THE DESEADAN LAND MAMMAL AGE IN URUGUAY AND THE REPORT OF *SCARRITTIA ROBUSTA* NOV. SP. (LEONTINIIDAE, NOTOUNGULATA) IN THE FRAY BENTOS FORMATION (OLIGOCENE-?LOWER MIOCENE).

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ABSTRACT

The first record of *Scarrittia* outside Argentina is herein presented. New evidence supporting the generic distinction between *Scarrittia* and *Leontinia* in mandibular morphology and an emended diagnosis of *Scarrittia* is offered: deep lingual groove in the trigonid of m3, size of the canine intermediate between i3 and p1 and shorter symphysial length in contrast to *Leontinia*. *Scarrittia robusta* nov. sp. is here diagnosed on the basis of mandibular remains from the Fray Bentos Formation in Uruguay. The new species is distinguished from *S. canquelensis* by subparallel and thicker mandibular rami and less procumbent incisors. This new record of *Scarrittia* in Uruguay widely extends the geographic range of the genus, which was previously known only in Patagonia. The associated fossil assemblage and the occurrence of *Scarrittia* in the Fray Bentos Formation supports previous referrals of the fauna to the Deseadan Land Mammal Age.

KEY-WORDS : DESEADIAN, *SCARRITTIA*, FRAY BENTOS FM., CHRONOLOGY, PALEOBIOGEOGRAPHY, URUGUAY.

RÉSUMÉ

On présente ici la première découverte de *Scarrittia* en dehors de l'Argentine. Le travail apporte de nouvelles données en faveur de la distintion des genres *Scarrittia* et *Leontinia* au niveau mandibulaire, et aussi une diagnose corrigée de *Scarrittia* : un sillon lingual profond dans le trigonide de m3, la grandeur de la canine intermediaire entre i3 et p1, et une longueur symphysaire plus petite par rapport à *Leontinia*. *Scarrittia robusta* nov. sp. est définie ici sur la base de restes mandibulaires provenants de la Formation Fray Bentos, Uruguay. La nouvelle espèce est distinguée de *S. canquelensis* par ses branches mandibulaires sub-parallèles et plus grosses, et par ses incisives moins proclives. Cette découverte augmente considérablement l'extension paléobiogéographique du genre, auparavant inconnu hors de la Patagonie. L'ensemble des fossiles et l'âge de cette unité sont discutés par rapport à des faunes sudamericaines isochrones. *Scarrittia* est en concordance avec des opinions ántérieures qui proposaient un âge Déséadien ("Land Mammal Age") pour la faune comprise dans les dêpôts référés.

MOTS-CLÉS : DÉSÉADIEN, *SCARRITTIA*, FM FRAY BENTOS, CHRONOLOGIE, PALÉOBIOGÉOGRAPHY, URUGUAY.

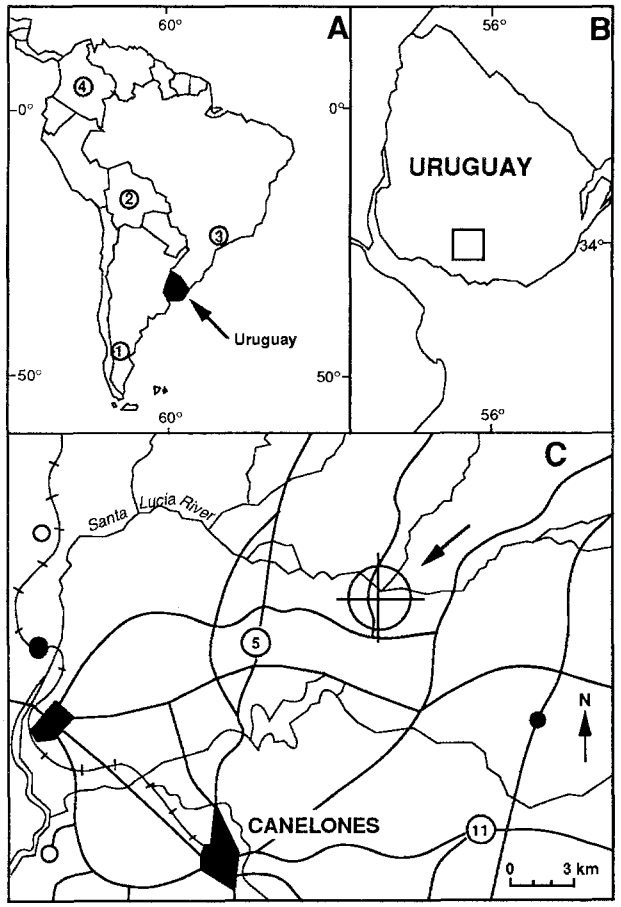


Figure 1 - Deseadan localities : **A** : 1) Chubut Province, Argentine, 2) Salla-Luribay, Lacayani, Bolivie, 3) Tremembé, Brazil, 4) Gualanday, Colombia ; **B and C** : Paso del Cuello, Canelones Department, Uruguay. *Localités déséadiennes.*

INTRODUCTION

Fossil faunas assigned to the South American Deseadan Land Mammal Age (Pascual *et al.* 1966) are known from localities in Argentina, Bolivia, Uruguay, Brazil and Colombia (Fig. 1A). The best known Deseadan Age faunas come from Argentina (Chubut Province) and Bolivia (Salla). The principal Deseadan Age fossil localities in South America were reviewed by Patterson & Marshall (1978) and by Marshall *et al.* (1983 ; 1986). Deseadan faunas have been reported from the Tremembé Formation in Brazil (Soria & Alvarenga 1989), at the Fray Bentos Formation in Uruguay (see Mones & Ubilla 1978), and the Gualanday Group in Colombia (Stirton 1947, 1953). Recent field work in Uruguay adds new information to our knowledge of the Fray Bentos Formation fauna and the Deseadan Land Mammal Age in Uruguay.

The Deseadan genus *Scarrittia* was established by Simpson (1934) for fossil material collected by the Scarritt Expedition to central Chubut, Argentina. This taxon is registered for the first time outside Patagonia, at a new locality, Paso del Cuello, Canelones Department, Uruguay, in fluvial sediments deposited in the Santa Lucía Basin (Figs. 1B-C, 2A). These deposits were originally included in the "Piso Santaluciense" of the "Deseadan" Age by Kraglievich (1932). In the present paper, we describe a new species of *Scarrittia*, discuss the taxonomy of the genus, and pursue its implications for faunal correlation.

Scarrittia belongs in the notoungulate family Leontiniidae, established by Ameghino (1895) to include forms which have brachydont to mesodont cheek teeth, the uppers composed of an external wall (ectoloph) with anterior (protoloph) and posterior (metaloph) lobes, but with *cristae* either lacking or little developed and with the second upper, and the third lower incisors developed into tusk-like, caniniform teeth. The type genus of the family, *Leontinia* AMEGHINO, 1895, is in some respects similar to *Scarrittia*. However, with the new material herein described, additional evidence from the mandibular ramus to support the differential diagnosis of the two genera is presented. Moreover, it is possible to distinguish both taxa by means of multivariate analysis based upon measurements of well preserved mandibles of *Scarrittia* and *Leontinia*, including the new specimens from Uruguay and material in the collections of the Museo de La Plata and the Museo Argentino de Ciencias Naturales.

The discovery of *Scarrittia robusta* nov. sp. in Uruguayan deposits of the Fray Bentos Formation extends the known geographic distribution of the genus, and permits us to discuss aspects of regional correlation.

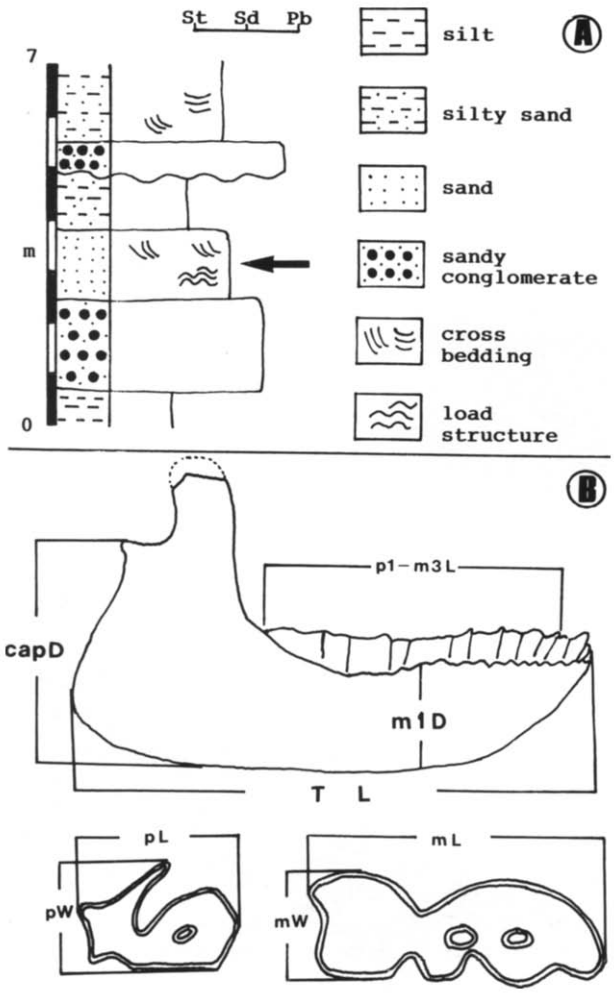
MATERIAL AND METHODS

Abbreviations : *MACN*, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires) ; *MLP*, Museo de La Plata (La Plata), Argentina ; *FC-DPV*, Facultad de Ciencias, Departamento de Paleontología, (Montevideo) Uruguay. The following specimens have been used in this study : *Scarrittia canquelensis* : MLP-s/n (*Sca*) ; MLP-66 V-11-4 (*Scb*) ; MLP- 66-V-II-12 (*Scc*) ; MLP-66-V-II-I (*Scd*) ; MLP 73-VII-1-1 (*Sce*), all collected from the Sarmiento Formation at Rinconada de Los López, Scarritt Pocket Local Fauna, Chubut Province , Argentina. *Leontinia gaudryi* : MACN A 52570 (*Lga*) MACN A 52571 (*Lgb*) ; MACN A 52575 (*Lgc*), all from the Sar-

Chs.	Sr	Sca	Scb	Scc	Scd	Sce	Lga	Lgb	Lgc
1 (i3L)	14.0	14.5	19.2	13.3	-	-	19.6	19.2	19.0
2 (i3W)	19.0	17.7	19.6	18.4	-	15.0	19.3	19.0	20.3
3 (cL)	13.0	11.8	-	13.4	-	-	9.6	12.2	-
4 (cW)	17.0	15.7	-	16.4	-	-	12.0	11.0	-
5 (p1L)	14.2	12.5	-	-	-	18.1	13.2	13.0	-
6 (p1W)	9.2	8.6	-	-	-	11.6	11.1	11.1	-
7 (p2L)	20.5	19.5	21.6	-	-	20.2	19.0	17.8	-
8 (p2W)	15.8	15.3	14.0	-	-	12.8	13.4	12.0	-
9 (p3L)	22.9	23.3	24.6	25.0	-	24.4	20.5	20.0	19.6
10(p3W)	19.3	14.1	12.4	17.3	-	14.1	16.2	13.1	13.8
11(p4L)	21.7	26.2	28.4	27.0	26.3	25.2	24.0	23.6	22.6
12(p4W)	18.2	21.0	15.2	18.0	-	13.4	19.6	14.3	15.0
13(m1L)	35.2	34.6	36.0	34.0	35.7	36.4	32.4	30.5	-
14(m1W)	20.0	15.8	16.8	18.3	17.5	14.4	17.5	15.7	-
15(m2L)	48.2	43.2	44.4	41.5	40.0	41.0	41.1	37.0	37.0
16(m2W)	18.7	16.0	16.5	17.5	19.5	13.8	17.2	17.5	15.5
17(m3L)	50.2	53.3	50.0	-	56.3	44.5	50.1	46.8	-
18(m3W)	15.7	14.7	15.3	15.6	18.0	13.6	16.6	15.4	15.2
19(p1-m3L)	211.0	-	-	-	-	-	176.2	183.0	-
20(TL)	402.0	-	450.0	-	-	363.0	-	-	-
21(capD)	177.3	-	195.0	-	-	162.0	-	-	-
22(m1D)	76.0	-	67.0	84.6	85.8	70.0	72.5	69.5	60.0
23(mandW)	39.0	-	35.0	33.6	34.0	-	-	34.0	30.4
24(sL)	87.7	-	80.0	91.4	-	78.5	96.0	102.0	92.0

TL:mandibular length; sL:simphysis length; L:anteroposterior length; W:maximum width; capD:depth from condyle to angular process; m1D: depth of mandible rami at lower m1; mandW:width mandibular rami at lower m2.

Table 1 - List of characters and individual measurements of ***Scarrittia robusta*** **(*Sr*),** ***Scarrittia canquelensis*** and ***Leontinia gaudryi*** (for abbreviations see Material and Methods). *Liste des caractères et mesures individuelles (les abbréviations se trouvent dans Material and Methods).*



miento Formation at Cabeza Blanca, Chubut Province, Argentina (see Table I).

Twenty-four linear dimensions were measured to the nearest 0.1 mm (Fig. 2B). Abbreviations for measurements are given in Table 1. These measurements were standardized, average taxonomic distance was calculated and a dissimilarity matrix produced following Sneath and Sokal (1973). A phenogram was produced using the dissimilarity matrix by the UPGMA (unweighted pair-group arithmetic average) clustering method. Principal components analysis (PCA) was performed on the character correlation matrix of standardized measurements, and a product moment correlation coefficient was computed. Onto the resulting three dimensional plots, we superimposed a minimun spanning tree (MST) computed from the matrix distances between OTU's. Standardization, phenogram, PCA and MST were performed using NTSYS-PC, the Numerical Taxonomy and Multivariate Analysis System of Rohlf (1988).

Figure 2 - **A**) schematic columnar section at Paso del Cuello, Canelones Department, Uruguay. The arrow show the stratigraphic position of *Scarrittia robusta*, **B**) mandibular and dental measurements recorded from leontinids and their recording points. Abbreviations as in Table 1. ***A)*** *soupe schématique de Paso del Cuello, Canelones, Uruguay. La flèche signale la position stratigraphique de* ***Scarritia robusta.*** ***B)*** *dimensions mandibulaires et dentaires utilisées chez les Leontiniidae.*

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order NOTOUNGULATA Roth, 1903
Family LEONTINIIDAE Ameghino, 1895
Scarrittia SIMPSON, 1934

Emended generic diagnosis - Very close to *Leontinia* but with I1 enlarged and caniniform, and I2 small. Lower incisors more procumbent and there are no lingual grooves on the protocones of P2-4 as there are in *Leontinia*. Deep lingual groove in the trigonid of m3, size of the lower canine intermediate between i3 and p1 and shorter symphysial length in contrast to *Leontinia*.

SCARRITTIA ROBUSTA SP. NOV. (Fig. 3)

Diagnosis - Leontiniid notoungulate of great size, about the same of *Scarrittia canquelensis*. *Scarrittia robusta* can be distinguished from *S. canquelensis* by subparallel and thicker mandibular rami and less procumbent lower incisors.

Etymology - Latin *robusta* in reference to its greater robustness (thicker mandibular rami) compared with *S. canquelensis*.

Holotype - FC-DPV-661 : mandible with complete dentition (Fig. 3).

Referred specimen - FC-DPV-641. Right mandibular fragment with p1 to m1.

Locality and horizon - Paso del Cuello on the Santa Lucía river, about 10 km Northeast of the town of Canelones, Department of Canelones, Uruguay (Fig. 1). Fray Bentos Formation, Oligocene to ?Lower Miocene in age (Fig. 2A).

Comparative description - Large and heavily built mandible, about 40 cm long. (Figs. 2B, 3). The new species displays the diagnostic family character of the third lower incisors developed into tusk-like, caniniform teeth. The mandibular rami are subparallel and thick, with a strong longitudinal internal groove. The coronoid process projects slightly backward. The symphysis is

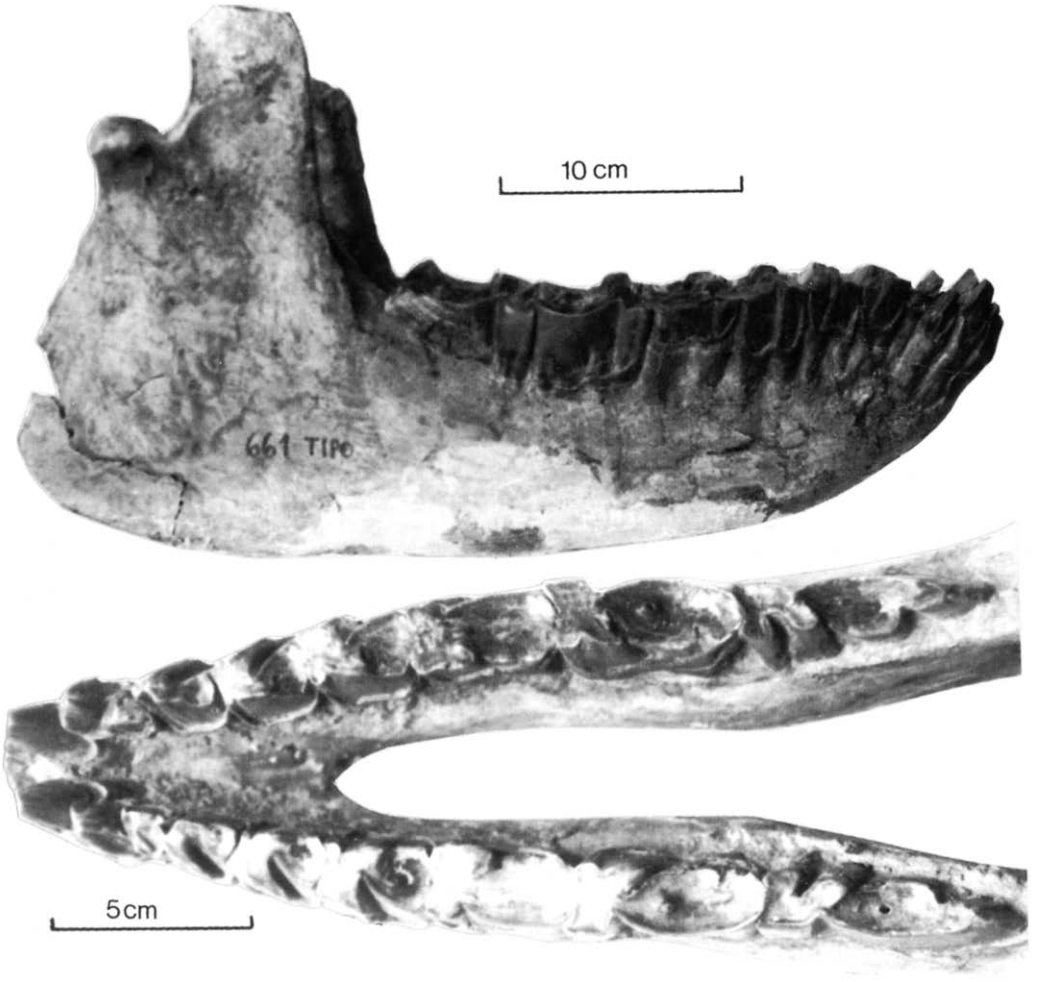


Figure 3 - Lateral (A) and dorsal (B) views of the mandible of ***Scarrittia robusta*** nov. sp. *Vue Latérale (A) et dorsale (B) de la mandibule de* ***Scarrittia robusta*** *nov. sp.*

long, but not as long as in *Leontinia*, terminating posteriorly at the level of pm3, as in *S. canquelensis*. The procumbent incisors are intermediate between the same two taxa in angle of implantation. The first and second lower incisors are small and narrow ; the caniniform i3 has well-developed cingula and is large, but not as large as the same tooth in *Leontinia*. The canine is intermediate in size betwen i3 and p1, as in *S. canquelensis* and in contrast to *Leontinia*, in which the canine is smaller than p1. The second lower premolar has nearly two times the crown area of p1. The premolars increase in size and in length-width ratio posteriorly from the second to the fourth, due to the enlargement of the talonid. The last premolar has a smaller length/width ratio than the molars. External and internal cingula are present on all teeth from i2 to m2. On all premolars the trigonid and talonid are separated by a deep groove on the labial side. In the holotype, all premolars have the protoconid crista better developed than *S. canquelensis*. The lower molars are long, narrow teeth, and differ from the premolars in having a posterior extension of the hypolophid. The lower molar trigonid is smaller than the talonid and is separated from it by lingual and labial grooves.

There is a lingual groove on both the trigonid and the talonid. This groove is present in all trigonids at all tooth positions except m1 ; in m3, the lingual groove is very deep, as in *S. canquelensis*, but in contrast to *Leontinia*. A valley or large fossette appears in the center of the talonid at all tooth positions, except on m1, perhaps because of wear. The molars appear to be very worn and display a concavity in the cementum exposed on the occlusal surface of the talonid. With wear, the postero-internal side of trigonid (metacone) protrudes from the dental series in molars and premolars.

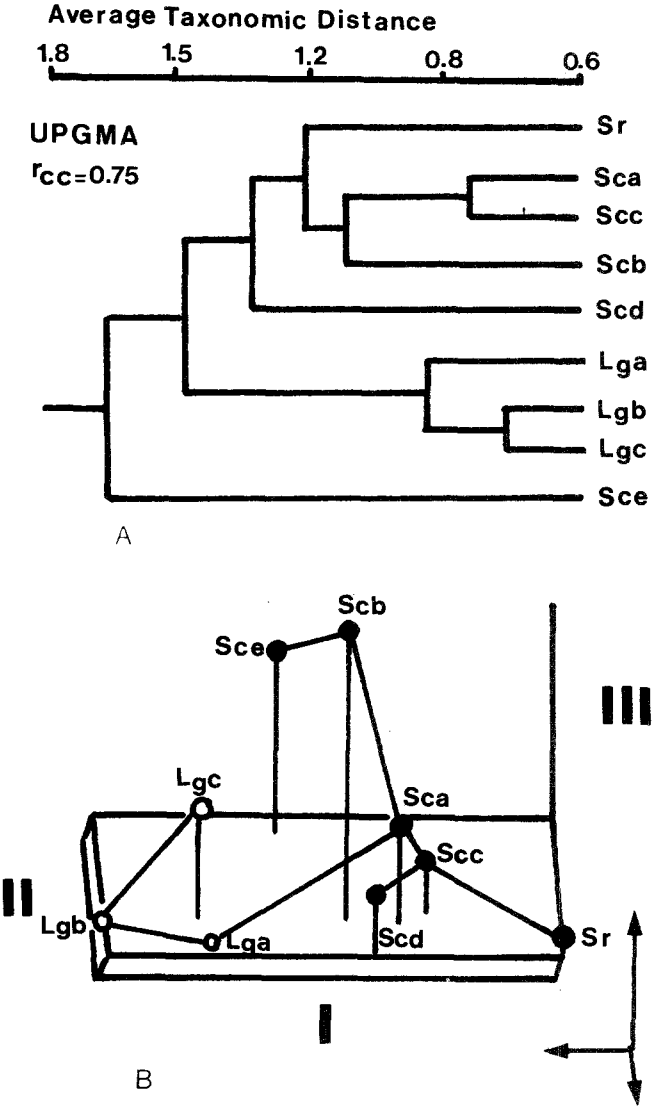


Figure 4 - **A** : phenogram depicting relationships of ***Scarrittia*** and ***Leontinia*** from transformed data matrix. **B** : projection of the first three axes from principal components analysis of 24 quantitative characters and MST superimposed on the PCA space (for abbreviations see Material and Methods). ***A** : phenogramme des relations de **Scarrittia** et **Leontinia** basé sur la matrice transformée de caractères. **B** : projection des trois premiers axes de l'analyse en composantes principales des 24 caractères quantitatifs et MST superposé sur l'espace ACP (les abbréviations se trouvent dans Material and Methods).*

DISCUSSION AND CONCLUSIONS

SYSTEMATICS

The Leontiniidae (Ameghino 1895) are notoungulates which exhibit a caniniform and enlarged third lower incisor, wide lower molar talonids and a hypolophid less than half of the length of the whole talonid (Chaffee 1952). These features enable us to place the newly described material from the Fray Bentos Formation in this family without doubt.

Leontinia, *Scarrittia*, *Ancylocoelus* and *Taubatherium* are the best known genera of the group (Ameghino 1895 ; Chaffee 1952 ; Soria & Alvarenga 1989). *Huilatherium* (Villarroel & Guerrero Díaz 1985), from the Miocene La Venta fauna of Colombia, probably among the best known leontiniids, is not yet fully described. *Leontinia* and *Scarrittia*, exhibit similarities in their great size, complete dental formula and general proportions. Nevertheless, it is possible to assign the newly described material from the Fray Bentos Formation to *Scarrittia* because of the distinctive featu-

Ch.	Principal Components		
	1	2	3
1	0.897	0.257	0.476
2	0.273	0.896	0.101
3	-0.595	-0.232	0.071
4	-1.058	-0.126	0.202
5	-0.280	-1.076	0.075
6	0.868	-0.558	-0.061
7	-0.654	-0.051	0.879
8	-0.904	0.320	-0.025
9	-0.740	-0.358	0.491
10	-0.626	0.168	-0.561
11	-0.052	0.029	0.655
12	-0.452	0.588	-0.287
13	-0.661	-0.439	0.429
14	-0.622	0.514	-0.298
15	-0.814	0.107	0.220
16	-0.439	0.690	-0.416
17	-0.500	0.805	0.054
18	0.049	0.861	-0.213
19	-1.117	-0.222	-0.129
20	-0.043	0.912	0.763
21	-0.047	0.924	0.748
22	-0.725	0.228	-0.448
23	-0.805	-0.316	-0.499
24	0.531	0.607	-0.617
*	42.61	31.74	19.47

Table 2 - Character loadings for the first three components of the principal componentes analysis using 24 quantitative mandibular characters and percent of total phenetic variance explained (*)(see Table 1 for list of characters). *Valeur des caractères pour les trois premières composantes de l'analyse des composantes principales basée sur 24 caractères mandibulaires quantitatifs et pourcentage de la variabilité phénétique totale (*) (voir liste des caractères dans le Tabl. 1).*

res of the genus (see above). The best known species of *Leontinia*, *L. gaudryi*, is stouter and displays a longer symphysis and greater symphysial surface in association with the greater development of i1 and i2 ; it also displays a more massive, caniniform i3 with much reduced basal cingula. Another resemblance between the material from Paso del Cuello and *Scarrittia* is the intermediate size of the canines between i3 and p1. In *Scarrittia* the internal trigonid groove of m3 is much more pronounced than in *Leontinia*, and the two specimens from Uruguay, FC-DPV 641 and 661, exhibit this feature. Although the new specimens show intermediate morphology between *Scarrittia* and *Leontinia* in some characters, they are herein referred to *Scarritia*.

To test this systematic hypothesis a multivariate analysis was performed using individual specimens as OTUs (Fig. 4A). The phenogram resulting from an average taxonomic distance matrix indicates phenetic distinctness for the genera *Scarrittia* and *Leontinia*. These genera are separated by low similarity values and the specimen from Uruguay, *S. robusta* (*Sr*), was clearly associated with the *Scarrittia* group. The immature specimen of *Scarrittia* (*Sce*) was isolated from the entire sample at lowest similarity values.

Principal Components were extracted to summarize phenetic variation among 24 linear mandible characters. The loadings of characters on the first three components are presented in table II and three-dimensional projections of the OTUs are depicted in fig.4B. The first three components explains 93.8% of the total variation (see Table 2). At component I some linear dental measurements denoted highest negative correlation loadings : p1-m3 length, canine width, p2 width, etc. Component II reflects p1 length, mandible depth from condyle to angular process, total mandible length, i3 and m3 width. Component III has its highest correlation with p2 length. The distribution of the specimens on the first three components agrees with the cluster exhibited in Fig. 4A. The individuals (including the Paso del Cuello specimen) previously regarded as *Scarrittia* and *Leontinia gaudryi* are respectively segregated by component I. A juvenile specimen of *Scarrittia canquelensis* (*Sce*) falls on the second axis far from the others. The projection of a MST onto a three-dimensional diagram helps avoid missinterpretation. MST calculated indicated little distortion of relationships among samples by reduction to three axes.

Qualitative comparisons, cluster and principal component analysis support the differentiation of *Scarrittia* and *Leontinia* by mandible features and the allocation of Uruguayan specimen to the former genus.

The proposed new species, *S. robusta*, represents a taxon clearly distinguished from the type-species of the genus, *S. canquelensis*, and displays a number of distinctive qualitative and quantitative characters (see Comparative description).

CHRONOLOGY AND PALEOBIOGEOGRAPHY

According to current knowledge, the Deseadan is the longest Land Mammal Age in South America, extending from about 34.0 Ma to about 21.0 Ma (early Oligocene-early Miocene). Paleomagnetic and radioisotopic data are taken into account to establish this temporal framework (MacFadden *et al.* 1985 ; Marshall *et al.* 1986). The Scarritt Pocket Local Fauna of Patagonia (Chubut, Argentina) is the youngest dated Deseadan Age fauna (about 21 Ma). The fauna includes *Scarrittia canquelensis*, *Proborhyaena gigantea*, *Platypittamys brachyodon* and several genera of notoungulates,

including *Rhynchippus* and *Archaeohyrax*. The oldest Deseadan local fauna includes the earliest records of *Pyrotherium* and hypsodont notoungulates below basalts dated to 33.6 Ma at Pico Truncado in Santa Cruz Province, Argentina (Marshall *et al.* 1986). *Scarrittia* has not been identified in Deseadan age faunas of Bolivia and Brazil. *Scarrittia* and *Leontinia* have not been found in association except doubtfully at Quebrada Fiera de Malargüe, in Mendoza Province, Argentina (Gorroño *et al.* 1979). *Scarrittia* has not yet been reported from the Deseadan type locality near La Flecha in Santa Cruz Province, Argentina. The Deseadan is a complex biostratigraphic unit including great faunal diversity and wide geochronologic range. Perhaps because of this fact, many other faunas, including those from Uruguay, can be assigned to this age (Deseadan s.l.).

Several years ago, Kraglievich (1932) recognized a fauna of "Deseadan stage" in Uruguay, contained in the fossiliferous Fray Bentos Formation. According to previous work and the data presented in this paper, deposits of the Fray Bentos Formation in the Santa Lucia basin include an association of characteristic Deseadan taxa : *Proborhyaena gigantea*, *Scarrittia robusta*, *Propachyrukhos schiaffinoi*, Notohippinae and Archaeohyracidae. The fauna can be assigned to the Deseadan based upon similarities with the Scarritt Pocket Local Fauna of Patagonia, and thus, a latest Deseadan age can be inferred for the fossiliferous Fray Bentos Formation. In previous work on the fauna from the Fray Bentos Formation (Mones & Ubilla 1978), the Deseadan was considered to be lower Oligocene in age. Since that time, its geochronologic scope has been extended (see Marshall *et al.* 1986). Therefore, the fossil-bearing deposits of this rock unit could correspond to an interval of time including the lower Miocene.

The discovery and description of a new species of *Scarrittia* indicates an enlarged geographic range for this genus (from 44^0 30'S to 34^0 30'S). At the present time, *Scarrittia* is represented by two species, *S. canquelensis* from the Scarritt Pocket local fauna from Chubut Province, Argentina and the newly described *S. robusta* from the Paso del Cuello local fauna in Uruguay. The Scarritt Pocket fauna is the youngest dated Deseadan fauna in Argentina. The precise chronostratigraphic range of *S. robusta* depends on its phylogenetic position with respect to its nearest relatives, *S. canquelensis* and *Leontinia*.

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