 2010), hegetotheriids (Cerdeño & Reguero in press), homalodotheriids (Seoane & Cerdeño 2014) and carnivorous metatherians (Forasiepi *et al*. 2014) have been studied in detail, and some other groups are currently under study (Hernández Del Pino *et al*. 2013). The present contribution deals with the leontiniid material that increases the knowledge of both the native ungulates from Quebrada Fiera and the diversity of the Family Leontiniidae during the Oligocene.

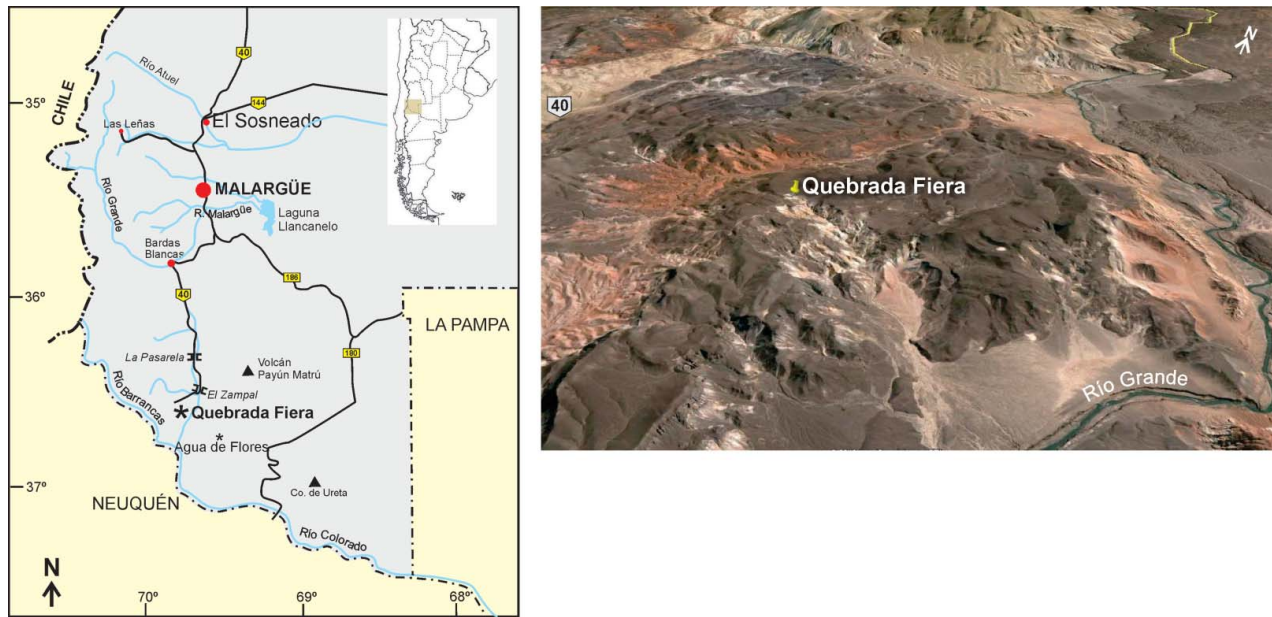*Corresponding author. Email: espe@mendoza-conicet.gob.ar

Figure 1. Geographical location of the Quebrada Fiera locality and detail of a Google Earth view of the site.

The Leontiniidae are a group of large South American notoungulates with complete, brachydont to mesodont dentition, which are known from the Eocene in northwestern Argentina (Bond & López 1995; Deraco *et al.* 2008) to the Middle Miocene in Colombia (Villarroel & Colwell Danis 1997) and Brazil (Ribero & Bond 2000). The greatest diversity and geographical distribution were reached during the Late Oligocene Deseadan SALMA, with seven recognized genera: *Leontinia* Ameghino, 1895, *Ancylocoelus* Ameghino, 1895, *Scarrittia* Simpson, 1934 (in Chaffee 1952), '*Henricofilholia*' Ameghino, 1901, and *Elmerriggsia* Shockey, Flynn, Croft, Gans & Wyss, 2012 in Patagonian localities, Argentina; *Anayatherium* Shockey, 2005 in Bolivia; and *Taubatherium* Soria & Alvarenga, 1989 in Brazil. *Scarrittia* was also recorded in Uruguay (Ubilla *et al.* 1994). Paula Couto (1983) recognized cf. *Leontinia gaudryi* Ameghino, 1895 in the Tremembé Formation, Brazil, but Soria & Alvarenga (1989) considered the leontiniid from this formation to belong to the genus *Taubatherium* (see also Ribeiro *et al.* 2010).

A comment is needed on the genus *Henricofilholia*. As Shockey (2005) summarized, Ameghino (1901) based different species of this taxon on inadequate material, *H. inaequilatera* being the only exception to this, but otherwise synonymized with *Ancylocoelus frequens* Ameghino, 1895 (Patterson 1952; Shockey 2005). However, Ribeiro *et al.* (2010) recorded two species (including a new one) of *Henricofilholia* from Gran Barranca (Patagonia, Argentina). The problem is that these authors considered *H. lustrata* Ameghino, 1901 as the type species of the genus, when actually Ameghino (1901, p. 405)

explicitly designated *H. cingulata* as the type of the genus. As the name of the type species *H. cingulata* was previously synonymized with *Ancylocoelus frequens* (Patterson 1952; Ribeiro 2003; Ribeiro *et al.* 2010), the name of the genus, *Henricofilholia*, is also synonymous with *Ancylocoelus* (ICZN 2000, art. 61.1, 61.3.1), as was noted by Soria & Alvarenga (1989, p. 159). Therefore, the name is not available and the Patagonian material referred to it should be renamed at generic level. For this reason, we use '*Henricofilholia*' in quotes, as already done by Shockey *et al.* (2012).

The material of Leontiniidae from Quebrada Fiera was previously identified as cf. *Scarrittia* and cf. *Leontinia* (Gorroño *et al.* 1979; Pascual & de la Fuente 1993) and more recently as *Scarrittia* sp. (Cerdeño 2011). Ribeiro *et al.* (2010, p. 179) also alluded to the leontiniid from Mendoza as *Scarrittia* cf. *S. canquelensis* Simpson, 1934 (in Chaffee 1952) without referring to any precise specimen. The present revision of these, as well as the new leontiniid remains, allows us to increase the diversity of this family during Deseadan times and to check the phylogenetic relationships of the group.

Material and methods

This study is mostly based on a skull and associated vertebrae, but some other remains are also referred to the same taxon. The skull is rather complete, somewhat distorted laterally and has some bone missing; the premaxillary and maxillary areas have been maintained separately from the rest of the skull because a perfect fit between both parts is

not possible even though there are some points of connection. Specimens are detailed in the Systematic palaeontology section below.

Material from recent expeditions was incorporated into the palaeontological collection of the Museo de Ciencias Naturales y Antropológicas "J. C. Moyano" (**MCNAM-PV**), Mendoza city, while previously recovered remains are stored at the Museo de La Plata (**MLP**).

The systematic study was achieved through direct and bibliographical comparisons with leontiniid specimens from Argentina and other South American countries. We especially relied on original photographs of specimens stored at: Amherst College Museum of Natural History (**ACM**), Amherst, Massachusetts, USA; American Museum of Natural History (**AMNH**), New York, USA; and Field Museum of Natural History (**FMNH-P**), Chicago, USA. For anatomical descriptions, we follow Cerdeño *et al.* (2012) in considering six main faces of each element: proximal (or dorsal in the skull), distal (or ventral in the skull), anterior, posterior (occipital in the skull), medial, and lateral, being anterior to the head position, medial to the sagittal plane, and lateral to the external side of the body. Limb bones are considered in a unique vertical axis independent of the actual anatomical position.

Cladistic methodology was used in the phylogenetic analysis. We assembled a character-taxon matrix based on that in Shockey *et al.* (2012). We performed the phylogenetic analysis with *Colbertia magellanica*, an Oldfieldthomasiidae from Itaboraí (Brazil), as the outgroup. The ingroup includes only species of Toxodontia: families Leontiniidae, Isotemnidae, Notohippidae and Toxodontidae, following one of the options in the analysis by Shockey *et al.* (2012), excluding Typotheria. The resulting data matrix comprises 23 taxa and 81 morphological characters (Online Supplemental Material). Concerning characters used by these authors, some comments are included in the section corresponding to the analysis (see below). Using the program TNT 1.1 (Goloboff *et al.* 2008), we conducted a tree bisection reconnection search (TBR), using 100 random addition sequences and saving 10 trees per round. After that, we repeated the search from previously obtained trees. The characters were treated as unordered and under equal and implied weights (Goloboff 1995, 1997).

Anatomical and dimensional abbreviations
Ant., anterior; APD, anteroposterior diameter; artic., articular; Aud. Bull., auditory bulla; B-OCC, basioccipital; BS, basisphenoid; C/c, upper/lower canine; Cond. F., condyloid foramen; Cris. Meat., crista meatus; dis., distal; dp, lower deciduous tooth; EAM, external acoustic meatus; ep., epiphysis; For. Mag., foramen magnum; For. Ov., foramen ovale; Fos. Subarc., fossa subarcuata; Glen. Fos., glenoid fossa; Glen. notch, glenoid notch; Gr., groove; H, height; Hy. Rec., hyoid recess; Hyp. F., hypoglossal

foramen; I/i, upper/lower incisors; IAM, internal auditory meatus; Ju. F., jugular foramen; L, length; Lambd. Cr., lambdoidal crest; M/m, upper/lower molars; Mas. F., mastoid foramen; max., maximal; Mc, metacarpal; Med. Lac. F., median lacerate foramen; Mt, metatarsal; Occ. Cond., occipital condyle; P/p, upper/lower premolars; Parocc. Pr., paroccipital process; Postglen. F., postglenoid foramen; Postglen. Pr., postglenoid process; Postym. Pr., posttympanic process; prox., proximal; PT, pterygoid hamulus; Scaph. Fos., scaphoid fossa; Spme. F., suprameatal foramen; Styl. F., stylomastoid foramen; sust., sustentaculum; TD, transverse diameter; tub., tuberosity; Vest. Aqued., vestibular aqueduct; W, width.

Systematic palaeontology

Order **Notoungulata** Roth, 1903
Suborder **Toxodontia** Owen, 1853
Family **Leontiniidae** Ameghino, 1895
Genus *Gualta* gen. nov.

Type species. *Gualta cuyana* gen. et sp. nov.

Diagnosis. As for the type and only species.

Derivation of name. *Gualta* is a word in Huarpes' native language meaning mountains or hills, in reference to the mountain where the fossiliferous levels outcrop.

Gualta cuyana sp. nov.
(Figs 2−10)

Holotype. MCNAM-PV 3951, nearly complete skull (with left and right I1−M3 series) and 11 associated cervical (seven) and thoracic (four) vertebrae.

Diagnosis. Longer nasals and more slender rostrum than *Scarrittia canquelensis*. External acoustic meatus separated by a well-developed septum from the suprameatal foramen. Crista meatus and post-tympanic process fused, very different from the independent condition in *Ancylocoelus frequens*. Unlike other toxodontians, the foramen ovale and median lacerate foramen do not share a common exit, the two being separated by a septum. Shallow fossa subarcuata. Internal auditory meatus as a unique large foramen. Complete dentition without diastema. Enlarged, but not hypertrophied I1 and i3, similar to *S. canquelensis*. I2 not reduced, similar in size and morphology to I3. Canine similar to I3, overlapping P1 as in *S. canquelensis*. P1 larger than C. Lingual sulcus on P3−P4 very shallow and lingual wall not posterolingually projected, different from *Scarrittia barranquensis*, *Leontinia*, *Elmerriggsia* and *Anayatherium*. Upper molars with lingual, but not labial cingula; lower molars with lingual and labial cingula. Total cervical length equivalent to total skull length, the neck being shorter than in *S.*

canquelensis. Calcaneum relatively shorter than in *S. canquelensis* and closer to *Elmerriggsia fieldia*, lacking navicular facet in contrast with *Scarrittia*, *Leontinia* and *Taubatherium*.

Derivation of name. *Cuyana* is an adjective that indicates native from, or pertaining to, Cuyo, the Argentinean region that includes Mendoza Province, where the type locality occurs.

Referred material. MLP 96-XI-20-2, right I1-M2 series and left I1−I2 and P1−M2 series of the same individual; MCNAM-PV 3995, maxillary fragment with part of a molar and the beginning of the zygomatic arch; MCNAM-PV 3842, broken upper right molar; MLP 96-XI-20-3, juvenile mandible with i1−i3 (left i3 broken), canine roots and both series p1−d2−d3−d4−m1 and m2 erupting; MCNAM-PV 3841, left mandibular fragment with p3−m2 and part of the symphysis, and isolated and incomplete right p3−m1; MCNAM-PV 4361, anterior part of axis; MCNAM-PV 3996 and PV 3997, incomplete cervical vertebrae; MCNAM-PV 3998 incomplete thoracic vertebra; MCNAM-PV 3938 and MCNAM-PV 4376, right humeri; MCNAM-PV 3916 and PV 4283, right calcanei.

Remarks. Some specimens previously assigned to or catalogued as Leontiniidae, such as MLP 77-VI-1-4 (*Leontinia*? sp. in Gorroño *et al*. 1979) and MLP 96-XI-20-1 (young cranial fragment), are considered to be Homalodotheriidae; and MLP 77-VI-1-11, proximal fragment of left Mc III, could belong to Toxodontidae. MLP 77-VI-1-4 is the only specimen assigned to the genus *Leontinia*, whose presence in Quebrada Fiera is rejected, as already suggested by Ubilla *et al*. (1994) and Cerdeño & Vera (2010). All recognized leontiniid remains from Quebrada Fiera are presently identified as the same new taxon.

Occurrence. Quebrada Fiera, Malargüe Department, Mendoza Province, central-western Argentina from the Agua de la Piedra Formation, Late Oligocene, Deseadan SALMA.

Description

Skull. The skull MCNAM-PV 3951 (Figs 2A, B, 3C) is long, narrow and relatively low (Table 1), with proportions more similar to *Scarrittia canquelensis* than *Leontinia gaudryi* Ameghino, 1895 (Loomis 1914; Chaffee 1952). Nasal bones are transversely convex, converging in a middle shallow groove; they are relatively short and narrow, widening posteriorly at the junction with the frontal bones (Fig. 2A). Anterolaterally, nasals form a slight convexity with the maxillae. Frontals are dorsally flat and slightly convex laterally at the postorbital apophyses. The latter are short and backwardly directed, well separated

Table 1. Skull dimensions (mm) of *Gualta cuyana* gen. et sp. nov. from Quebrada Fiera, Mendoza. Values in parentheses are approximate.

Skull	
Total length	(386)
L occipital crest−nasal tip	318
L of sagittal crest	99.2
Nasal length (middle line)	126
Frontal length (middle line)	83.8
Length orbit−nasal tip	137
Length orbit−premaxillary tip	164.5
Length orbit−nasal notch	105
Anterior nasal width	33.1
W postorbital apophyses level	(140.8)
Bizygomatic width	203.7
Temporal width	76.3
W of occipital crest	98.2
W cristae meati level	148.5
W paraoccipital apophyses level	100.4
W occipital condyles	85.4
W of foramen magnum	39.9
H occipital face	109
Palatal width between P1	(36)
Palatal width between M1	(51)
Palatal width between M3	59.1

from the zygomatic arch. The frontals narrow behind these apophyses, and develop two thin temporal crests that converge into a narrow, long and low sagittal crest. *Leontinia gaudryi* (e.g. ACM 3290, ACM 3293; Loomis 1914, fig. 72) shows a significantly different configuration of nasals and frontals, and the strong postorbital processes almost close the orbit. *Scarrittia canquelensis* differs from MCNAM-PV 3951 by its shorter and stouter nasals and larger size (Chaffee 1952, table 16).

In lateral view (Fig. 2B), premaxillary and maxillary bones are partially preserved. A narrow interpremaxillary crest develops over the I1s. The orbit is posteriorly open, large and oval in outline; on the anterior border there is a small rugosity as a slightly developed tuberosity, probably corresponding to the lacrimal tuberosity. The lacrimal bone is not observed on the external face, contrary to *Leontinia gaudryi*. The broken bone just allows a partial observation of the antorbital foramen. The zygomatic arch starts at the level of M2; the jugal ramus of the arch has an irregular lateral surface, with a small, mediodistal tuberosity. The anterodistal border of the arch is regularly convex, without forming a marked angle. From the jugal ramus, a convex zygomatic plate develops at the base of the orbit. The squamosal ramus of the arch is high and has a smooth surface. Its posterior end rises almost to the level of the sagittal crest, and joins the nuchal crest at a marked angle (around 100°). Its ventral border forms a lateral
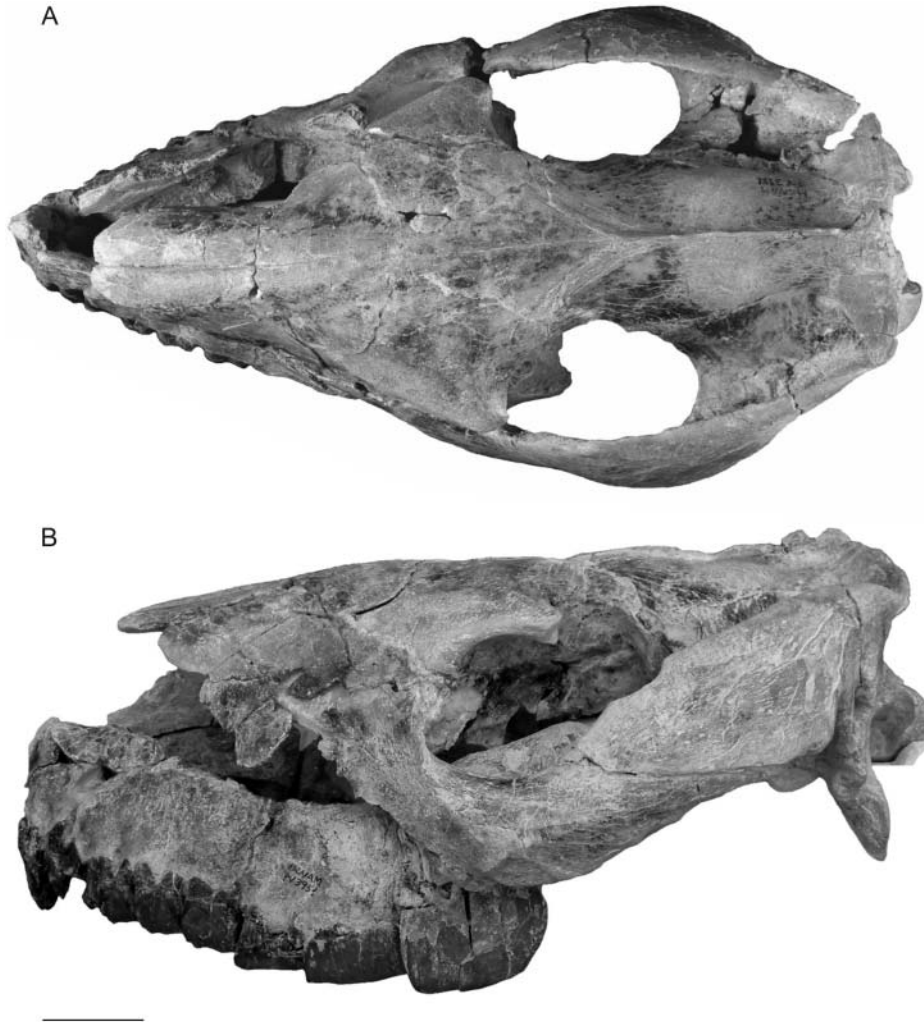
Figure 2. Skull MCNAM-PV 3951 of *Gualta cuyana* gen. et sp. nov. **A,** dorsal view; **B,** lateral view. Scale bar = 50 mm.

wide and deep notch that ventrally subdivides the glenoid fossa. The notch is posteriorly limited by the postglenoid (or retroarticular) process. The latter does not develop as a ventrally detached apophysis, but forms a regular, curved border fused with the crista meatus (see below). Both structures together with the post-tympanic process surround a cavity where the rounded external auditory meatus (EAM) is separated by a well-developed septum from the anterior, smaller, and circular suprameatal foramen (Fig. 3A). Basal to the EAM, there is another foramen that corresponds to the dorsal opening of the postglenoid foramen (see basicranium description below), which is partially hidden by the crista meatus in lateral view. The whole cavity with the three foramina opens lateroventrally by means of a shallow groove that separates the postglenoid process and the crista meatus (Fig. 3A).

Compared with the ear region of the leontiniid *Ancylocoelus frequens* (Gabbert 2004, fig. 14.2), there are several differences. In MCNAM-PV 3951, the mentioned septum is narrower. The crista meatus and the post-tympanic

process are not well differentiated as occurs in *Ancylocoelus*. Instead, a unique, ventrally projected process is observed, which is interpreted as both the crista meatus and the post-tympanic process fused without clear limits. On the posterior side of this process there is a foramen that would correspond to the stylomastoid foramen, in a very different way from that of *Ancylocoelus* (Gabbert 2004, fig. 14.2), and would mark the limit between the post-tympanic process and the crista meatus; then, the crista meatus is the ventrally projected part whereas the post-tympanic process is reduced to the posterodorsal area of the structure. The crista meatus shows an acute border that laterally runs posteriorly to the EAM, whereas in *Ancylocoelus* the crista meatus runs anteriorly to the EAM, reaching the above-mentioned septum. In *Ancylocoelus*, the groove between the postglenoid process and the crista meatus only reaches the suprameatal foramen.

Behind the ear region and well separated from the post-tympanic process, there is a long, transversely flattened and distally pointed paroccipital (paracondylar or jugular)
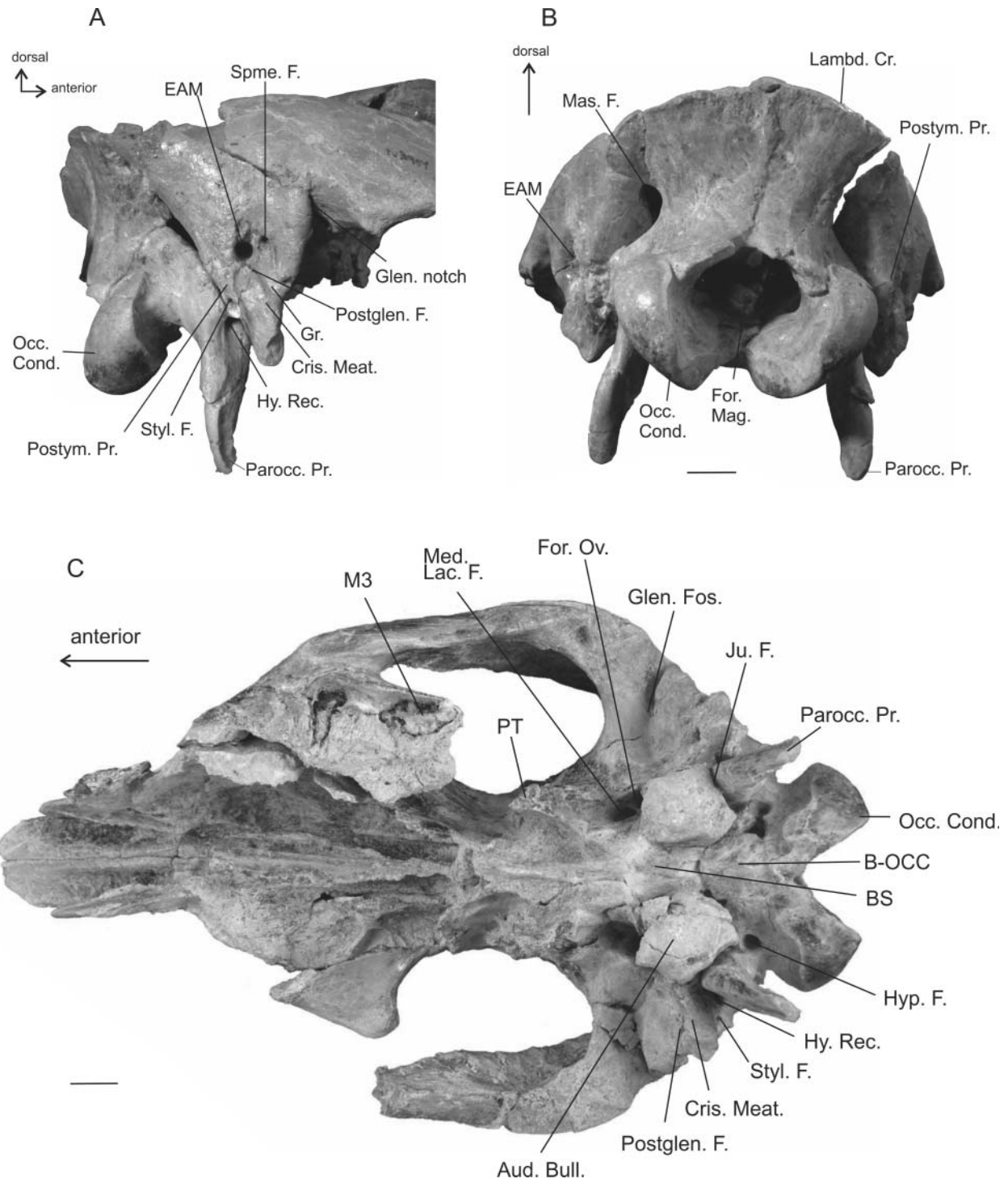
Figure 3. Skull MCNAM-PV 3951 of *Gualta cuyana* gen. et sp. nov. **A,** detail of ear region; **B,** occipital view; **C,** ventral view. See abbreviations in text. Scale bars = 20 mm.

process that shows some sigmoid curvature along its height. In this lateral view, the occipital condyles project backward (Figs 2B, 3A).

The occipital face is relatively narrow. The narrowing below the lambdoidal crest borders two large lateral mastoid foramina (Fig. 3B). Each foramen is deep, high and

distally pointed, and is laterally limited by the posterior end of the squamosal. The foramen magnum is large, wider than high, and the condyles are narrow and rather vertical.

In ventral view, the separated condition of the two skull portions allows the observation of the ventral face of frontal and nasal bones (Fig. 3C). On the frontal, there is a

median, narrow crest that fades anteriorly and becomes a groove flanked by two crests that diverge anteriorly to the nasals. The median groove continues on the nasals transformed into a blunt crest that reaches the anterior tip of the bones, where it becomes flatter and less marked. Laterally to the median crest-groove, there are several oblique thin crests on this ventral surface; the most anterior crests are longer and continue on the maxillary surface.

The basicranium is rather complete (Fig. 3C). A suture is observable between the basioccipital and the basisphenoid. Two sphenoid tuberosities converge posteriorly in a median crest on the basioccipital.

According to Gabbert (2004), the ectotympanic bone forms the auditory bulla and the EAM. The bulla is very inflated, although reduced in relation with the size of the cranium; it is in contact with the crista meatus and the paraoccipital process, as well as with the basisphenoid. The jugular foramen is a narrow opening placed between the bulla and the paraoccipital process. Behind it, a large, rounded hypoglossal foramen is at the base of the paraoccipital process, between the latter and the occipital condyle. A condylar foramen is not observed. In turn, between the paraoccipital process and the crista meatus, the hyoid recess (tympanohyal recess in Billet *et al*. 2008) is a wide foramen, placed medially to the stylomastoid foramen (Fig. 3C). On the anterior side of the crista meatus and medially to the postglenoid lateral border is the postglenoid (retroarticular) foramen; close and ventrally to it there is a groove running anteromedially, surrounding the bulla; Gabbert (2004, p.182) describes a groove in the notohippid *Puelia*, which leads ventrally from the retroarticular foramen. In our skull, the groove reaches a fossa (anterior to the bulla) where two deep, large foramina are separated by a short septum: the foramen ovale (posterior) and the median lacerate foramen (anterior); these

foramina do not form a unique opening, the sphenotympanic fissure, as stated by Gabbert (2004) for toxodontians or Billet *et al*. (2008) for the mesotheriid *Trachytherus*. Anterior to these foramina, the scaphoid fossa (following Gabbert 2004) develops at the base of the pterygoid hamulus. These processes are incomplete at both sides, but they are large at their base and would be ventrally long (Fig. 3C). Their medial surface is concave. Between the processes, the sphenoid forms a median ridge that becomes more acute anteriorly (tip broken). Dorsally to this sphenoid surface (not seen in ventral view but laterorostrally), a large foramen, the optic canal, opens at each side into the temporal fossa. Two ethmoidal foramina open ahead the optic canal.

The right bulla, petrosal and zygomatic arch were at first separated from the skull, allowing the observation of both petrosals in anatomical position (Fig. 4A, B), and the right one was later removed during the preparation process. The petrosal seems less expanded than that of *Scarrittia canquelensis* figured by Gabbert (2004, fig. 14.6) and Billet (2011, fig. 7A). In cerebellar view, the bone shows a shallow fossa subarcuata and the internal auditory meatus (IAM) that appears as a unique large foramen (Fig. 4B); the separation of both the foramen acoustic superior and foramen acoustic inferior would be very deep. A large vestibular aqueduct is placed posteriorly to it. The right petrosal permitted observation of the tympanic face, but it is badly preserved, with a wide, convex border on its mastoid region. This rounded border is observed on the petrosal of the leontiniid from the Tremembé Formation, Brazil, figured by Paula Couto (1983, fig. 9), which would correspond to *Taubatherium* (Soria & Alvarenga 1989).

Upper dentition. Both upper dental series of the skull are almost complete, just the left canine is broken off (Fig. 5A).
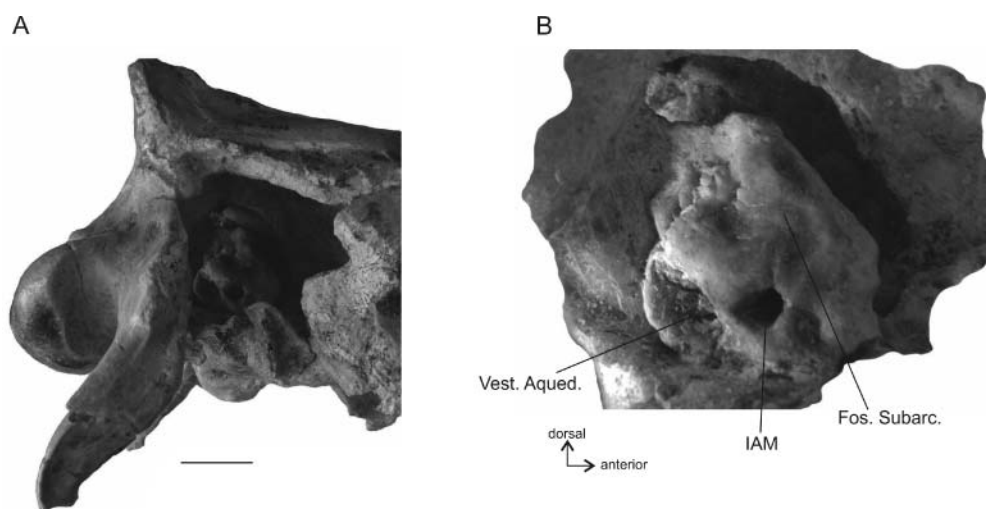

Figure 4. Details of petrosals of *Gualta cuyana* gen. et sp. nov. from the skull MCNAM-PV 3951. **A,** left petrosal in anatomical position; **B,** the same in detail (without scale). Scale bar = 20 mm.
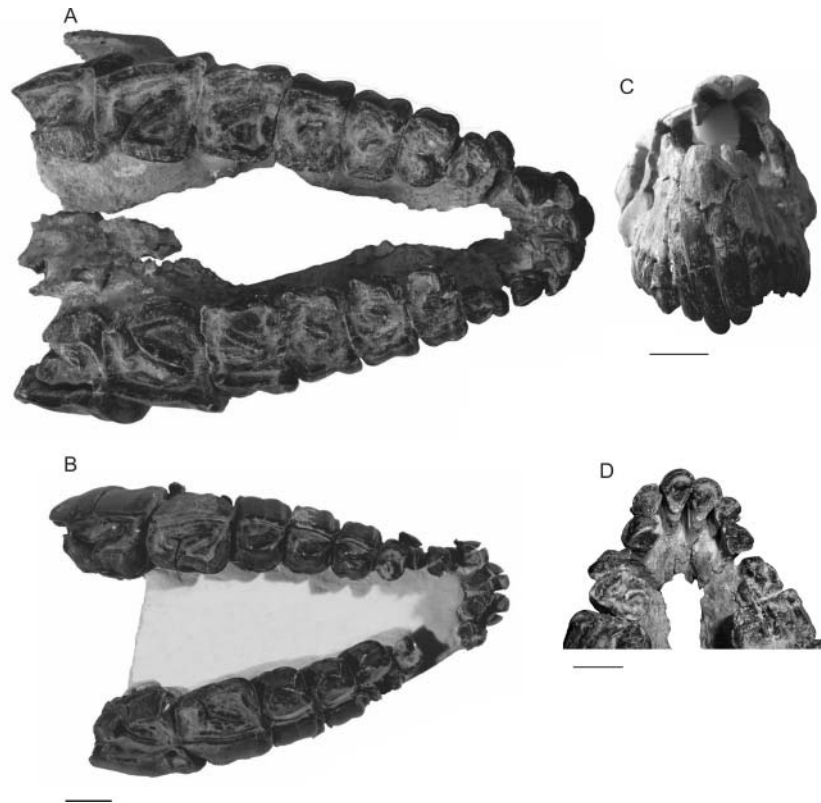
Figure 5. Upper dentition of *Gualta cuyana* gen. et sp. nov. **A,** complete dental series of the skull MCNAM-PV 3951, occlusal view; **B,** MLP 96-XI-20-2, right I1−M2 and left I1−3 and P2−M2, occlusal view; **C,** anterior view of the skull MCNAM-PV 3951 showing upper incisors; **D,** detail of incisors, lingual view. Scale bars = 20 mm.

Among the incisors, the I1 of the skull MCNAM-PV 3951 are clearly higher crowned than I2 and I3 (Table 2; Fig. 5C); this condition occurs in *Scarrittia* (Chaffee 1952) and *Anayatherium ekecoa* Shockey, 2005, though in the latter the I1 seem to be more hypertrophied (Shockey 2005, fig. 2). They are high, narrow teeth, with a bevelled wear surface (Fig. 5D) and convex labial wall; the crown enlarges and points lingually to the base and

Table 2. Upper tooth dimensions (mm) of *Gualta cuyana* gen. et sp. nov. from Quebrada Fiera, Mendoza. PV corresponds to MCNAM material. Values in parentheses are approximate.

		I1	I2	I3	C	
MLP 96-XI-20-2	L	(13.2) (13.0)	(15.2) 12.4	15.5 —	(19.0) —	
	W	(11.9) (12.3)	12.8 13.3	13.3 —	(10.0) —	
PV 3951	L	11.5 11.5	12.6 13.0	14.0 15.5	— 15.1	
	W	15.7 15.8	12.5 11.7	12.4 13.6	— (10)	
		P1	P2	P3	P4	
MLP 96-XI-20-2	L	13.0 13.4	20.2 19.7	23.5 23.2	24.0 24.8	
	W	17.6 >15.9	25.9 26.9	30.6 31.4	35.5 (34)	
PV 3951	L	>11.8 12.8	18.6 17.9	21.4 20.6	23.3 22.9	
	W	— 18.6	28.0 27.1	33.7 30.6	34.6 34.4	
		M1	M2	M3	LP1−4	LP1−M2
MLP 96-XI-20-2	L	37.0 40.7	47.1 48.6	— —	81.0 79.5	162 158.2
	W	38.0 37.6	43.4 42.4	— —		
PV 3951	L	31.4 33.0	43.7 45.2	58.2 55.8	(77.5) 75.0	LP1−M3
	W	36.4 37.3	44.4 44.2	47.5 42.5		192.6 192

root, becoming well triangular in section. There are well-developed basal lingual and labial cingula, which strongly rise laterally. I2 is similar to I1, but it is slightly longer and narrower (Table 2), and lower-crowned. I3 is similar to C, lingually placed with respect to I2, closing the incisor series; it has a stronger labial cingulum than the I2. The canine, in turn, is labially placed to P1 and transversely oriented. It is more flattened than I3. Incisors are also preserved on MLP 96-XI-20-2 (Table 2). They are complete but fractured, with little wear. They show a similar morphology to those of MCNAM-PV 3951. The comparable position of I3 and C (right ones preserved) is also observed in AMNH 29613 of *S. canquelensis* (Chaffee 1952, pl. 9).

Cheek teeth of MCNAM-PV 3951 and MLP 96-XI-20-2 (Fig. 5A, B) show the same morphological characteristics, with minor differences. Both specimens belong to adult individuals, MCNAM-PV 3951 having a greater degree of tooth wear. The one-rooted, subquadrangular P1 has a strong, V-shaped labial cingulum, more similar to that of the incisors and canine than to that of P2−4. On the occlusal face, there is an L-shaped fossette, anterolingually elongated, close to the anterior wall and connected to the anterolingual cingulum. The latter is already partly worn and incorporated to the occlusal face. The most central extreme of this fossette has been isolated as a tiny, circular fossette in the P1 of MLP 96-XI-20-2. The P1 is smaller than the posterior premolars (Table 2).

The P2 shows the protocone as the unique lingual cusp, centrally placed and joined to the metaloph; it is better differentiated on MLP 96-XI-20-2 due to its lesser wear degree. A mesiolingual ridge develops from the tip of the protocone to the anterior cingulum (protocone−cingulum ridge in Shockey *et al*. 2012). The protoloph is a short, low, poorly developed, narrow crest (Fig. 5A). The anterior cingulum is strong, and continues lingually at the base, reaching the posterior cingulum. The latter forms an acute border rising to the protocone tip, though it is lower and expands posteriorly. The paracone fold is well developed and projects labially; the parastyle forms a thin, backwardly projected border that really corresponds to the anterolabial cingular rim. There is an anteroposteriorly elongated central fossette, with two small cristae (hardly observable on the P2 of MCNAM-PV 3951). At the posterolabial extreme of the occlusal face there is another tiny circular fossette, which would have already disappeared on MCNAM-PV 3951.

The P3 and P4 have the protoloph better developed than in P2. In MLP 96-XI-20-2, the less worn P3−4 show the lingual wall with the protocone well developed and joined by a short crest to the end of the metaloph, which can be interpreted as a hypocone or pseudo-hypocone as in M2 (see below), but not as a divided protocone, because it does not seem to have the same condition as in P1−2. The

lingual wall is straighter than in *Scarrittia canquelensis* and *S. barranquensis* Ribeiro, López & Bond, 2010, both species showing a greater posterolingual projection, especially *S. barranquensis* (Chaffee 1952, pl. 9; Ribeiro *et al*. 2010, fig. 11.2), independently of the cusp interpretation. There is also a centred, lingual depression that deepens to the base, better observed in P4 of MCNAM-PV 3951; it is much smoother than the lingual sulcus in *S. barranquensis* and *Anayatherium*, which is absent in *S. canquelensis* (Chaffee 1952; Shockey *et al*. 2012). The general aspect of P3−4 is more similar to those of *Elmerriggsia fieldia* Shockey, Flynn, Croft, Gans & Wyss, 2012, even though this taxon also has deeper lingual sulcus and a 'grooved protocone' (Shockey *et al*. 2012, fig. 5). The central fossette also has two cristae. These folds are not so clearly defined on the premolars of the skull due to wear. Premolars do not have detached metastyle; they present labial cingulum. With wear, premolars become clearly wider than long.

Molars are longer than wide; however, this outline varies with wear in such a way that the M1 of MCNAM-PV 3951, rather worn, is short and wide (Table 2). The M1 presents wide protoloph and metaloph due to wear (lingually fused on MCNAM-PV 3951); there is no crista. Parastyle and paracone folds are much smoother than in premolars. The cingulum is continuous on anterior, lingual and posterior faces, being less developed at the base of the hypocone. The central valley is Y-shaped in the younger specimen (lingual arm separates metaloph from protoloph), whereas in MCNAM-PV 3951 the Y becomes a simple, stretched and anteroposteriorly inclined fossette. The M2 of MLP 96-XI-20-2 shows an unworn hypocone (pseudo-hypocone in Shockey *et al*. 2012), as a pointed cusp that rapidly enlarges through its base. The lingual cingulum interrupts at the base of the hypocone and does not connect with the posterior cingulum; there is a small basal tubercle at the entrance of the median Y-shaped valley. The posterior cingulum limits a large postfossette. This fossette is not present on the worn M2 of the skull, which resembles the M1 of MLP 96-XI-20-2. The M3s preserved on MCNAM-PV 3951 are trapezoidal, with no posterior lingual cusp developed. The central valley opens posteriorly, above a low, V-shaped posterior cingulum. There is a very small fossette almost obliterated in the posterior part of the ectoloph. The lingual cingulum of these M3s is weakly developed, more as a rugose cingular rim. Molars lack the labial cingulum, as occurs in *Scarrittia*, *Leontinia* and *Anayatherium* (Shockey *et al*. 2012).

The specimen MCNAM-PV 3842 is also assigned to *Gualta cuyana* gen. et sp. nov. It is an upper right molar preserving the ectoloph (29.4 mm) and a portion of the central area, with some enamel remain of the fossette. Paracone and metacone folds are smoothly marked, resulting in a smooth undulation.

Lower dentition. MLP 96-XI-20-3 is a juvenile mandible with all incisors (di1−di3; left i3 broken), canine roots, and p1−dp2−4−m1 and m2 erupting in both series. The mandibular bone is fragmented, but teeth are well preserved (Fig. 6A−C; Table 3). The mandibular symphysis is narrow and forms an obtuse angle (about 140°) with the horizontal ramus. Its posterior end reaches the level of the anterior part of dp3. The horizontal ramus is low, with ventral border rather straight until the posterior inflexion at the level of m2 (Fig. 6A). There is a rounded mandibular foramen at the level of p1−dp2. Ascending rami are lacking. From p1 to the anterior part of m1, teeth form smoothly convex series that converge both anteriorly and posteriorly, but the talonid of m1 and the m2 are rather parallel, even slightly divergent (Fig. 6B).

Incisors are interpreted as deciduous teeth because of their small size. Dimensions increase from di1 to di3, but the latter is not developed as a tusk (Table 3); all of them present labial and lingual V-shaped cingula; lingually, a medium small vertical fold is formed to the cingular base, which enlarges the occlusal surface, fusiform in outline. The root of the canine is similar in size to that of the i3, slightly more compressed.
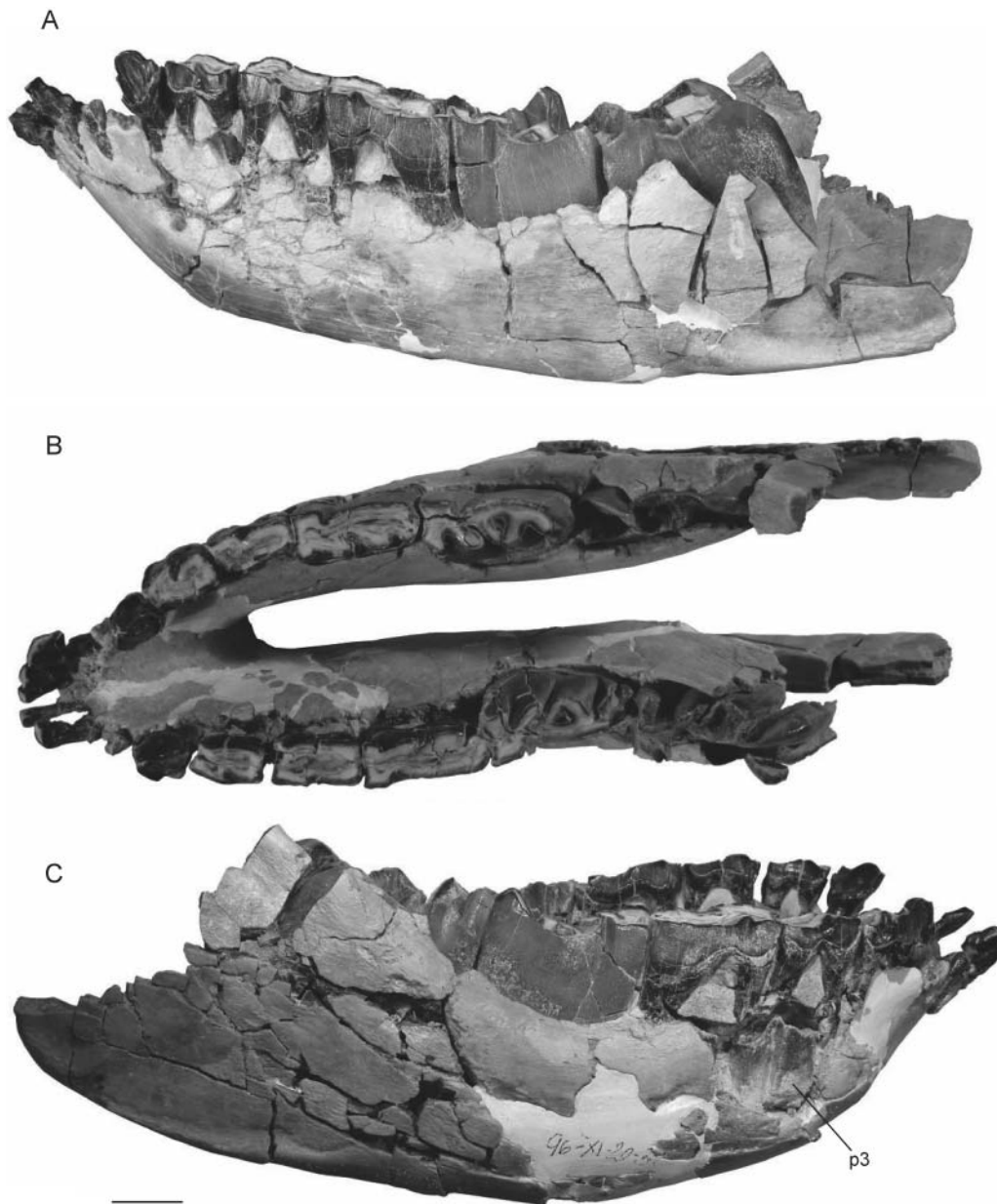

Figure 6. *Gualta cuyana* gen. et sp. nov. MLP 96-XI-20-3, juvenile mandible with right di1−3 (left di3 broken), canine roots and both series p1−d2−4−m1−2. **A,** left lateral view; **B,** occlusal view; **C,** right lateral view showing the permanent p3 below the dp3. Scale bar = 20 mm.

Table 3. Lower teeth dimensions (mm) of *Gualta cuyana* gen. et sp. nov. from Quebrada Fiera, Mendoza. PV corresponds to MCNAM material. Values in parentheses are approximate.

		di1		di2		di3		c	
	L	5.0	4.5	7.5	7.3	—	11.0	—	—
MLP 96-XI-20-3	W	6.4	6.1	7.1	7.7	—	6.9	—	—

		p1		p2		p3		p4		m1		m2		m3	
PV 3841	L					22.2	21.2	24.9	(25)	35.5	—	(42.2)	—	51.8	—
	W					19.6	17.8	23.3	—	23.0	—	22.6	—	24.7	—
				dp2		dp3		dp4							
MLP 96-XI-20-3	L	12.7	12.5	17.5	17.2	21.6	21.2	32.3	31.1	38.6	39.8	44.7	46.7	—	—
	W	12.8	12.6	13.6	14.0	14.7	>13	15.4	16.0	17.8	18.9	(11.2)	(13)	—	—

	Lp1−m2		Lp1−dp4		Lm1−m3
MLP 96-XI-20-3	167.2	171.0	81.0	87.0	
PV 3841					(126.5)

The p1 are barely worn, subtriangular but with similar maximal dimensions (Table 3). With respect to the trigonid, the talonid is reduced with only a crest. The trigonid valley is scarcely developed as a smooth, shallow lingual sulcus. A crest starts from the metaconid, posterolingually directed, which encloses a long, narrow posterior fossettid, also limited by the posterior cingulum. A strong labial fold also develops from the protoconid, which subdivides the labial wall. Labial and lingual cingula are strong. The deciduous teeth (dp2−4) are heavily worn, longer than wide, and the talonid length increases markedly from dp2 to dp4 (Fig. 6B; Table 3). All deciduous teeth present labial and lingual cingula. On dp2 and dp3, the labial fold directs backward, leaned against the talonid wall. The dp4 is more similar to the m1; the trigonid has a straight labial face, well separated from the talonid by a wide groove. Lingually, there are three grooves; the anterior one is hardly marked; the other two are on the talonid, one behind the metaconid (meta-entoconid fold) and forwardly directed, whereas the posterior groove (ento-hypoconid fold) is more transverse and shorter. The fractured mandibular bone allowed inspection of the tip of the p4 below the right dp4; as performed radiographic images did not provide good views of the permanent tooth, we removed a piece of bone and checked the presence of p3−4 in place (Fig. 6C). The m1 of MLP 96-XI-20-3 exhibits some degree of wear. Its lingual cingulum is low and strong (seen by the mandibular border); the labial cingulum is not observable. Beside the three lingual grooves commented for the dp4, m1 and m2 show a fourth shallower sulcus in the middle of the talonid that separates two convergent crests that fuse with wear enclosing an accessory fossettid (see Madden 1990; posterior fossettid in Ribeiro et al. 2010); they are fused in m1 (on the right m1, it would be 1 mm below the border) and in contact in m2, which is still unworn and hardly emerging from the bone. The anterior

fold becomes very shallow to the base of the crown. The slightly curved talonid directs backward, with rounded end. The lingual cingulum rises at this point, becoming smoother (observed on m1). Dimensions of the deciduous teeth (Table 3) are greater than those of the specimen from the Tremembé Formation described by Paula Couto (1983, p. 12).

MCNAM-PV 3841 (Fig. 7A, B; Table 3) includes two associated mandibular fragments, one with left p3−m3 and part of the symphysis, and another with right p3−m1 and a small fragment of m2. The posterior edge of the symphysis reaches the anterior level of p4. The horizontal ramus is relatively low, with little difference in height from p4 to m3 level (*c*. 69 mm at p4−m1 level, *c*. 68.8 mm at m2−3, and 92.5 mm behind m3); its transverse diameter varies from 34.5 mm (p4 level) to 38.4 mm (m2 level). According to data provided by Ribeiro et al. (2010, p. 172), the height of the horizontal ramus of the mandible is close to that of *Scarrittia canquelensis* (65 mm at the level of m1) and greater than that of *S. barranquensis* (54 mm) and *Leontinia gaudryi* (60−62 mm). However, Ubilla et al. (1994, table 1) included other higher values for both *S. canquelensis* and *L. gaudryi*, as well as for *Scarrittia robusta* Ubilla, Perea & Bond, 1994.

The p3−4 present a strong, backwardly directed labial fold in the trigonid, as in the described dp2−4. The p3 and p4 are relatively shorter than dp3−4 of MLP 96-XI-20-3 (Table 3). The lingual groove between trigonid and talonid is near to being closed in p3 whereas it has already formed a fossettid in p4, without traces of bifurcation as observed in other leontiniids (see character 34 in the phylogenetic analysis). Lingual and labial cingula are strong in premolars and molars. In the latter, the cingula develop along the trigonid and anterior part of talonid, fading on the posterior part. The meta-entoconid fold in molars is deep and anteriorly curved; a remnant of the accessory

Figure 7. *Gualta cuyana* gen et sp. nov. MCNAM-PV 3841, mandibular fragments with right p3−m1 (broken) and left p3−m3. **A,** occlusal view; **B,** lateral view. Scale bar = 20 mm.

fossettid is observable only on m2 (wear is advanced and occlusal surfaces are badly preserved); the m3 also shows the ento-hypoconid fold. Folds, fossettid and cingula of the lower cheek teeth are similar to those of *S. canquelensis* and *S. robusta*.

Vertebrae. As commented before, the skull MCNAM-PV 3951 was found associated with part of the vertebral column (Fig. 8A).

The atlas is rather complete, wide and short (Table 4); the wings are not very extended laterally (Fig. 8B, C). In ventral view, the two foramina appear close, but separated, in a single elongated fossa; their dorsal exit is instead totally independent; they would correspond to the transverse or intervertebral and the lateral foramina; a third foramen, dorsally observable and anterodorsally placed is the alar foramen.

The axis exhibits a relatively long, high odontoid process (dens) (Fig. 8D, E); its ventral surface is longitudinally slightly concavo-convex. The lateral facets for the atlas are sub-triangular in outline and smoothly convex. The spinous process is high, lacking the proximal border. It enlarges posteriorly and is short, not reaching the level

of the odontoid process. The articular posterior processes project backward, with the facets distally oriented. The transverse processes are missing, but it can be observed that they start close to the caudal facet and are slightly distally directed; before each process there is a well-developed transverse foramen. The vertebral body is long (Table 4), with a medial narrowing. The caudal articular facet is wide and low, slightly inclined forward.

An isolated axis fragment, MCNAM-PV 4361, preserving the odontoid process and part of the body, is comparable in morphology and size (odontoid process, 19.5 mm × 19.7 mm; anterior articulation: TD, 77 mm, H, 31.2 mm) to that of MCNAM-PV 3951.

The remaining cervical vertebrae are incomplete (Fig. 8A), lacking the spinous processes, which would not be very elevated. The vertebral body shortens from the third to the seventh vertebra (Table 4); it is first longer than wide, becoming wider than long on the fifth to seventh cervical vertebrae. The inclination of the cranial and caudal facets slightly diminishes through the series. They are quadrangular in outline, becoming more trapezoidal towards the last one. Cranial and caudal articular processes are close to the horizontal plane, the former slightly
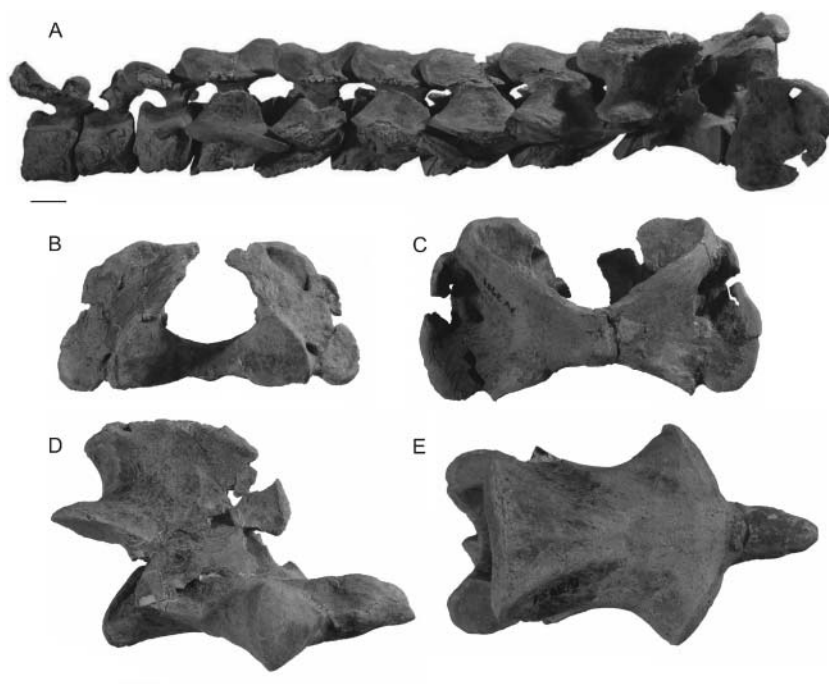
Figure 8. Vertebrae of *Gualta cuyana* gen. et sp. nov., associated with the skull MCNAM-PV 3951. **A,** 11 cervical and thoracic vertebrae in anatomical connection, dorsolateral view; **B, C,** atlas, posterior and dorsal views; **D, E,** axis, lateral and distal views. Scale bars = 20 mm.

medioproximally oriented, and the latter distolaterally oriented. The vertebral channel is large and rounded; there are two small foramina at its base (also present on the thoracic vertebrae). The preserved transverse foramina are circular.

Chaffee (1952) noted that the cervical vertebrae of *S. canquelensis* are exceptionally long, the neck being longer than the skull in contrast with the toxodontids *Nesodon* and *Adinotherium*, and the homalodotheriid *Homalodotherium*. For the specimen MCNAM-PV 3951, however, the anatomical length of the seven vertebrae is 387 mm, practically identical to the estimated total skull length (386 mm). Shockey *et al*. (2012, p. 25) stated that the neck of *Leontinia* would be shorter than that of *Scarrittia*, and the exceptional length would not be a general characteristic for leontiniids, which is now confirmed with the

Table 4. Dimensions (mm) of the vertebrae associated to the skull MCNAM-PV 3951 of *Gualta cuyana* gen. et sp. nov. from Quebrada Fiera, Mendoza. Values in parentheses are approximate.

Vertebrae	Atlas	Axis	3rd	4th	5th	6th	7th	T. 1st	T. 2nd	T. 3rd	T. ?
Maximal TD	129.2		78.5	77.6	83.0	—	85.6	—	—	—	59.1
Maximal APD	72.0	110.5	76.2	74.8	77.5	65.5	62.5	—	—	—	39.9
Maximal H	>64	—	—	—	—	—	—	—	—	>78	(63.5)
APD vertebral body		76.9	55.6	52.0	50.0	45.6	41.7	34.2	35.5	33.0	27.2
APD spinous process		(79)									14.3**
Max. TD spinous pr.		(30.4)									16.4
Axis dens		19 × 23.5									
Ant. TD artic. level	100.0										37.2
TD cranial facets	88.4*	72.9	45.0	46.0	46.0	44.1	44.7	(37)	39.4	35.5	26.5
H cranial facet	39.0	31.4	38.0	31.9	35.2	32.6	37.0	35.4	35.9	34.1	19.6
TD caudal facet	83.0	53.6	52.3	54.3	53.0	52.7	48.5	37.2	(35.5)	—	26.6
H caudal facet	35.1	32.9	33.1	34.3	34.5	35.6	34.8	34.6	33.9	35.2	20.0

*TD including both cranial facets of the atlas. **Depth at the base. T., thoracic.
Ant., anterior; artic., articular; Max., maximal; pr., process.

present material. The atlas described by Paula Couto (1983) from the Tremembé Formation has a smaller transverse diameter, but in the figure it appears to be relatively longer (APD) than our specimen (Table 4; Fig. 8C).

The three thoracic vertebrae of the anatomical series are rather incomplete. With respect to the cervical, the body and processes are short; the body becoming relatively higher (Table 4). The spinous process is developed, as well as the costal foveae. The transverse processes are short, blunt, and bear two costal foveae. A fourth thoracic vertebra appeared together with the former, but it is clearly smaller (Table 4), and does not match well with the third. Considering its small size and the posterior inclination of the spinous process, it could correspond to a more posterior thoracic vertebra (fifth to seventh) according to Chaffee's (1952) data. This author stated that the anterior thoracic vertebrae have a smaller and shorter centre than the posterior ones, and that the neural spine backward inclination increases from the third to the seventh vertebra, later decreasing to the vertical condition in the last three thoracic vertebrae.

Some incomplete vertebrae could pertain to the same taxon, particularly the cervical vertebral bodies MCNAM-PV 3996 and MCNAM-PV 3997, and the thoracic MCNAM-PV 3998.

Based on the skull, jaws and vertebrae, a life reconstruction of *Gualta cuyana* gen. et sp. nov. has been created (Fig. 9).

Appendicular skeleton. Among the great amount of isolated postcranial elements found at Quebrada Fiera, some can be assigned to leontiniids and are preliminarily considered to belong to the same species as the described skull.

MCNAM-PV 3938 is a very fragmented right humerus lacking the proximal epiphysis (Fig. 10A) that was recovered very near the skull, and MCNAM-PV 4376 is a complete right specimen (Fig. 10B−E). MCNAM-PV 4376 is a little smaller and more slender than MCNAM-PV 3938 (Table 5). It shows a large torsion between both epiphyses; the deltoid tuberosity is anteriorly directed, not laterally. The greater tuberosity (tuberculum majus) is also directed anteriorly and laterally, whereas the humeral head remains posteriorly placed. The lesser tuberosity

Figure 9. Life reconstruction of *Gualta cuyana* gen. et sp. nov. (created by Jorge Blanco).

(tuberculum minus) projects anteriorly but is placed medially to the head and is well separated from the greater tuberosity by a wide intertuber groove (sulcus intertubercularis). As a whole, the proximal epiphysis is massive, with a developed articular extension from the head to the greater tuberosity, also observed by Chaffee (1952, p. 538) in *S. canquelensis*. The transverse section of the shaft is elliptical at its greatest part (breakage level in MCNAM-PV 3938), transversely flattened with respect to the distal epiphysis; below the deltoid crest, the section becomes much smaller and triangular. The deltoid crest is little projected; it draws a sigmoid crest lateroanteriorly directed; its most lateral area appears as a wide, rugose, curved, grooved-crest that continues into the anterior crest (MCNAM-PV 3938 shows some discontinuity between both areas); both parts occupy more than a third of the

Table 5. Dimensions (mm) of the humeri of *Gualta cuyana* gen. et sp. nov from Quebrada Fiera, Mendoza. Values in parentheses are approximate.

	L	Head		Prox. ep.		Deltoid tub.		Diaphysis		TD max. dis.	Dis. artic.	
		TD	APD	TD	APD	TD	APD	TD	APD		TD	APD
PV 3938	> 386*	—	—	—	—	49.1	(86)	53.0	(63)	136.0	90.0	71.5
PV 4376	398	84.3	74.0	114	141	39 .0	83.6	(53.5)	54.8	121.5	92.0	65.8

*without proximal epiphysis, probably over 400 mm
artic., articular; max., maximal.

Figure 10. *Gualta cuyana* gen. et sp. nov. **A,** MCNAM-PV 3938, incomplete right humerus, anterior view; **B–D,** right humerus MCNAM-PV 4376, posterior, anterior and lateral views; **E, G,** calcaneum MCNAM-PV 3916, anterior and lateral views; **F, H,** calcaneum MCNAM-PV 4283, anterior and lateroposterior views. Scale bars = 20 mm.

humeral length. In the distal epiphysis there is no foramen connecting the coronoid and olecranian fossae, although the bone in this zone is very thin and it is broken off almost completely in MCNAM-PV 3938. The coronoid fossa is shallow and rugose (observed on MCNAM-PV 4376); the radial fossa is smaller and deeper, placed above the capitulum. The olecranian fossa is very deep and relatively narrower in MCNAM-PV 3938 than in MCNAM-PV 4376. The whole distal articulation (capitulum and trochlea) forms a slightly inclined surface with respect to the vertical axis of the bone. The medial border of the trochlea is acute and much more developed than the lateral border. The capitulum is slightly different between the specimens. It is more laterally elongated in MCNAM-PV 4376, where it appears transversely concavo-convex,

but regularly convex in MCNAM-PV 3938. The lateral epicondyle is slightly projected and continues proximally as a smooth lateral supracondylar crest; the medial epicondyle forms an acute crest but is not very projected medially; there is no supracondylar foramen. Dimensions of these specimens are smaller than those provided by Chaffee (1952, table 18) for *Scarrittia canquelensis* but greater than those of *Leontinia gaudryi*.

MCNAM-PV 3916 and MCNAM-PV 4283 are two right robust calcanei, with strongly wrinkled areas of ligamentary insertion (Fig. 10A–D; Table 6). Their tuber calcis is wide, short in APD, and posteromedial–anterolaterally oriented. In lateral view, the fibular facet forms a detached, regular convexity proximodistally directed; it is wider proximally than distally. The flattened ectal facet for the

Table 6. Dimensions (mm) of calcanei of *Gualta cuyana* gen. et sp. nov. from Quebrada Fiera, Mendoza. Values in parentheses are approximate.

Calcaneum MCNAM	H	Tuber TD APD	TD sust.	Maximal APD	Distal artic. APD TD	Maximal Distal TD	Minimal posterior TD
PV 1916	97.1	42.0 44.8	>43	53.5	— —	—	31.5
PV 4283	102.2	43.0 (48.9)	(49.5)	55.8	39.0 30.2	39.0	—

sust., sustentaculum.

astragalus (better preserved on MCNAM-PV 4283) is medially oriented; it is relatively small, rounded, slightly convex, and more proximally placed than the fibular facet. The sustentaculum is short, and bears a flattened astragalar medial facet whose proximodistal dimension is greater than its transverse diameter. A deep, vertical sulcus separates the sustentaculum from the ectal facet. The distal area is broad and the cuboid facet extends on the posterior face; this facet is not well preserved, but it is wide, little concave and very inclined. Both the sustentacular facet and the cuboid facet are more flattened than in *Scarrittia canquelensis* (Chaffee 1952) and the cuboid facet is more inclined posteriorly; the general outline of the bone is closer to the calcaneum of *Elmerriggsia* in having a shorter neck, wider tuber and less developed sustentaculum (Shockey *et al.* 2012, fig. 7). There is no facet for the navicular, which differentiates the studied calcanei from other leontiniids such as *Scarrittia*, *Leontinia* and *Taubatherium*; the presence of a calcaneonavicular articulation has been considered as an 'advanced toxodont' trait of leontiniids, shared with notohippids and toxodontids (Shockey *et al.* 2012).

There is no complete metapodial to be confidently referred to leontiniids. However, MCNAM-PV 3871 is a distal fragment very similar to those of AMNH 29582 of *S. canquelensis*. It shows a smooth keel on the posterior part of the trochlea; the anterior face has a very convex border surrounded by a marked depression. The epiphysis does not enlarge much above the articulation. A similar fragment is MCNAM-PV 4123, but this is much eroded.

Other postcranial bones (e.g. MLP 77-VI-1-12, distal fragment of femur; MLP 77-VI-1-14 and 15, proximal fragments of tibiae; and MLP 77-VI-1-19, distal fragment of metapodial) from Quebrada Fiera have been catalogued as possible leontiniids, but it is difficult to determine their accurate affinities at this moment, considering the presence of other large toxodontians (homalodotheriids and toxodontids) and the lack of detailed descriptions or associated bones. A comparative study on postcranial elements from this locality is planned for the future.

Phylogenetic analysis

The pioneering phylogenetic analysis for Leontiniidae was performed by Cifelli (1993). This author and later Villarroel & Colwell Danis (1997) and Shockey (2005) based their studies on dental characters at the generic level. Recently, Shockey *et al.* (2012) presented a more complete analysis for leontiniids, evaluating the group at the species level and incorporating postcranial characters for the first time. Based on the latter analysis we evaluated the phylogenetic position of the new taxon within Leontiniidae.

Concerning characters used by Shockey *et al.* (2012) and their codification in *Gualta cuyana*, some comments are needed. Character 12: the relative height of M1 was inferred from the height of the less worn M2, resulting in a mesodont tooth. Character 21: the lingual groove on premolars is only observed on P3 and P4, not in P2, but it is codified as present (21^1). Character 22: the protoloph ridge is present on P2 and it is low in P3 and P4, in a similar way to *Anayatherium* and *Leontinia*. Character 27: the presence of a posterior fossette on upper molars is observed in M2, but not in M1 where it was possibly at a higher level of the crown and has consequently disappeared by wear. Character 32: the only specimen with premolars, MCNAM-PV 3841, does not show any trace of metaflexid bifurcated, in contrast for instance with the specimen FMNH-P 13384 assigned to *Leontinia*. In addition, we detected an error in the character states of characters 16 and 21 and their corresponding codification: two states in the list and three states in the matrix, and vice versa (Shockey *et al.* 2012); as a consequence, they were eliminated from our analyses. The data matrix and the list of characters, almost the same as in Shockey *et al.* (2012), are provided in the Online Supplemental Material.

Our analysis under equal weights recovered 315 equally parsimonious cladograms (L: 156, CI: 0.62, RI: 0.76), while applying weights (k: 3−100) the search yielded 10 trees for all the explored k-values. The majority consensus trees of each case are shown in Figure 11. In both topologies, the Leontiniidae form a monophyletic group (Fig. 11A, B, nodes 5 and 4, respectively), whereas the Notohippidae results in a paraphyletic assemblage in the analysis under implied weights (Fig. 11B, nodes 2 and 3). Regarding Leontiniidae, both topologies present substantial differences.

Under equal weights (Fig. 11A), there is a large polytomy (node 5) that includes two minor clades: one of these groups the Miocene genera *Huilatherium* and *Colpodon*

Figure 11. Consensus trees from the phylogenetic analyses of Leontiniidae: **A,** under equal weights; **B,** under implied weights.

(node 6), and the other (node 7) includes *Leontinia gau-dryi* as the sister group of a more inclusive clade (node 8) formed by *Gualta cuyana*, the species of *Anayatherium* and *Scarrittia canquelensis*. The relationships of both these taxa and the other Palaeogene leontiniids are poorly resolved (nodes 5 and 7).

In the analysis using implied weights, the two species of the Miocene genus *Colpodon* form a clade (Fig. 11B, node 5) as the sister group of the remaining leontiniids (node 6). In this clade, the other Miocene taxon, *Huilatherium pluriplicatum*, appears basal to the Palaeogene leontiniids (node 7). Node 7 shows *Gualta cuyana* as the sister group of a more inclusive clade (node 8), which includes the species of *Anayatherium* and *Scarrittia canquelensis* forming a polytomy with a monophyletic group (node 9) integrated by Deseadan and Mustersan taxa gathered into two clades: *L. gaudryi* and *A. frequens* on the one hand, and (*T. paula-coutoi*, *M. fernandezi* (*E. fieldia*, *C. bondi*)) on the other hand. The result of this second analysis implies an incongruity between the phylogenetic hypothesis and the temporal record of the taxa. Nevertheless, the obtained topologies show that the phylogenetic relationships among Leontiniids are still poorly resolved; a more exhaustive analysis is required, taking into account their palaeobiogeographical and biostratigraphical distributions.

Discussion

The best-known leontiniid is *Scarrittia canquelensis*, described in detail by Chaffee (1952). Even though there are clear similarities with this species, the leontiniid from Quebrada Fiera exhibits distinctive characters that allow its recognition as a new taxon. After Chaffee (1952) and the revised diagnosis of *Scarrittia* presented by Ribeiro *et al.* (2010, p. 171), *Gualta cuyana* shares most characters, but differs in the presence of a lingual sulcus on P2−4, which nevertheless is slightly developed. The diagnostic feature 'small I2' and Chaffee's (1952) description indicate the I2 as the smallest upper tooth, as a simple cone, but this is not so evident in our specimens, where the I2 is rather similar to I3 and canine; in fact, the length of I2 in MCNAM-PV 3951 is slightly greater than that of I1 and little shorter than I3 (Table 2). Concerning the I1 of *G. cuyana*, it is not really as much developed as Chaffee (1952) described for *Scarrittia*: greatly enlarged into a caniniform tooth, greater than the I2 of *Leontinia*. However, the specimen AMNH 29613 of *S. canquelensis* (Chaffee 1952, table 10) shows similar dimensions to the studied first incisors, which detach from the I2−3 mainly by their higher crown. In this sense, our taxon is closer to *Scarrittia* or *Anayatherium* than to *Leontinia* that has the I2 developed as a tusk (ACM 3290; Loomis 1914). At the same time, the completeness of the dental series of the new taxon precludes assignment to taxa such as

Ancylocoelus or the Miocene *Colpodon*. The canine overlapping P1 is present in *Scarrittia canquelensis*, whereas the presence of lingual sulcus on P3−P4 is shared with *S. barranquensis*, *Leontinia*, *Anayatherium* and *Elmerriggsia*, although these taxa have a much deeper sulcus.

Some features of the skull are also different from *Scarrittia canquelensis*. In this species, nasals are described as broad and thick (Chafee 1952, p. 531), whereas MCNAM-PV 3951 has narrow nasals and a more slender rostrum, not as shortened as in *S. canquelensis*: the length orbit−premaxillary tip represents 25% of the total skull length in this species (Chaffee 1952, fig. 5), whereas it is 35.4% in our specimen. Concerning the postcranial skeleton, the cervical vertebrae reflect a shorter neck than in *S. canquelensis*. The humerus of *S. canquelensis* described but not figured by Chaffee (1952) is roughly coincident with the studied specimens. However, according to this author, the olecranian fossa is not deep, which does not agree with our description. The calcanei are similar to that figured by Chaffee (1952, pl. 11) and to left calcaneum AMNH 29585 of *S. canquelensis*, but the general outline is closer to the smaller calcaneum of *Elmerriggsia fieldia* figured by Shockey *et al.* (2012), mainly by the shorter neck and more medially projected tuber.

The phylogenetic analyses under equal and implied weights provide two poorly resolved consensus trees, which show differences regarding the relationships among leontiniids. In the analysis using equal weights, *Gualta cuyana* appears more related to the species of *Anayatherium* and *Scarrittia canquelensis* (*Anayatherium* and *Scarrittia* are sister taxa in the analysis of Shockey *et al.* [2012], but not in Shockey [2005]), whereas applying weights *Gualta cuyana* appears as the sister group of a greater monophyletic clade including all the remaining Palaeogene leontiniids, which implies a conflict between the obtained phylogenetic hypothesis and the chronological distribution of several species.

Conclusion

The new leontiniid described for the Quebrada Fiera locality adds to other endemic taxa identified in this Deseadan site, such as *Mendozahippus fierensis* (Notohippidae; Cerdeño & Vera 2010, 2014), *Fieratherium sorex* (Metatheria; Forasiepi *et al.* 2014), *Prohegetotherium malalhuense* (Hegetotheriidae; Cerdeño & Reguero in press), *Asmodeus petrasnerus* (Homalodotheriidae; Seoane & Cerdeño, 2014) and other still unpublished taxa preliminarily considered to represent new species among rodents (Cerdeño 2011) and toxodontids (Hernández Del Pino *et al.* 2013).

Gualta cuyana gen. et sp. nov. reinforces the peculiarity of this mammal fauna from Mendoza, and also provides evidence of the affinities with taxa from both higher and

lower latitudes, i.e. Patagonia and Bolivia, respectively. This is a characteristic of the mammal assemblage that has been previously interpreted as reflecting an area of contact between two palaeobiogeographical areas (Cerdeño & Vera 2010; Cerdeño *et al.* 2010).

The leontiniid remains recovered from Quebrada Fiera are still relatively uncommon, representing around 6% of the notoungulate material identified at the family level (small postcranial bones excluded from this count), in contrast, for instance, with the 25% reached by hegetotheriids (Cerdeño & Reguero in press). This low proportion of leontiniids is closer to their representation in Salla (Bolivia) than to that in Patagonia, where *Scarrittia canquelensis* and *Leontinia gaudryi* are the most common taxa in localities such as Scarritt Pocket and Cabeza Blanca or La Flecha, respectively (Chaffee 1952; Shockey *et al.* 2012). *Taubatherium* is also the best-represented mammal in the Tremembé Formation (Soria & Alvarenga 1989). A higher diversity of leontiniids also occurs in the Deseadan levels of Patagonia, but no more than two species are coeval at the same site (Ribeiro *et al.* 2010).

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Supplemental data

Supplemental material is available online http://dx.doi.org/10.1080/14772019.2014.982727.

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