NEOLICAPHRIUM RECENS FRENGUELLI, 1921, THE ONLY SURVIVING PROTEROTHERIIDAE (LITOPTERNA, MAMMALIA) INTO THE SOUTH AMERICAN PLEISTOCENE

by

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ABSTRACT

The litoptern Proterotheriidae are extinct endemic South American ungulates frequently used as an example of evolutionary convergence with the horses. They were considered to be exclusively Tertiary representatives with the youngest record being in the late Pliocene, before the appearence of the equids and cervids during the Great American Interchange. Two undoubted Pleistocene records in Argentina and the specimen here described from Uruguay, confirm the persistence of the proterotherids into that period. In the Quaternary, these ungulates are found outside the typical pampean region and probably were confined to a few northern and warmer more forested relictual microhabitats.

RESUMEN

Los litopternos de la familia Proterotheriidae son ungulados extinguidos y endémicos de América del Sur comúnmente utilizados como ejemplo de evolución convergente con los caballos. Han sido considerados representantes exclusivos del Terciario registrados por última vez en el Plioceno tardío previamente a la aparición de los équidos y de los ciervos conjuntamente con la inmigración masiva que formó parte del denominado Gran Intercambio Faunístico. Se confirma la persistencia de los proterotéridos en el Pleistoceno en base a dos registros de Argentina y del especimen de Uruguay que se describe. Estos ungulados existieron en el Cuaternario fuera de la región pampeana típica y estuvieron probablemente confinados algo más al norte en escasos microhábitats relictuales más cálidos y forestados.

RESUME

Les litopternes Proterotheriidae sont des ongulés éteints, endémiques de l´Amérique du Sud, souvent utilisés comme un exemple de convergence évolutive avec les chevaux. Ils ont été considérés comme des répresentants exclusifs du Tertiaire, avec leur dernier régistre dans le Pliocène supérieur, avant l´apparition des équidés et des cervidés pendant l´évennement immigratoire massif nommé "Grand Echange Américain". Deux registres indubitables du Pleistocène de l´Argentine et le spécimen décrit de l´Uruguay confirment la persistance des protérothéridés dans cette période. Dans le Quaternaire, ces ongulés se rencontrent en dehors de la région pampéenne typique et probablement ils ont été confinés à quelques microhabitats rélictuels plus chauds et boisés, situés plus au nord.

INTRODUCTION

During most of the Tertiary, South America was an "Island Continent", inhabited by a peculiar and diverse endemic mammalian fauna (Simpson , 1980). Within this fauna, the native ungulates or "Meridiungulata" (McKenna, 1975) were conspicuous, especially since some of its representatives (v. gr. typotherian "rodent-like" notoungulates and the "pseudo-horse" proterotheriid litopterns), had developed adaptive types convergent with unrelated holarctic mammalian groups. Consequently, the native South American ungulates are often mentioned as classic examples of convergent evolution (McKenna, 1975; Scott, 1937).

The litopterns of the family Proterotheriidae ranged in size from that of a rabbit to that of peccaries (*Tayassu*) and huemuls (*Hippocamelus*), cursorial forms which have a particular significance in the referred context. This group is known since the Paleocene (Itaboraian Age) and recorded at several localities of South America from Patagonia to Colombia. Proterotheres show a "horse-like" tendency towards monodactyly, with an enlarged metapod III, digits I and V lost, and lateral digits II and IV reduced. In the Miocene (Santacrucian Age) proterotherids have tridactyle, although functionally monodactyle limbs, similar to those of the anchitherine horses (*Mesohippus*, *Parahippus*) (Simpson, 1980; Scott, 1910, 1937; Patterson and Pascual, 1972). The most extreme representative of the proterotherid tendency towards monodactyly is Thoatherium, of the Santacrucian Age also, in which the lateral digits II and IV were even more reduced than those of *Equus* (Scott, 1937).

In South America, accordingly to their traditionally accepted fossil record, the proterotherid litopterns were considered extinct before the Pleistocene (Stucky and McKenna, 1993; Pascual *et al.*, 1996), well before the arrival of its ecological "parallels", the equids, after the Great American Biotic Interchange (Cifelli, 1985), not cohabiting with them and, of course, not involved as "victims" of the replacement of "southerner" ungulates by the more "apt" "northerner" ungulates (Webb, 1991). Thus, apparently, the proterotheriids were one of those native ungulate groups that disappeared before the climax of the Interchange and its demise being related to the environmental changes occurring between the Chapadmalal-Marplatan ("Uquian") Ages (Pliocene-Pleistocene), that decimated many other South American mammals (e.g. the "rodent-like" pachyrukine notoungulates and argyrolagid marsupials) (Simpson, 1970; Cione and Tonni, 1995, Cerdeño and Bond, 1998).

So, until recently, the "meridiungulates" survivors into the Pleistocene were represented only by one litoptern (Macraucheniidae) and two notoungulates (Toxodontidae and Mesotheriidae). The records of Pleistocene Proterotheriidae (Frenguelli, 1921; Alvarez, 1974) were not accepted as an empirical fact until now. Curiously, the article of Frenguelli (op.cit.) was disconsidered by most of posterior authors, perhaps owing to the idea that the material collected by Frenguelli was not enough evidence to support a biochron extention.

In this paper a new record of *Neolicaphrium recens* FRENGUELLI, from the Pleistocene of Uruguay (fig.1 and pl. 1) is described, thus resolving this question. The finding allows to improve the diagnosis of this taxon and to postulate the survival of the Family in the Quaternary. Stratigraphic problems and evolutionary implications are also discussed.

Abreviations and Methodology:

MLP, Departamento Científico Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina. FC-DPV, Collection of fossil vertebrates, Facultad de Ciencias, Montevideo, Uruguay. CTES-PZ, Colecciones de Paleontología Vertebrados, Facultad de Ciencias Naturales de Corrientes, Argentina. CORD-PZ, Museo de Paleontología de la Universidad Nacional de Córdoba, Córdoba, Argentina. Topographical nomenclature of the crown morphology follows Reig (1977), Soria (1981) and Soria & Hoffstetter (1985). Highness of the crown is taken in accord to Janis (1988). All the measurementes

are in millimetres (mm).

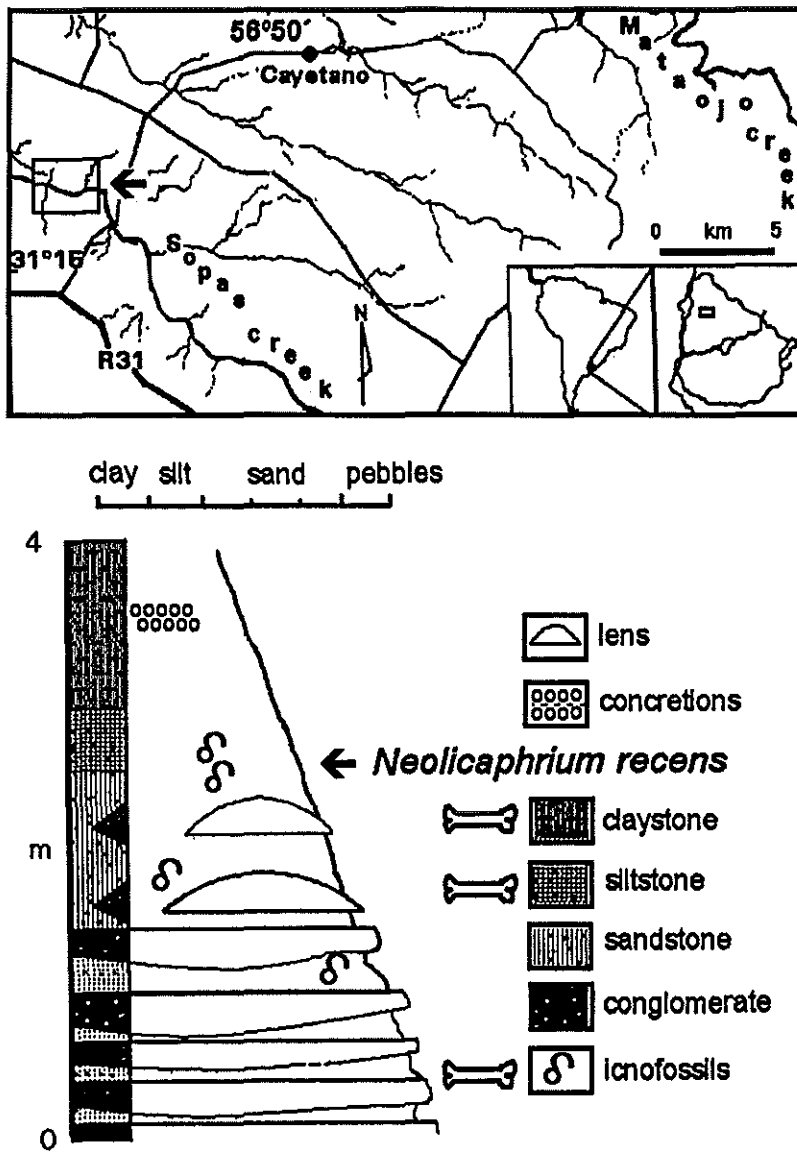

Figure 1.— Geographic location and stratigraphic section showing the colecting site of *Neolicaphrium recens*, FC-DPV-776.

SYSTEMATIC PALEONTOLOGY

Order **LITOPTERNA** AMEGHINO, 1889
Suborder **LOPHOLIPTERNA** CIFELLI, 1983
Superfamily **PROTEROTHEROIDEA** AMEGHINO, 1887
Family **PROTEROTHERIIDAE** AMEGHINO, 1887
Subfamily **PROTEROTHERIINAE** AMEGHINO, 1887

Genus *NEOLICAPHRIUM* FRENGUELLI, 1921

Type Species: *Neolicaphrium recens* FRENGUELLI, 1921

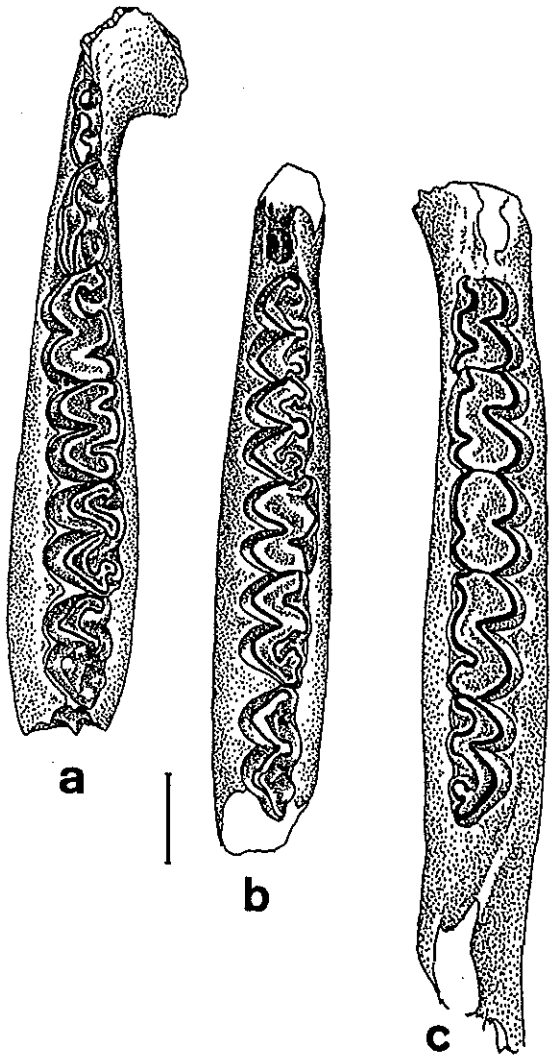

Figure 2.— *Neolicaphrium recens*. Occlusal view of: (a), left dp1-m2, PZ-Ctes 1604; (b), left p3-m3 of MLP 34-V-22-12, type; (c), right p3-m3, FC-DPV-776. Scale bar: 1 cm. Drawings by C. Vildoso Morales.

Diagnosis: A proterotheriid of medium to small size, comparable to that of *Thoatherium* minusculum or to the extant cervid *Ozotoceros bezoarticus*. Molariform teeth, especially m1-m3, with crown relatively high, but still "mesodont" not hypsodont. p3-m3 with a very well-developed entoconid connected by a short crest (postentolophid) to a lingually projecting hypoconulid. The m3 with a more posteriorly projected hypoconulid, forming some kind of rudimentary "third lobe". Valleys of the trigonid and talonid (metaflexid and entoflexid respectively) narrow, reaching deep to the bottom of the crown and relatively penetrating ones. Labial fold (ectoflexid) very deep and penetrating. Labial and lingual cingulum not continuous, the labial one restricted to the anterior and posterior parts of the lower molariform teeth; the smooth

lingual cingulum forms a rim at the base of the lingual valleys. A well developed layer of cementum is present at least in the p3-m3 of m3.

Distribution: middle to late Pliocene (Chapadmalalan Age), latest Pliocene or early to middle Pleistocene (San Andresan or Ensenadan Age) of Argentina, and middle to late Pleistocene (Bonaerian and Lujanian Ages) of Argentina and Uruguay .

Neolicaphrium recens FRENGUELLI, 1921

(Fig. 2 and pl. 1)

Diagnosis: as for the genus, and aproximately a third smaller than N. major, with entoconid in the m1-m3 better developed than in N. major.

Distribution: latest Pliocene or early Pleistocene (Sanandresan or Ensenadan Age) of Argentina, and middle to late Pleistocene of Argentina and Uruguay (Bonaerian and Lujanian Ages).

Holotype: MLP 34-V-22-12, incomplete left mandibular ramus with p3-m3 of and adult individual. Altos de San Vicente, near the city of Córdoba, province of Córdoba, Argentina. "Bonaerian", Pampean Formation (Bonaerian Age, middle to late Pleistocene). This specimen, first described by Frenguelli (1921), formerly retained part of the ascending ramus and the p2, as the result of later damages, this two elements are now missing.

Hypodigm: CTES-PZ 1604, incomplete left mandibular ramus, with part of the symphisis and the dp1-dp4, m1-m2 of a young individual. Toropí rivulet, near Bella Vista, province of Corrientes, Argentina. Yupoí Formation (Bonaerian Age?, Pleistocene). CORD-PZ 1767-1769, fragmentary right and left mandibular ramus with dp3-m1 and p3-m1 respectively. Also there is CORD-PZ 1769, a fragmentary fore foot autopodium, wich was described by one of the authors (Tauber, 2000). Near Corralito, Department of Tercero Arriba, province of Córdoba, Argentine Republic. Beds of Ensenadan Age (early to middle Pleistocene). FC-DPV-776, incomplete mandible with left p2-m2 and right p3-m3, aged individual. Sopas creek, Department of Salto, Uruguay Republic. Sopas Formation (Lujanian Age, late Pleistocene), (fig. 1).

Measurements: see Table 1.

Comments:

The type specimen was thoroughly described by Frenguelli (1921), and nothing sustantial can be added. One important point, that apparently was not observed by Frenguelli (1921), is that in *Neolicaphrium recens* the premolars and molars have the crown covered by a well developed layer of cementum, a feature at least not observed in other proterotheriids, except the Montehermosan (early Pliocene) species of Eoauchenia and Epitherium. The new specimen of N. recens from Uruguay (FC-DPV-776), unfortunately has lost its symphyseal region and the preserved teeth (p2-m3) belong to an aged individual having most of the crown features obliterated by wear. Nothwithstanding, we can observe that FC-DPV-776 has the typical bicrescentic lophoselenodont molariform teeth of the Proterotheriidae. The p2 is elongate and not molariform, its trigonid has a projecting anterior crest (paralophid), curved lingually; the

talonid is relatively wider than the trigonid. The molariform p3-p4 fit very tightly, and also the m1-m3. The enamel cap is very thin in the anterior and posterior part of these teeth, so with the use, each molariform presures into the anterior one, becoming imbricated into the other tooth's crown, recalling what normally happens in living aged artiodactyls, especially some camelids as Lama. The m1-m2 are not different from those of the other known specimens of N. recens. The m1, has lost nearly all the features but still retains its ectoflexid; in the m2, the metaflexid and entoflexid are present.

	FC-DPV-776	MLP-34-V-22-12	CTES-PZ-1604
Heigth at m3	23.6	-	20.8
Height at m4	18	18	17.8 (dp4)
Thickness at m2	13.9	12.5	12
m1-m3 length	39.4	38.3	38.4
Length p2	9.7	-	8 (dp2)
Anterior width of p2	5	-	3 (dp2)
Posterior width of p2	5	-	3.1 (dp2)
Length of p3	11.4	11.7	10.3 (dp3)
Anterior width of p3	7	5.5	4.5 (dp3)
Posterior width of p3	8.5	6.6	4.7 (dp3)
Length of p4	11	11.4	14.4 (dp4)
Anterior width of p4	8.8	7.5	7 (dp4)
Posterior width of p4	9.5	8.8	8 (dp4)
Length m1	11.8	10.4	12.5
Anterior width of m1	9.7	8.2	7.5
Posterior width of m1	10.5	8.3	8
Length of m2	13.6	13.2	13
Anterior width of m2	10.3	8	7.3
Posterior width of m2	9.7	8.1	7.8
Length of m3	14.6	19.4	14.1
Anterior width of m3	8.8	6.6	7.2
Posterior width of m3	6.6	5.3	7

Table 1.— Dental and mandibular measurements (mm) of the specimens of *Neolicaphrium recens.*

The m3, with lesser wear, presents a distinct entoconid, connected posterolabially to the hypoconulid by a short crest. All molariform teeth (p3-m3) have a layer of cementum. The CTES-PZ 1604 specimen is interesting in that it belongs to a young individual. Its m1-m2 are slightly worn, so all the features already present in the type specimen (MLP 34-V-22-12) are shown. Also, the deciduous premolars (dp1-dp4) are present. The dp1 and dp2, are elongate, not molariform. The crown of the dp1 is very slender, implanted by two well separated roots. It has a central cusp (protoconid) a short projecting conule (a hint of a paralophid) and a short talonid with a small central cusp. The dp2, resembles the p2 in its morphology, although more longer and wide. The

trigonid has a principal cusp (protoconid) with a lingually projecting crest (paralophid) which has an anterolingual cusp, so the anteriormost part of the paralophid looks somewhat "bifid". The talonid is relatively short and wide, lingually to it is a small cusp (entoconid?). The internal folds and valleys are well-developed. A very smooth lingual cingulum is observed in the dp2. The dp3 is the largest of the deciduous series, especially because of its longer paralophid. Except for its better defined metaconid, this tooth is very similar to the dp2. The dp4 is molariform and very similar to the p4, although larger. Apparently, there was an entoconid well developed as in the p4, but the wear has obliterated this feature and we only observe a posterior crescentic lophid, somewhat enlarged at is lingual end. Smooth and discontinuous labial and lingual cingula are observed in the dp3-dp4.

Part of the symphysis has been preserved in CTES-PZ 1604, but unfortunately it is badly damaged. It can be observed, however, that there are two alveoli for the incisors (i2-i3). Anterior to the dp1, is a short diastema, and the c1, if present was very small. The symphysis extends backwards onto the level of the anterior part of the dp1.

From the material preserved *Neolicaphrium recens*, appears to be a Proterotheriinae proterotheriid, with some progresive features such as relatively high crowns and a cementum layer. It appears not to be particularly related to the high-crowned proterotheriines from the Montehermosan Age as Eoauchenia and Epitherium. In these forms, there is also a layer of cementum, but the lower molars referred to these taxa (the types are crania and postcranial elements) have a larger entoconid, slenderer cingula, and deeper internal valleys which are completely filled up with cementum, being apparently more specialized than *Neolicaphrium recens*, at least in this respect. The ancestral forms related to N. recens, the last proterotheriid, are probably related to the "Araucanian" (Huayquerian and Montehermosan Ages) species described as *Neobrachytherium intermedium* (MORENO & MERCERAT, 1891) (Soria, 2001), which is very similar in its molar morphology to N. recens, especially in the form and connection of the entoconid to the hypoconulid. Soria (2001) described a new species for Neolicaphrium, N. major, based on a very imperfect jaw of Chapadmalalan Age (middle to late Pliocene), this species is nearly a third larger in size than N. recens, but has molars with a more gracile entoconid. There is an urgent need for revision of the Proterotheriidae, especially for the latest Miocene and Pliocene proterotheriids, and till this task is partially fullfilled (e.g. Soria, 2001), the relationships of *Neolicaphrium recens* will remain unclear.

GEOCHRONOLOGY

The first remains of *Neolicaphrium recens* were found at Córdoba province, Argentina (fig. 3), in deposits probably of early Lujanian Age ("Bonaerian", late Pleistocene). The holotype (No. MLP- 34-V-22-12), a mandibular ramus with dentition (fig. 2), pertained to a middle-sized (i.e. the living cervid *Ozotoceros bezoarticus*) proterotheriid, different from other known species and was clearly associated to Pleistocene fauna such as the "saber tooth" *Smilodon populator* and the edentates

Scelidotherium leptocephalum and *Panochthus tuberculatus*, among others. Its taxonomic status was unanimously accepted (e.g. Soria, 2001) but its stratigraphic provenance was questioned. The remains of this proterotheriid were thought to be coming from older (Pliocene) beds, although this was not fundamented.

Posteriorly, another proterotheriid remain was found in outcrops of the Pleistocene Yupoí Formation, at Toropí stream (Corrientes province, Argentina) (Álvarez, 1974; Marshall *et al.*, 1984). In the first paper, several remains of typical Pleistocene mammals were described (*Panochthus*, *Toxodon*, *Megatherium*, *Equus*, *Stegomastodon*), and a mandibular fragment with teeth (fig. 2) corresponding to an undoubted Proterotheriinae was figured and cited. The presence of this ungulate was explained as reworked (remanie) from older deposits or, elliptically, due to some kind of zoogeographical differences between this area and the typical Pampean zone, but without any clear reference to the survival of this group into the Pleistocene.

It is important to remark that the Proterotheriidae from Toropí (CTES-PZ-1604) was collected in situ, without any evidence of reworking, and has no specific differences with the holotype of *Neolicaphrium recens*. Marshall *et al.* (1984) suggested that either the proterotheres survived into the Quaternary of Corrientes or the specimen was collected from underlying Pliocene beds. Except this, or some comments by Bond (1986, 1999) and Alberdi *et al.* (1993), the possible survival of this group into the Pleistocene, was considered very dubious by other authors (Bond, Cerdeño y López, 1995).

Similar in morphology and size, the Uruguayan specimen is referred to *Neolicaphrium recens* (fig. 2) and it is associated to late Pleistocene "panoply" mammal taxa (*Glossotherium robustum*, *Glyptodon clavipes*, *Panochtus tuberculatus*, *Macrauchenia patachonica*, *Equus* (*Amerhippus*) *neogeus*, *Hippidion principale*, *Neochoerus aesopi*, and others) (Ubilla *et al.*, 1994; Ubilla & Perea, 1999). The importance of this new record is that it proves undoubtedly that the Proterotheriidae survived into the Pleistocene, in coexistence with the immigrant ungulates, its supposed ecological "parallels". The fauna of the Sopas Formation comes from fluvial deposits (conglomerates, sandstones, sandy siltstones and soils) with a 14C date of >43.000 years b.P.. Some species of this mammalian assemblage (especially *Tapirus terrestris*, *Coendou* cf. *C. magnus*, "*Catagonus*" group" and "*Tayassu*" group) suggest warmer climatic conditions than today at the same latitude (Ubilla and Perea, 1999).

The mammalian fauna of the Sopas Formation indicates clearly a Lujanian Age (late Pleistocene), and reveals some interesting differences with the typical lujanian faunas of the Guerrero Member of the Luján Fm., Buenos Aires province. In a marked contrast to the drier and more steppic typical "pampean" faunas", the presence in the Sopas Formation of mammalian taxa as *Tapirus terrestris*, *Coendou*, *Hydrochoerus* cf. *H. hydrochaeris*, *Lundomys molitor*, *Lontra longicaudis*, among others, and several mollusc species, are eco-indicatives of ripparian forest and streams. Other mammals recorded at this unit as *Equus* (A) neogeus, *Macrauchenia patachonica*, *Microcavia criolloensis* and glyptodont species are indicatives of more open areas, revealing a mosaic environment conformed with diverse microhabitats (Ubilla, 1996; Ubilla *et al.*, 1999).

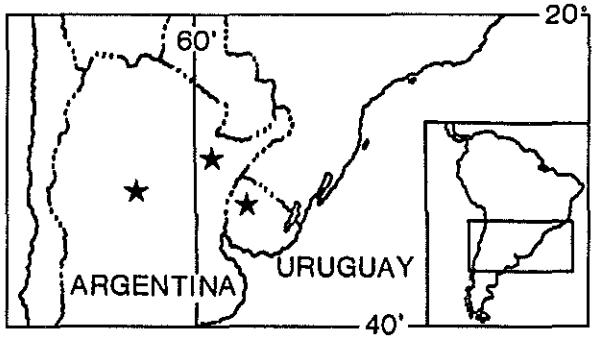

Figure 3.— Geographic distribution of the Pleistocene Proterotheriidae. From left to right, location of specimens from Córdoba and Corrientes (Argentina) and Salto (Uruguay).

MORPHOLOGICAL FEATURES AND "CONVERGENCE"

One relevant aspect related to the proterotherid monodactyl condition is that, unlike equids, they bear "inadaptive" carpal and tarsal articulations (sensu Kowalewsky, 1896; Osborn, 1910). In equids, the carpal and tarsal bones underwent a rearrangement with respect to the enlargement of the middle toe (digit III) and diminution of the lateral digits (II and IV). Thus, in horses, the carpal and tarsal bones related to the reduced digits disappear, and those articulating with specialized metapods enlarge. This condition, was considered traditionally as the "adaptive" one (sensu Kowalewsky, 1896; Osborn, 1910). On the contrary, in proterotherids, as in other extinct ungulates, the rearrangement was considered to be "imperfect" or "inadaptive", because the lateral digits, no matter how reduced they are, retained their corresponding carpal and tarsal articulations. From the point of view of the late XIX and early XX century evolutionary theory, this fact was important as an example of "progressive adaptation", because almost all holarctic ungulates, essentially the Artiodactyla, that had the "inadaptive" limb pattern disappeared during Oligocene and Miocene (Kowalewsky, 1896; Osborn, 1910) and none of them lives at present. This fact, could be used as an evidence of the "superiority" of the more "adaptive" design over the "inadaptive" one. In this classical view, the "inadaptive" Proterotheriidae becoming extinct in the Pliocene and being replaced directly or indirectly by the more "adaptive" immigrant ungulates coming from North America seems to be a good example of that evolutionary process.

Today, it is widely accepted that changes and replacement patterns within the ungulate faunas of the Northern Hemisfere are more likely due to complex phenomena, basically related to environmental changes (Janis, 1993) than, merely, the result of the "superiority" of one kind of structure.

Besides its similarities to horses, based essentially on its monodactyly and its anchiterine-like brachyodont teeth (Simpson, 1980), the proterotheriid tarsus resemble in some aspects that of artiodactyls (Ameghino, 1905; Cifelli , 1983; 1985). Also in their teeth, the selenodont structure of the proterotheriids somehow reminds that of some artiodactyl Cervidae and Camelidae. Another interesting point, is the peculiar proterotherid anterior teeth specialization, with the second upper pair of incisors (the I1 and I3 are absent) enlarged and conforming in many of the taxa little "tusk-like" structures. In the mandible, the third pair of incisors are also enlarged though not much

as the upper ones, and behind the incisors there is a short diastema between them and the respective second premolars. These specializations, indicate the adaptive singularity of the Proterotheriidae (Scott, 1937), and that this particular ungulate group is not merely an "iteration" of an ecological holarctic "pair", as the equids; they are instead a neotropical evolutionary "experience", convergent with horses basically in the acquisition of a monodactyl condition.

The traditional view of the Proterotheriidae as "vicariant equids" may suggest a similar way of life. For that reason the proterotherids were considered, in most cases, open environment dwellers, like extant horses. This curious interpretation is probably the result of comparing the most extreme monodactyly in both groups (*Thoatherium* vs. *Equus*), since the anchitherine equids, cited by several authors as proterotherid ecological "equivalents", generally are considered as inhabitants of forest environments (MacFadden, 1994). Nevertheless, in the case of the proterotherids, it was not considered that generally the remains of this family seem to be much more frequent in fossil assemblages related to forest habitats. For example, their abundance in Santacrucian Age beds (Scott, 1937) associated with some mammals clearly related to forested environments such as monkeys and erethizontid rodents (Tauber, 1991), provides strong evidence to support the referred ecological adaptation for most proterotherids. Also, after the Santacrucian Age, and following an increase of the open habitats in southern South America, the proterotheriid remains are clearly more abundant in those fossil assemblages that indicate a more forested environment than others, as the late Miocene Huayquerian Age beds of Catamarca and the "Mesopotamian" of Entre Ríos in Argentina. *Neolicaphrium recens* (fig. 2) was part of a relictual lineage probably confined to warmer and more forested environments, than the "pampean" ones, during the Pleistocene in South America, and until now, registered in the latitudinal band now conformed by Uruguay and the Argentinian provinces Córdoba and Corrientes (fig. 3).

Looking at these latest proterotheriids, an interesting point is that *Neolicaphrium recens* has higher crowned teeth than other taxa. Following Janis (1988) quantification of hypsodonty (m3 crown height/wide), and compared with living ungulates, the proterotherids from the late Oligocene to middle Miocene (Colhuehuapian to Friasian Ages) of Patagonia and also from Colombia have brachyodont teeth, for example in Patagonia they present values ranging from 0,83 to 1,16. From the late Miocene (Huayquerian Age) the teeth of some proterotherids show higher crowns (e.g. 1,62-1,75), falling in the mesodont category, shifting from more strictly browsers to some kind of "mixed feeders" in closed habitats. Very probably these last proterotheriids in Argentina and Uruguay, inhabited relatively more open habitats, similar to those of the forested savannas, and the increase in the crown height was probably due to the incorporation of more abrasive elements (grasses and grit) (Janis, 1988) in its diet. This process very probably was related to the restriction of forested areas in southern South America (e.g. Argentina) and a greater expansion of the grasslands. The fact that N. recens has a relatively high value of mesodonty for the proterotherids (i.e. 2,00 to 2,50) and the presence of cement in its teeth reveals this tendency in the proterotherids, that survived into the Pleistocene.

Neolicaphrium recens is the last known proterotheriid, a straggler of a group

widely represented in the early and middle Tertiary; its last record during the late Pleistocene, can be seen as part of the process, very probably related to environmental changes, that steady decimated the extraordinary endemic southern ungulate radiation and apparently had nothing to do with the holartic ungulate "invaders" in South America.

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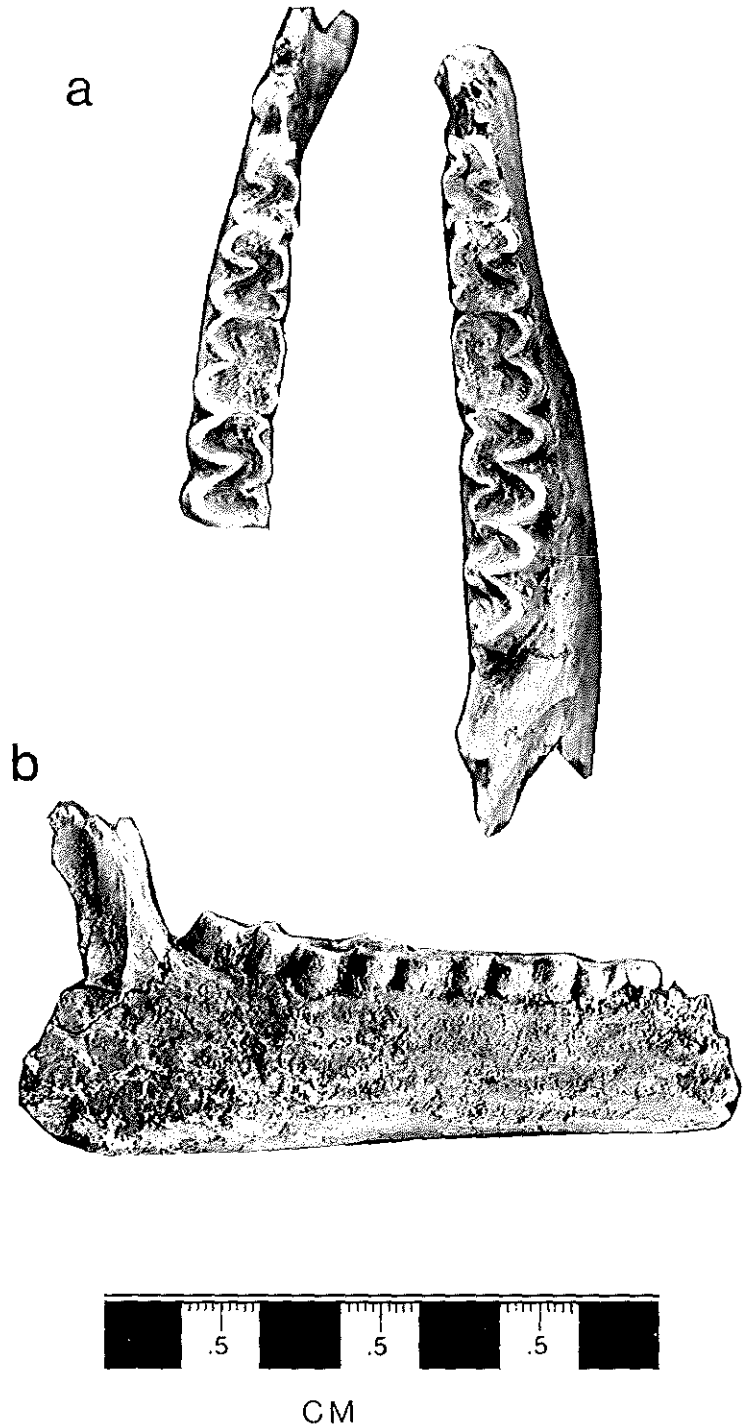
CAPTION OF THE PLATE

PLATE 1

Neolicaphrium recens, FC-DPV-776, a: occlusal view of left and right mandibles, b: lateral view of right mandibular ramus.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