

NEW LEONTINIDIDS (CLASS MAMMALIA, ORDER NOTOUNGULATA, FAMILY LEONTINIIDAE) FROM THE SALLA BEDS OF BOLIVIA (DESEADAN, LATE OLIGOCENE)

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A revised diagnosis of the Leontiniidae (Class Mammalia, Order Notoungulata) is provided and leontiniids of the Deseadan South American Land Mammal “age” (SALMA; late Oligocene) are summarized. Two new species of leontinids from the Deseadan Salla Beds of Bolivia are described and placed within the new genus, *Anayatherium*: the smaller *A. ekecoa* and a much larger *A. fortis*. A phylogenetic analysis suggests that these species are closely related to the derived Patagonian genera *Ancylocoelus* and *Colpodon*, with the loss of the canine serving as a putative synapomorphy uniting these taxa. Although leontiniids are the most frequently encountered taxa at many other Deseadan localities, they are exceedingly rare at Salla. This scarcity, the scarcity of other ungulates with low crowned cheek teeth, and the heavy tooth wear of a relatively young individual of *A. ekecoa* suggest that ungulates with low crowned teeth were at a selective disadvantage at Salla.

Key Words: Notoungulata; Leontiniidae; Salla; Deseadan; new taxa

INTRODUCTION

The Deseadan (late Oligocene) South American Land Mammal “Age” (SALMA) has been of considerable interest to students of South American paleontology for over a century. This interest has been stimulated by the great diversity of Deseadan mammals, including the “immigrant” taxa, rodents and monkeys (Ameghino 1895, 1897; Gaudry 1906; Loomis 1914; Hoffstetter 1968, 1969; Patterson & Pascual 1972). Historically, the massive *Pyrotherium* and leontiniids have served as “guide fossils” to indicate Deseadan horizons. These large mammals were the most conspicuous faunal elements for the early students of the Deseadan (Ameghino 1895, 1897; Gaudry 1906; Loomis 1914; Simpson 1934).

Salla (pronounced sál-ya by the local Aymaran Indians), Bolivia contains Deseadan beds that have received much attention in the last 30+ years. This is due largely to the discovery of the primate *Branisella* (Hoffstetter 1969), the earliest known of monkey in South America, as well as Salla’s diverse fauna of marsupials, rodents, and ungulates (see faunal list in Shockey 1997a). Fortuitously, Salla is interbedded with several layers of volcanic ash which have helped to firmly establish the Deseadan as being late Oligocene (MacFadden et al.

1985; Kay et al. 1998) rather than early Oligocene (Simpson 1933) or much older (Cretaceous per Ameghino 1895, 1897). Salla records about 40 species of mammals in over 25 families from 8 or 9 orders of mammals (Shockey 1997a).

Leontiniids were medium-sized to large notoungulates, known from the Mustersan SALMA (Bond & Lopez 1995; early Oligocene, see Kay et al. 1999) to the middle Miocene of La Venta, Colombia (Villarroel & Colwell Danis 1997). Their greatest diversity was, by far, in the Deseadan SALMA, where five genera are here regarded as valid (see also Simpson 1945; McKenna & Bell 1997). Although leontiniids are common members of many Deseadan faunas of Patagonia (e.g., La Flecha [Ameghino 1895; Gaudry 1906], the locality now known as Cabeza Blanca [Ameghino 1897; Loomis 1914] and Scarritt Pocket [Chaffee 1952]) and of the tropical Tremembé Formation of Brazil (Soria & Alvarenga 1989), they are remarkably uncommon at Salla. The two specimens described below, however, are complete enough to greatly improve our understanding of the leontiniids of Salla. Prior to this work, only fragmentary remains had been noted in published accounts of Salla.

In his first publication regarding Salla, Hoffstetter (1968) mentioned the probable presence of leontiniids there, but noted that the remains were rare and too frag-

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mentary to rule out the possibility that they were homalodontotheriids. Hoffstetter (1976) noted the absence of homalodontotheriids on a revised faunal list and gave *Henricofilholia* as the genus of leontiniid present. MacFadden et al. (1985) did not include leontiniids on their faunal list, but mentioned leontiniid genera (i.e., *Henricofilholia*, *Leontinia*, and *Ancylocoelus*) in their discussion of isotemniids, suggesting that these leontiniid genera were erroneously considered to be isotemniids.

Subsequent to Hoffstetter's expeditions to Salla, teams led by Bruce J. MacFadden of the University of Florida, in collaboration with GEOBOL (Servicio Geológico de Bolivia, La Paz, Bolivia), and Masanaru Takai of the Primate Institute of Kyoto, Japan, in collaboration with Federico Anaya, then with the MNHN-Bol, have recovered material that permits a much-improved understanding of leontiniids of Salla. This present work describes two specimens, each representing a new species referred to the new genus, *Anayatherium*.

MATERIALS, METHODS, ABBREVIATIONS

Specimens of leontiniids were studied in the following collections (given with their abbreviationst): **UATF**, Universidad Autónoma "Thomas Frias", Postosí, Bolivia, **MNHN-Bol**, the department of paleontology, Museo Nacional de Historia Natural, La Paz, Bolivia; **UF**, Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.; **AMNH**, the American Museum of Natural History, New York, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; and **ACM**, the Pratt Museum at Amherst College, Amherst, Massachusetts, U.S.A.

Dental terminology follows the convention of using upper case letters for the upper incisors, canines, premolars and molars (i.e., I, C, P, M) and lower case for the lower series. Deciduous teeth are prefixed with "d."

The phylogenetic position of *Anayatherium* was estimated by evaluating its characters in terms of those defined by Villarroel and Colwell Danis (1997) for their recent phylogenetic analysis of the Leontiniidae. Only the characters (1-14) regarding the upper teeth could be scored for *Anayatherium* since the lower jaws and teeth remain unknown. Typographic errors of Villarroel & Colwell Danis (1997) were corrected (character scores of "3" were printed, but were not defined). This revised taxon/character matrix, with *Anayatherium* and its character scores added, was analyzed in PAUP, version

4.0b10. An "exhaustive search" was employed to generate hypothetical phylogenetic trees. The most parsimonious hypothesis is reported and discussed.

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth 1903

Suborder TOXODONTIA Owen 1853

Family LEONTINIIDAE Ameghino 1895

Revised Diagnosis.—Brachydont to mesodont Toxodontia with reduced canines. Canines incisiform or absent. Tendency for enlargement of an upper incisor to caniniform or tusk-like form. Molar protoloph much greater length than metaloph. Anteroposteriorly oriented median valley containing simple cristae, forming small fossettes in some species. Lingual wall of molar ectoloph with longitudinal grooves, obscured early with wear. Third lower incisor enlarged or caniniform. Broad, robust entolophid of molars containing early-formed fossettid that is not the result of a union of entolophid and hypolophid. Hypolophid of m1-2 less than half the total length of the talonid (diagnosis modified after Chaffee 1952).

Discussion.—Florentino Ameghino (1895) honored his wife Leontina by naming the genotype of this family *Leontinia* (see Simpson 1948). In the same publication he also named three other genera of leontiniids, *Ancylocoelus*, *Rodiotherium*, and *Loxocoelus*, the latter two of which were represented by mere fragments. Three species of *Leontinia* were named in this first paper regarding the Deseadan (Ameghino 1895): *Leontinia gaudryi*, *L. lapidosa*, and *L. garzoni*. *Leontinia gaudryi* is regarded as the type for the genus, whereas *L. lapidosa* was based on a mandibular fragment with a single molar from an animal about the same size as *L. gaudryi*. Loomis regarded *L. lapidosa* as a junior synonym of *L. gaudryi*. *Leontinia garzoni*, however, is clearly differentiated from *L. gaudryi* by its distinctly small size, but was considered indistinguishable from *Ancylocoelus frequens* Ameghino 1895 by Patterson in his unpublished catalog of the Ameghino collection in the MACN. Ameghino's initial description of the family was based on somewhat fragmentary material, leading him to erroneously report that *Leontinia* lacked canines and that the caniniform incisors were I3 and i3. After receiving and studying superior material of *Leontinia* spp. collected by his brother Carlos at Cabeza Blanca, he corrected these errors (Ameghino 1897), noting that the caniniform incisors were I2 and i3 and that *Leontinia* had both upper and lower incisiform canines. In this

Table 1. Synonymy of Deseadan leontiniids based on Loomis (1914), Chaffee (1952), Patterson's unpublished catalog, and this study.

Anayatherium gen. nov.

Anayatherium fortis sp. nov.

Anayatherium ekecoa sp. nov.

Ancylocoelus Ameghino 1895

Ancylocoelus frequens Ameghino 1895 (= *Henricofilholia inaequilatera*, Ameghino 1901 = *Leontinia garzoni* Ameghino 1895 = *Rodiotherium armatum* Ameghino 1895)

Leontinia Ameghino 1895

L. gaudryi Ameghino 1895 (= *L. lapidosa* Ameghino 1895 = *L. oxyrhyncha* Ameghino 1897 = *L. stenognatha* Ameghino 1897 = *L. fissicolis* Ameghino 1897)

Scarrittia Simpson 1934

S. canquelensis Simpson 1934

S. robusta Perea & Bond 1994

Taubatherium Soria & Alvarenga 1989

T. major Soria & Alvarenga 1989

T. paulacouttai Soria & Alvarenga 1989

second work on the Deseadan (Ameghino 1897), Ameghino named three additional species of *Leontinia*, all of which were the same size as *L. gaudryi*.

Loomis (1914) synonymized several species in four genera of leontiniids, regarding these as *Leontinia gaudryi*. Based on his large sample of leontiniids from Cabeza Blanca (the most commonly encountered animal there), he inferred that there was but one sexually dimorphic species, regarding those with large caniniform incisors as being males and those with smaller ones (*L. oxyrhyncha* Ameghino 1897) females. He believed that the sexual dimorphism and changes in the appearance of the teeth that occur with wear accounted for much of the variation seen within this species.

Soon after the discovery of Scarritt Pocket, Simpson (1934) named and hastily described the "most common quarry species" from that locality. Without adequate explanation, he designated "a specimen not collected and now unidentifiable (Simpson 1934: p. 2)" as the holotype for *Scarrittia canquelensis*, despite the fact that many specimens were at hand, though unprepared. In naming *Scarrittia*, Simpson (1934) did not

closely compare it to *Leontinia*. Of it he wrote that "there is no reasonable possibility of very close relationship" (Simpson 1934: 2), but indicated that it was similar in the reduction of the canine and "some other details" which he did not specify. He believed that *Scarrittia* was closest to *Henricofilholia*, but did not indicate which species (species then referred to *Henricofilholia* are now referred to both *Astrapotheria* and *Leontiniidae*; see below) but tentatively referred *Scarrittia* to the *Leontiniidae*.

Chaffee (1952) revised the diagnosis of *Scarrittia* and indicated that it was "very close to *Leontinia*" (1952: 517) differing only in that it was the I1 of *Scarrittia* that was caniniform, its lower incisors were more procumbent, and P2-4 lacked lingual grooves on the protocones. He proposed an informal grouping of these two genera and suggested that *Scarrittia* may be found to be a subgenus of *Leontinia*.

The poorly known and poorly defined genus, *Henricofilholia* Ameghino 1901 should be discussed since it has appeared on faunal lists of Salla as a leontiniid (Hoffstetter 1976) and as an isotemnid (MacFadden et

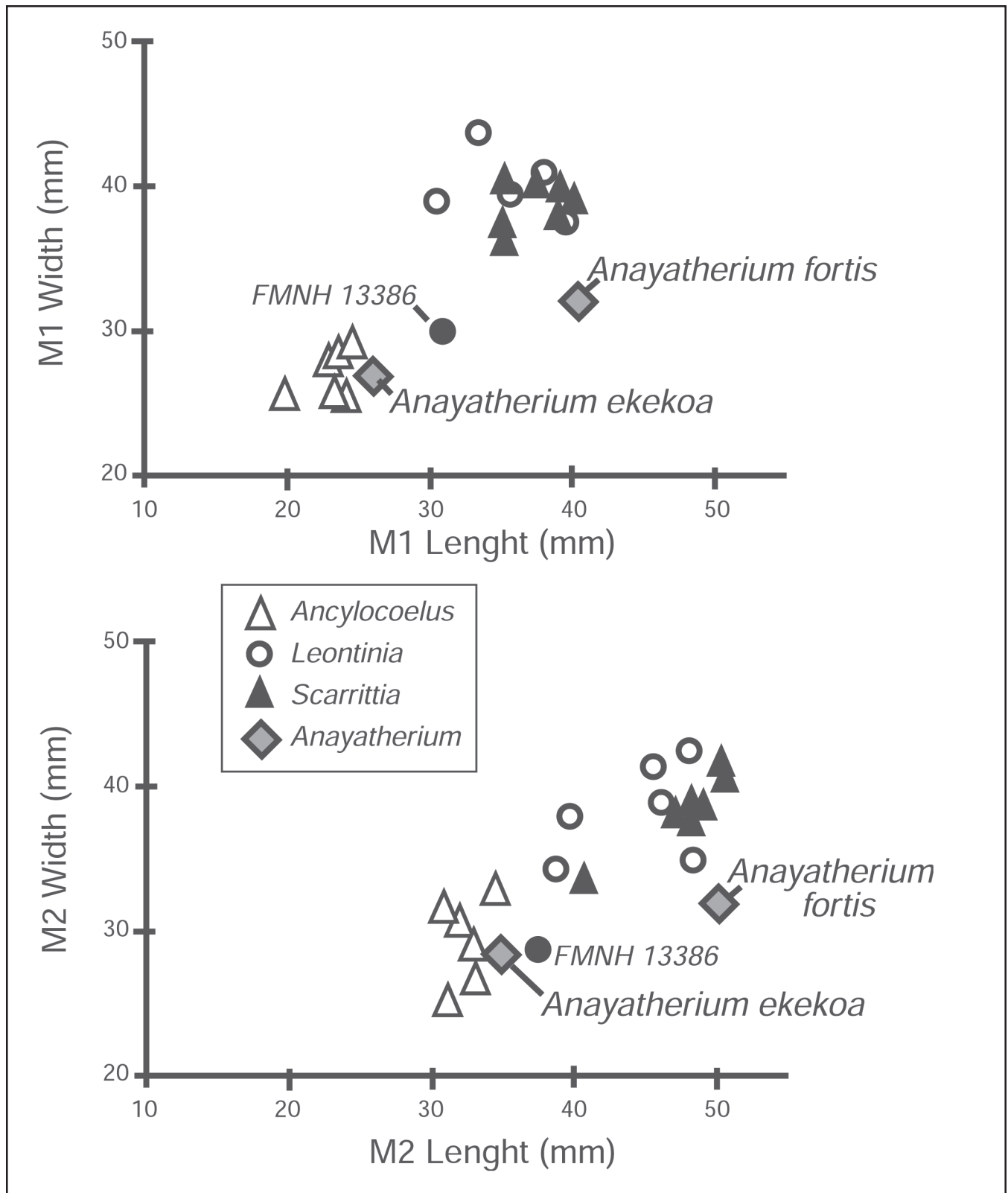


Figure 1. Molar dimensions (widths vs. lengths of M1 and M2) of selected Deseadan leontiniids.

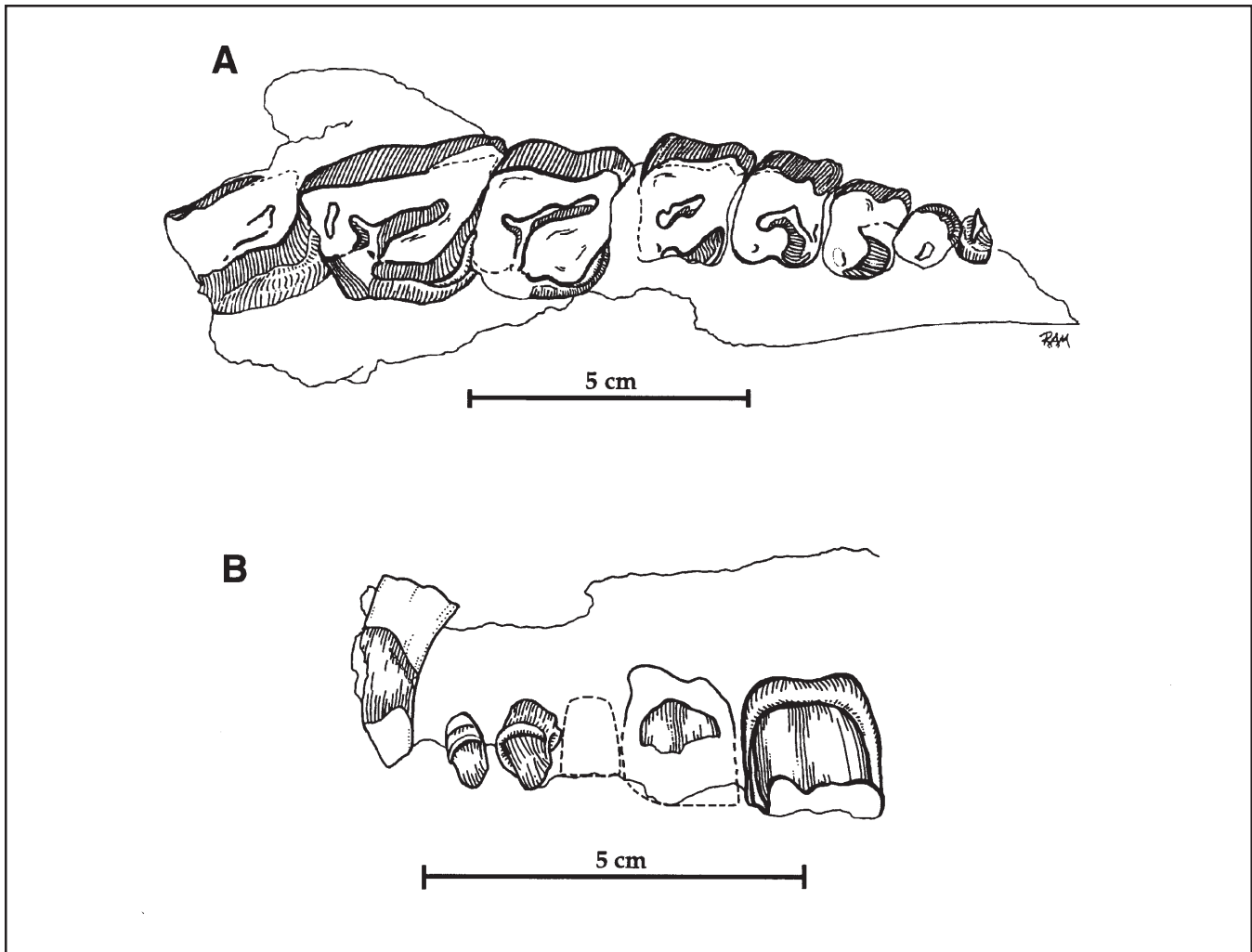


Figure 2. Views of the holotype of *Anayatherium ekecoa* n. gen. & sp. (MNHN-Bol-V-5521). A, occlusal view of right I3 (or C?), P1 – M3 and B, lateral view of left rostrum, I1, I2, I3?(or C), position of P1 (not preserved), and P2-3.

al. 1985). The genus was based largely on inadequate type material and the resulting chaos illustrates the futility of naming fragmentary remains (see also Pascual 1965). *Henricofilholia* (Ameghino 1901) was first applied to *?Parastrapotherium cingulatum* Ameghino 1894, with Ameghino explicitly designating *?Parastrapotherium cingulatum* as the type species for *Henricofilholia* (Ameghino 1895). He simultaneously named two new species of *Henricofilholia*, all of which he considered as belonging to Order Astrapotheria Lydekker 1894.

Later, Ameghino (1904b) indicated that *Henricofilholia* was closer to *Colpodon* than *Astrapotherium* and included it among the Leontiniidae. Though he clearly stated in the text that he placed the

genus in the Leontiniidae, the heading was erroneously printed as “Isotemnidae.” This “typo” is the apparent source of erroneous assignment of *Henricofilholia* to Isotemnidae by later workers (i.e., Loomis 1914; MacFadden et al. 1985). Ameghino’s inclusion of *Henricofilholia* (and *Colpodon*) in the Leontiniidae was tentative as he added that the definitive allocation depended upon the familial placement of *Colpodon*. This “colocación definitiva” appeared soon after (Ameghino 1906) and *Henricofilholia* was placed in the Colpodontidae which in turn was included in the order Hippoidea. Hippoidea was composed of “colpodontids”, notohippids, and equids.

With one exception, species of *Henricofilholia* were based upon one or two isolated teeth. Chaffee

Table 2. Dimensions (in mm) of upper teeth of the holotypes of *Anayatherium fortis* and *Anayatherium ekecoa*, two new species of leontiniids from Salla, Bolivia.

		<i>Anayatherium fortis</i> n. sp. UATF-V-00134	<i>Anayatherium ekecoa</i> n. sp. MNHN Bol-V- 5521
I1 (alveolus)	breadth	10.0	————
	depth	13.2	————
I2 (alveolus)	breadth	8.3	————
	depth	8.0	————
P1	length	————	11.1
	width	————	12.5
P2	length	————	12.1
	width	————	18.0
P3	length	21.7	15.3
	width	28.0	21.0
P4	length	(22.5)	16.8
	width	————	22.6
M1	length	39.4	24.8
	width	32.3	28.3
M2	length	48.2	34.7
	width	36.4	30.5

(1952) regarded *H. intercincta* and *H. lemoinei* as synonyms for *Parastrapotherium ephebicum*, an astrapothere, not a notoungulate. Other species of *Henricofilholia* are based on such inadequate type material that they are best ignored. The exception is *Henricofilholia inaequilatera* Ameghino 1901, which is based upon a nearly complete cheek-tooth row (MACN A 52-528, P2-M3; Ameghino 1904a:fig 466). It is indistinguishable from the leontiniid *Ancylocoelus frequens*, showing the same suite of characters seen in *A. frequens* and is well within the size range of this

species (Fig.1). Bryan Patterson regarded *Henricofilholia inaequilatera* as a junior synonym of *A. frequens* in his 1952 unpublished catalog of specimens in the Ameghino Collection.

Summary and revision of Deseadan species of leontiniids recognized in this work are presented in Table 1. Villarroel and Colwell Danis (1997) presented a recent and credible phylogentetic analysis of leontiniid genera. Synapomorphies for the Leontinidae suggested by the phylogenetic analysis include 1) hypertrophied i3 and 2) demarcated “leontiniid basin” (sensu Villarroel &

Colwell Danis 1997) of the upper premolars.

***ANAYATHERIUM* n. gen.**

Type Species.—*Anayatherium ekecoa* n. gen. & sp.

Referred Species.—*Anayatherium fortis* n. gen. & sp.

Generic Diagnosis.—Snout short, with corresponding loss of an anterior upper tooth; apparently, but not definitely, the canine. I1 greater than I2. P3-P4 with vertical, lingual grooves (as in *Leontinia*), but indistinct or lacking in P2. Differs from *Leontinia* by incisiform, rather than caniniform, I2 and apparent loss of canine. Like *Scarrittia*, I1 is larger than I2, but differs from *Scarrittia* by presence of the grooved premolar protocones.

Geographic and Temporal Range.—Two species of *Anayatherium* are described below. *Anayatherium ekecoa* is from Unit 5 of Salla, immediately below the carbonate layer that underlies the *Branisella* level, and *A. fortis* is from the geologically older Unit 2. The best fit of paleomagnetic horizons to those containing radioisotopically dated ashes of Kay et al. (1998) would place the paleomagnetic horizon from which the holotype of *A. ekecoa* came as being in C8n.2n, between 25.99 and 26.55 (Kay et al. 1998). The holotype of *A. fortis* is from Unit 2, regarded as being Chron 10n.2n (Kay et al. 1988), which has an age of about 28.6 Ma (Berggren et al. 1995). *Anayatherium* is only known from Salla, Bolivia.

Etymology.—A tribute to Federico Anaya Daza, for his heroic efforts to advance the science of paleontology in Bolivia.

***ANAYATHERIUM EKECOA* n. sp.**

Holotype.—MNHN Bol V-005521 (cast, UF 177203), upper dentition within fragmentary maxillae and premaxillae containing left I1-I3 and P1-M3 and right I3 (or C?) - M3 and complete upper left dentition (Fig. 2; Table 2).

Diagnosis.—Considerably smaller than *Anayatherium fortis*, *Leontinia gaudryi*, and *Scarrittia canquelensis*. Similar size to *Ancylocoelus frequens*, but distinct from *Ancylocoelus frequens* by the presence of grooved protocones of P3-P4, and the lack of well-defined and persistent trista that gives the branched appearance to the major fossette of the upper molars of *A. frequens*.

Type Locality.—The holotype was found at Tapial

Pampa in the Salla Beds in Unit 5, just below the El Planimiento (a carbonate horizon that immediately underlies the *Branisella* Level of Unit 5). The holotype was found during a MNHN-Bol expedition sponsored by Masanaru Takai of the Primate Institute of Kyoto, Japan. The holotype of *A. ekecoa* is the only known specimen.

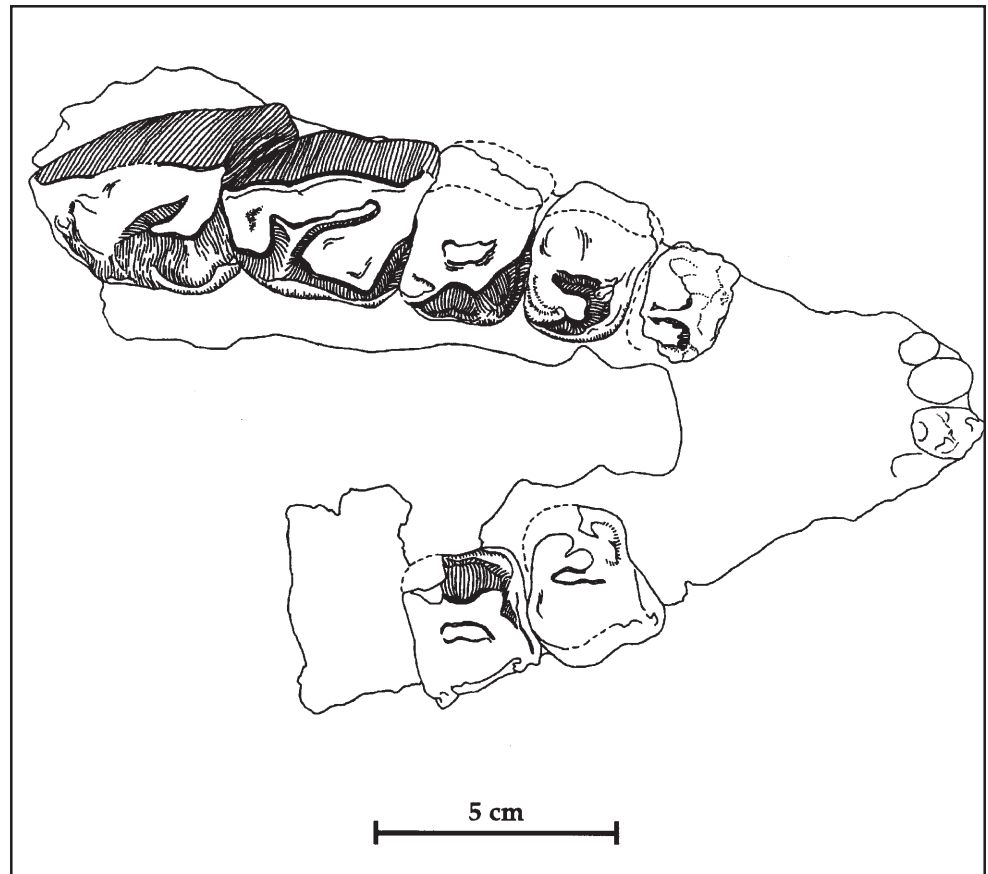
Etymology.—After *Ekeco*, a diminutive deity to whom Aymaran people give miniature offerings. This is in reference to the small size of the animal and to the geographic location of the type locality, now occupied by Andean Native Americans.

Description.—The holotype, MNHN-Bol V-005521 (Fig. 2), preserves nearly the entire upper dentition of this small leontiniid. Only the right I1-I2 and left P1 are missing. I1 is caniniform and significantly larger than the other incisors and appears to have only recently erupted prior to the death of the animal. It has a weak external cingulum and a robust root, which is broken but does not show any sign of tapering. I2 and I3 (C?) are significantly smaller than I1, are anteroposteriorly compressed, and have strong cingulae. The canine (or I3) appears to be absent; the exact determination of the absent tooth is difficult because the premaxilla and maxilla are solidly fused. Cracks and scratches on the specimen are more conspicuous than any suture that may remain. One palatal suture-like line follows immediately from the anterior root of the first premolar, suggesting that the absent tooth is the canine. This feature, however, may be a crack and not a suture. In any event, the animal lacks a complete upper dentition. The formula of the upper dental series is likely 3-0-4-3, but may be 2-1-4-3. The lower series is unknown.

The first premolar (likely an un-replaced dP1, which is characteristically not replaced in notoungulates) is much smaller than the following premolars (Table 2) and is preserved only on the right side. It is so worn that its crown is essentially featureless, except for a shallow fossette. A deep, conspicuous cingulum is present on the external surface. The tooth has worn down nearly to the external cingulum and has worn to such an extent that the anterolingual cingulum has formed a fossette.

Though heavily worn, P2-P4 are comparable to those of FMNH P13386, an unnamed species described and figured by Patterson (1934a:fig. 10c) and referred to *Leontinia* sp. The external enamel undulates around a distinct parastyle and paracone ridge then follows a smoother path to a shallow metacone ridge. A distinct external cingulum is present on P2-P4, but absent on the molars. The protocone is not connected at the occlusal

Figure 3. Occlusal view of the holotype of *Anayatherium fortis* n. gen. & sp. (UATF-V-00134) with partial dentition (alveoli of right I1-2, right P2-M2 and left I1, alveolus of I2, and P3-4).



level to the parastyle, except on the more heavily worn P4. An anterolingual cingulum, deep to the level of occlusion, contacts the protocone with the protoloph. The protocones of P3-P4 have longitudinal lingual grooves, as in *L. gaudryi* and the unnamed P13386 (and unlike *Scarrittia canquelensis* [Chaffee 1952]).

The molars have the same general appearance as those of *Leontinia* and *Scarrittia*. M1 is roughly square in occlusal view, but has a projection of the anterolabial corner such that it imbricates the P4 (evident on left P4-M1, not figured). Though the I1 and M3 have not come into complete occlusion, the M1 is worn to the level of the internal cingulum. The M1 protoloph is narrow labially, but broadens rapidly to form a bulbous structure at the protocone. The valley between the protoloph and ectoloph is narrow and lacks branches or fossettes. M1 lacks a posterior fossette. The M2 is relatively and absolutely longer than the M1, has a narrower protoloph, and a narrow, transversely oriented posterior fossette. M3 is incompletely erupted and badly damaged. A distinctive internal cingulum is present on it, and all the molars, but none of these upper molars have external cingula.

ANAYATHERIUM FORTIS n. sp.

Holotype.—UATF-V-00134 (cast, UF 90959). Right maxilla with P3-M2, of which P2 and M3 are poorly preserved; right and left premaxillae with left I1 and roots of right I1 and roots of both I2s; and left maxilla containing fragments of P3-4 (Fig. 3; Table 2). Crowns of incisor and premolars are damaged.

Diagnosis.—Larger than *A. ekecoa*, similar size to *Leontinia gaudryi*, *Scarrittia canquelensis*, and *Taubatherium major*. Muzzle shorter than those of *L. gaudryi* and *S. canquelensis*. Alveolus of I1 larger than that of I2. I1 not greatly enlarged, but similar to I1 of *L. gaudryi*. Differs from *L. gaudryi* by small size of I2 and reduction of anterior dentition (no apparent canine). Differs from *S. canquelensis* by smaller I1 and presence of longitudinal lingual groove in protocone of upper premolars (lingual protocone groove is absent in *S. canquelensis*). Molars relatively narrower than those of *S. canquelensis* and *L. gaudryi*. Lacks the distinct molar cristae of *T. major*. The referral of this species to *Anayatherium* is tentative as it is based upon a shared suit of characters (premolar grooves of P3-4 and en-

larged I1) rather than an unambiguous synapomorphy.

Type Locality.—From Unit 2 at Pasto Grande, Salla Beds, Bolivia.

Etymology.—*Fortis*, Latin for “strong,” in reference to the robust nature of the beast and to the character of the namesake (F. Anaya) of the genus.

Description.—The holotype (UATF-V-00134) is the only known specimen, so the following description is based solely on this specimen.

The I1 has the same general form as that of *Leontinia gaudryi*. An external cingulum is present, but indistinct. The crown of I1 is broken. No posterior cingulum is seen, but this may have been lost in the break-

age of this tooth since the posterior cingulum occurs closer to the occlusal level than the anterior cingulum. Both I2s are missing, but the alveoli and roots of I2 are not enlarged, as in *L. gaudryi* (see Loomis 1914 and discussion below). The specimen does not preserve I3-P1 and is so poorly preserved in the region that nothing can be said of them, not even whether or not any or all of these teeth were present.

The first premolars are not preserved and P2 is badly damaged. P3 is not heavily worn and preserves some of the crown features. The protocones of P3-P4 have the vertical, lingual grooves as seen in *L. gaudryi* and *Leontinia* sp. of Patterson (1934a:fig. 10c). The

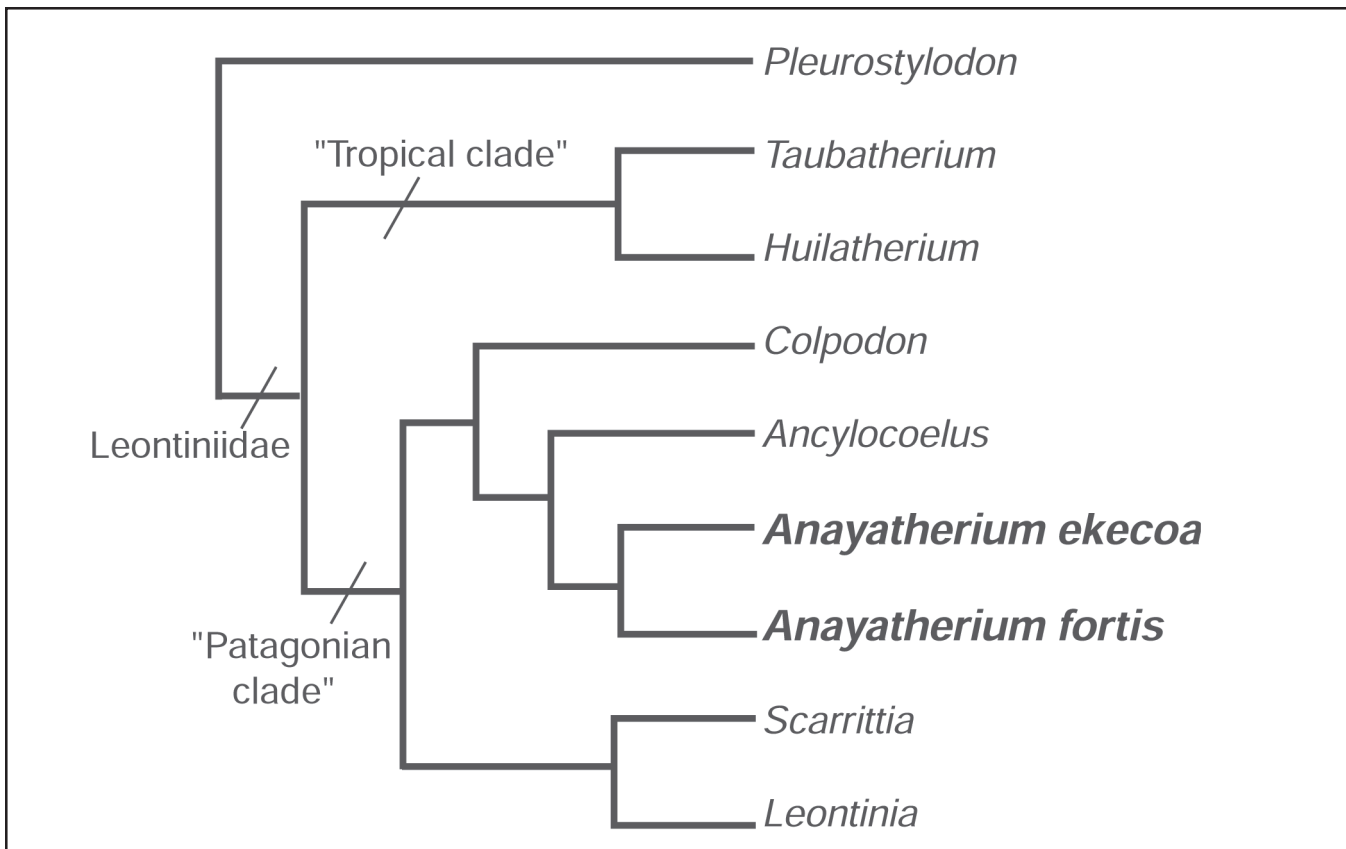


Figure 4. Phlogenetic hypothesis based upon most parsimonius phylogenetic tree. Tree Length = 47; Consistency Index = 0.7234; Homoplasy Index = 0.2766. Analysis based upon a taxon/character matrix modified from Villarroel & Colwell Danis (1997) to include *Anayatherium* and its character states. Evaluated with the “exhaustive search” of PAUP, version 4.0b10.) Putative synapomorphies for the Leontiniidae and the “tropical” and “Patagonian” clades (numbered character states of Villarroel & Colwell Davis 1997) are as follows: Node Leontiniidae: 5, Basins of “leontiniid depression” incompletely separated; 15, i3 somewhat hypertrophied; 20, Lower molar post fossetid U-shaped; 21, Lower molar entoflexid rounded. “Patagonian” node: 5, Leontiniid depression well separated; 6, P4 labial cingulum weak or absent; 8, Posterior arm of upper premolar hypofossette weakly developed; 9, Cheekteeth mesodont. “Tropical” clade: 13, Upper molar anterior lingual cingulum absent; 14, Upper molar anterolingual enamel border of hypflexus conspicuous in relief with wear; 23, Lower molar labial cingulum absent.

badly damaged P2 lacks this groove. On the P3, the occlusal surface of the protocone is isolated, save for a connection to the metaloph. An unworn ridge connects the protocone with the posterior cingulum. The anterior cingulum is well removed from the occlusal surface and becomes incorporated into the protoloph. The parastyle is distinct and a sharp groove cuts into the ectoloph between the parastyle and the paracone ridge. P3-P4 have an external cingulum.

P4 is more worn than the P3. It also has a better-developed protoloph that unites the protocone with the ectoloph. The posterior lingual cingulum forms a cup that projects this region of the tooth's surface medially. This appears rather conspicuous, compared to the rather weak protocone.

The M1 is but moderately worn. Cingula are present from the anterolingual portion of the tooth to the posterior border. All are removed from the occlusal level, except for the posterior cingulum, which has come into wear. None of the molars have a labial cingulum. The central valley is Y-shaped, with the anterior arm being conspicuously longer. This anterior arm lacks any bifurcation such as is present in *Ancylocoelus*, *Taubatherium* and *Colpodon*.

The posterior cingulum of the M2 had not come into wear. This tooth has a similar form to the M1, though with significantly less wear.

Only the anterior-most portion of the M3 had broken the gum line. Most of this tooth is missing, but part of the ectoloph was recovered. The internal wall of this ectoloph demonstrates the vertical ridges described by Patterson (1934a:fig. 10b) of an unworn molar of *Leontinia gaudryi* (FMNH P14659).

DISCUSSION

PHYLOGENY

Villarroel and Colwell Danis (1997) presented a phylogeny of leontiniids that illustrated two distinct clades for the family (Fig. 4). One branch contained Patagonian genera (*Leontinia*, *Scarrittia*, *Ancylocoelus*, and *Colpodon*) whereas the other branch contained the Tropical genera *Taubatherium* and *Huilatherium*. The tropical plus Patagonian clades are shown as a monophyletic group with the isotemnid *Pleurostylodon* as the sister taxon (Villarroel & Colwell Danis 1997).

Using the 23 characters and scoring criteria of Villarroel and Colwell Danis (1997: appendix), *Anayatherium ekecoa* was scored as follows: 10011 00110 0010 and *A. fortis* was scored as ?0011 00110 0010, since the presence-absence of the canine is un-

known in *A. fortis*. Only characters 1-14 could be scored for the species of *Anayatherium* as the lower jaw is unknown. The lower jaw characters were all scored as "?". An exhaustive search using PAUP, version 4.0b10, produced a single most parsimonious phylogenetic hypotheses (tree length = 47; consistency index = 0.7234; homoplasy index = 0.2766). This analysis placed *Anayatherium* within the "Patagonian" clade, more specifically, among *Ancylocoelus* and *Colpodon* with the loss of the canine as the hypothetical synapomorphy uniting the three genera (Fig. 4). The two species of *Anayatherium* appear to form a distinct clade. The loss of enamel-lined pits of the upper molars appeared as a putative synapomorphy uniting these two species.

The *Scarrita-Leontinia* "sub-group" of Chafee (1952) is supported in this and the original analysis of Villarroel & Colwell Danis (1997). It is noteworthy that the characters that unite these two genera are those from the lower dental series, which is lacking in both species of *Anayatherium*, thus comparison in this analysis was impossible. Nonetheless, *Anayatherium* appears to be firmly established within the "Patagonian" clade of leontiniids, distinct from the tropical genera, *Taubatherium* and *Huilatherium*. Putative synapomorphies for this clade of Patagonian taxa plus *Anayatherium* include a well-demarcated leontiniid depression of P3-P4, poorly developed labial cingulum of P4, and mesodont dentition.

The nesting of *Anayatherium* within the Patagonian genera is significant in terms of the biogeography of the Salla leontiniids. Such a phylogenetic placement is consistent with the previous observation that most other ungulates of Salla were closely related to Patagonian Deseadan taxa, with most being cogenetic, though specifically distinct (Shockey 1997a).

PALEOECOLOGY

Although leontiniids are among the most common specimens collected at most Deseadan localities (see Introduction), they are exceedingly scarce at Salla. The two specimens described here are the only instructive specimens encountered in large collections of fossils of Salla (MNHN-Bol, MNHN-Paris, FLMNH, and PU). This scarcity of leontiniids suggests some ecological difference between Salla and other well-known Deseadan localities where leontiniids are common.

Salla is at a significantly lower latitude than the classical Deseadan localities of Patagonia, so one might consider the possibility there was a regional effect; that is, conditions were more favorable for leontiniids in higher

latitudes than the more tropical latitude of Salla. The relative abundance of leontiniids in the Deseadan of Brazil, however, does not support the notion that there was a gross regional effect. Soria and Alvarenga (1989) noted that leontiniids were the most commonly encountered fossils in the Taubaté Basin, which lies near the Tropic of Capricorn (only about 6° south of Salla). Also, the fact that leontiniids survived into the middle Miocene at La Venta, Columbia (Villarroel & Guerrero Diaz 1985), 13.8 - 11.8 Ma (Flynn et al. 1997), but became extinct at the end of the Colhuehuapian in Patagonia also argues against any notion that tropical regions were unfavorable to them.

A curious fact regarding the ungulate fauna of Salla is that high crowned notoungulates (mesotheres, interatheriids, archaeohyracids, hegetotheriids, and notohippids) are much more common than any ungulate with lower crowns (litopterns, pyrotheres, astrapotheres). Other low-crowned notoungulates (i.e., homalodontotheriids and isotemniids) appear to be absent from the fauna. The abundance of hypsodont taxa suggests that the vegetation of Salla was abrasive; either external grit or biogenic silicates (see Shockey 1997b and references therein). Either source of the abrasives suggests a more open habitat, having little in the way of non-abrasive vegetation to support a putative browser like *Anayatherium*. The extreme wear of the cheek teeth prior to the eruption of I1 and M3 in the holotype of *A. ekecoa* suggest that the animal had some abrasive foods in its diet. Having the cheek teeth wear so much at a relatively young age likely had a negative effect on the fitness of these animals.

Ecological factors relating to body size may also be a factor in the scarcity of leontiniids at Salla. Though a rigorous ecomorphological comparison of the Salla fauna with those of other Deseadan localities is wanting, the scarcity of large animals at Salla is fairly conspicuous. For example, astraptheres are exceedingly rare at Salla, known only from a few fragments and the common pyrothere of Salla, *Pyrotherium macfaddeni*, is much smaller than *P. romeroi* of Patagonia (Shockey & Anaya 2004).

CONCLUSIONS

Unlike Deseadan localities of Patagonia, and even Brazil, leontiniids are scarce at Salla. Two reasonably well preserved and instructive specimens, however, are sufficient to illustrate that the leontiniids of Salla represent a distinct genus of two species described here: *Anayatherium ekecoa* and *Anayatherium fortis*. A phylogenetic analysis suggests that these two species

are more closely related to Patagonian taxa than they are to other low latitude leontiniids. Though phenetically similar to *Scarrittia* and *Leontinia*, *Anayatherium* is more derived by its apparent loss of the canine. This loss of canine may represent a synapomorphy uniting *Anayatherium* with *Ancylocoelus* and *Colpodon*.

The scarcity of leontiniids is likely due to local conditions that were more favorable to high crown ungulate taxa (tyotheres, and notohippids) than to lower crowned herbivores. Indeed, the extreme wear of the teeth of the holotype of *A. ekecoa*, a young animal at the time of death, is vivid testimony regarding the effect of abrasives in or on the vegetation at Salla.

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