

THE FIRST CRANIAL REMAINS OF THE PLEISTOCENE PROTEROTHERIID *NEOLICAPHRIUM* FRENGUELLI, 1921 (MAMMALIA, LITOPTERNA): A COMPARATIVE APPROACH

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ABSTRACT—The first cranial and upper dental remains of a proterotheriid referred to *Neolicaphrium* cf. *N. recens* Frenguelli, 1921, are described from the late Pleistocene of northern Uruguay (Sopas Formation). An isolated molariform from the Pleistocene of northeastern Pampean Argentina is considered as *Neolicaphrium* sp. It is the last surviving Pleistocene Proterotheriidae. An expanded diagnosis of this genus—based until now only on mandibular characters—is provided. The following combination of characters distinguish it from other genera of proterotheriids for which characters of the skull have been described: dorsal surface of skull almost parallel to the occlusal surface of the cheek teeth series; relatively large orbits and diastema; very large caniniform upper incisors; upper premolars and molars relatively low crowned; P2 nearly quadrangular; molariforms (at least P4 and M1–3) with anterolingual cingulae; anteroposteriorly short upper molar series; M1–3 with metaconule reduced to a small transverse crest connecting the hypocone to the metacone; hypocone reduced (or nearly absent), particularly in M3; M3 located below the orbit. A principal component analysis places it near the smallest species of proterotheriids, which were separated very well along the second component, usually related to shape.

INTRODUCTION

The South American ungulate Proterotheriidae were small- to medium-sized cursorial litopterns conspicuously characterized by the reduction of the lateral digits II and IV (I and V having disappeared), very early acquiring a ‘functional monodactyly’ similar to that of extinct anchitheriine equids or, in certain cases, even more extreme than that of living equids (see Soria, 2001). Thus, the proterotheriids have been considered as South American ‘pseudohorses’ or ‘horse-like,’ and often have been mentioned as classic examples of convergent evolution (Scott, 1937; McKenna, 1975; Carroll, 1988). The Proterotheriidae reach significant levels of diversity, particularly in the Miocene Santacrucian (13 species and 7 genera) and Huayquerian (10 species and 7 genera) South American Land-Mammal Ages (Villafañe et al., 2006).

In the Pleistocene, proterotheriid diversity dramatically decreased to only one species: *Neolicaphrium recens* Frenguelli, 1921. According to available information, this Pleistocene proterotheriid is only recorded in central and northeastern Argentina and northern Uruguay (Bond et al., 2001) (Fig. 1).

Neolicaphrium recens was described by Frenguelli (1921) on the basis of an incomplete left mandibular ramus (Pleistocene, Provincia de Córdoba, Argentina). Later, a mandible fragment of a young individual was figured by Alvarez (1974), in a faunistic study of the Yupoi Formation (upper Pleistocene, Provincia de Corrientes, Argentina). Later, Bond et al. (2001) referred this specimen to *N. recens*. Tauber (2000) reported a manus tentatively referred to the same species, considering it Pleistocene in age (Provincia de Córdoba, Argentina). Bond et al. (2001) added more mandibular remains (Pleistocene, Córdoba, Ar-

gentina) and, in particular, the most complete mandible known for an individual of *Neolicaphrium recens* (Sopas Formation, late Pleistocene, Uruguay). Pitana et al. (2006) referred an astragalus to an undetermined proterotheriid of the Pleistocene of southern Brazil. In addition, Vezzosi et al. (2009) referred a right mandibular ramus from the Tezanos Pinto Formation (late Pleistocene–early Holocene; southern Provincia de Santa Fé, Argentina) to *N. recens*.

At first, the discoveries of Frenguelli (1921) and Alvarez (1974) were rejected as Pleistocene in age owing to the fact that the Proterotheriidae were considered to be extinct as a group in the Pliocene (Chapadmalalan Stage/Age) (Kraglievich, 1934; Stucky and McKenna, 1993). Bond et al. (2001) corroborated the group’s persistence in the Pleistocene of South America (Ensenadan to Lujanian Stage/Ages according to Cione and Tonni, 1999), with *Neolicaphrium recens* being the last known representative of the group. It was coeval with Nearctic ‘invader’ ungulate mammals and became extinct in the late Pleistocene together with other northern and southern ungulates such as notoungulates, horses, some camelids, and some deer. As ‘vicariant equids’ or ‘pseudohorses,’ an open habitat lifestyle comparable to that of the more advanced equids was sometimes suggested for proterotheriids (Scott, 1937). But as has been pointed out, the observed anatomical differences in the skull, dentition, and postcranial skeleton, combined with the fact that proterotheriid remains are more abundant in areas where there is evidence of more closed habitats, clearly places into question those early suppositions and support more forested habitats, such as woodland savannas, for the Proterotheriidae (see Cifelli and Guerrero, 1997; Bond et al., 2001).

Neolicaphrium recens was represented until now only by mandibular remains. The purpose of this paper is to provide a comparative description of significant Pleistocene cranial and upper dental remains referred to *Neolicaphrium* cf. *N. recens* (from

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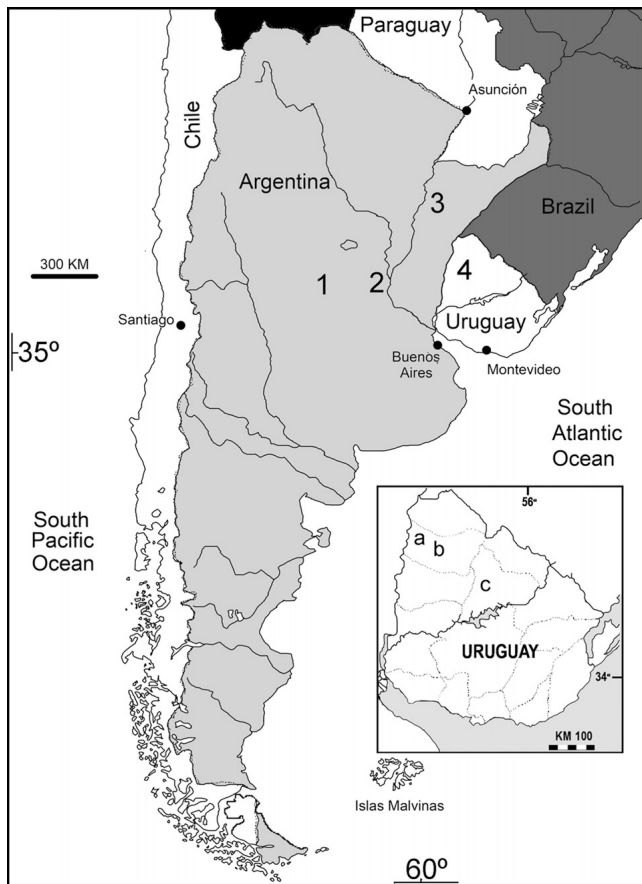


FIGURE 1. Geographic localities with Pleistocene remains of *Neolichaphrium recens*, including the material described here. 1, Córdoba (Argentina); 2, Santa Fé (Argentina) (MACN-Pv-16603b); 3, Corrientes (Argentina); 4, Salto and Tacuarembó (Uruguay); a, Río Arapey, departamento de Salto (MACN-S-92); b, Arroyo Sopas, departamento de Salto; c, Arroyo Malo, departamento de Tacuarembó (FC-DPV-749). Occurrences 1, 3, and b are based on Bond et al. (2001).

northern Uruguay, Río Arapey Grande and Arroyo Malo) and an isolated upper molar from northeastern Pampean Argentina (Río Coronda) referred to *Neolichaphrium* sp. (Fig. 1). In addition to insights about the skull morphology of this extremely poorly known and last surviving proterotheres, an expanded generic diagnosis is provided.

MATERIALS AND METHODS

The following skulls with upper cheek teeth were used for comparative purposes: *Anisolophus minusculus*: MACN-Pv-9026; *Diadiaphorus majusculus*: MLP-12-301, MACN-Pv-2711, -9181, -9208, and MACN-A-9137; *Eoauchenia primitiva*: MACN-Pv-8002; *Epitherium laternarium*: MACN-Pv-8001; *Neobrachytherium intermedium*: MACN-Pv-8428; *Neobrachytherium* sp.: MACN-Pv-8477; *Prollichaphrium specillatum*: MACN-Pv-52239; *Tetramerorhinus cingulatum*: MACN-Pv-5971; *Tetramerorhinus lucarius*: MACN-Pv-3067, -1859, -8660-61; *Tetramerorhinus mixtum*: MACN-Pv-8970; *Thoatherium minusculus*: MACN-A-9080. The ages of the mentioned taxa based on Soria (2001) are: *Anisolophus minusculus*: Santacrucian to Colloncuran; *Diadiaphorus majusculus*: Santacrucian; *Eoauchenia primitiva*: Montehermosan; *Epitherium laternarium*: Montehermosan; *Neobrachytherium intermedium*: Huayquerian;

Prollichaphrium specillatum: Colhuehuapian; *Tetramerorhinus cingulatum*, *T. lucarius*, and *T. mixtum*: Santacrucian; *Thoatherium minusculus*: Santacrucian.

We follow the taxonomic arrangement at generic and specific levels proposed by Soria (2001), until now the most recent and complete review of the family. For comparative purposes, we selected the most complete skulls with upper cheek teeth of proterotheriids, particularly those that include a comparable set of characters. Despite the fact that some taxa are in need of revision, we believe that the available sample is suitable to offer an adequate description of the new material here studied. This material was good enough to perform qualitative morphologic comparisons and some statistical treatment.

Bivariate and principal component analyses were performed using Statistica v. 6.0 (2004) and PAST v. 1.8 (Hammer et al., 2008) software. The minimum-length spanning tree (MST) was computed in order to show the nearest neighbors of taxa based on their positions in a multidimensional space. Measurements of the studied and comparative material are presented in Table 1. Because P1 is not preserved in the MACN-S-92, measurements including it were estimated and taken based on the anterior border of the alveolus.

Institutional Abbreviations—FC-DPV, colección Paleontología de Vertebrados, Facultad de Ciencias, Montevideo, Uruguay; MACN-A and -Pv, colección Ameghino y de Paleontología de Vertebrados respectivamente del Museo Argentino y de Ciencias Naturales 'Bernardino Rivadavia'; MACN-S, Museo Arqueológico y de Ciencias Naturales de Salto, Uruguay; MLP, colección Paleontología de Vertebrados, Museo de La Plata, Argentina.

Other Abbreviations—BP, before present; MST, minimum-length spanning tree; PCA, principal component analysis.

GEOLOGICAL SETTING AND BIOSTRATIGRAPHIC FRAMEWORK

The remains of Uruguay were collected from the Sopas Formation, which crops out mainly in river, stream, and creek banks of northern Uruguay in sections up to 15 m high. The Sopas Formation is considered to be late Pleistocene in age (Ubilla and Perea, 1999), with dates of >43,000 years. BP based on radiocarbon (mollusc shells and woods samples) and thermoluminescence. It includes a rich vertebrate fauna with mammals as the dominant group, ichnofossils, wood, and molluscs from numerous outcrops along its distribution area (Martínez and Rojas, 2004; Ubilla, 2004, 2007; Ubilla et al., 2004; Tambussi et al., 2005; Verde et al., 2007). The mammal fauna is biostratigraphically correlated to the Lujanian Stage/Age of the Provincia de Buenos Aires (late Pleistocene to early Holocene sensu Cione and Tonni, 1999) and includes some 'Brazilian' taxa, which indicate a relation with the Oxygen Isotopic Stage 5e last interglacial or OIS 3 last interstadial (Ubilla et al., 2004). The fossil content is also indicative of various habitats (permanent lacustrine and fluvial contexts, soils, open to semi-open and forested areas) (Ubilla et al., 2004; Ubilla, 2007).

The Sopas Formation has conglomerates with clay and calcareous matrices, conglomerate-sandstones, and siltstones and sandy-siltstones, predominantly deposited under fresh-water environmental conditions, and in some places show the development of paleosols on fluvial flood plains (Ubilla et al., 2004; Verde et al., 2007). Little was known about the fossil content of the Río Arapey outcrops where the skull of *N. cf. N. recens* (MACN-S-92, see below) was found. From the same place was collected an incomplete skull and mandible that was preliminarily identified as *Tapirus terrestris* by Ubilla et al. (2004). The lithological features observed in the outcrops of the Río Arapey Grande and also in its tributary Río Arapey Chico consist of conglomerate-sandstones intercalated with sandstones and friable siltstone levels.

TABLE 1. Measurements (mm) of the material studied and comparative taxa.

	DL	PI-4L	PI-MIL	MI-3L	PI-M3L	APWI	IL	BicW	P2L	P2W	P3L	P3W	P4L	P4W	M1L	M1W	M2L	M2W	M3L	M3W	DL/PI-M3
MACN-S-92	24.1	35.6	44.3	35.2	70.8	7.2	19	32.5	7.9	7.9	9.2	10.5	10.3	12	14	14.9	12.5	15.5	12.6	14.3	0.34
FC-DPV-749	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12.5	16.5	11.7	12.8	—
MACN-Pv-16603	24.4	—	—	—	114.5	7	—	—	—	—	—	—	—	—	—	—	—	14.3	—	—	—
MLP-12-301 Dm	21.9	56.8	73.7	—	—	6.7	—	—	14.9	12.9	15.8	18.2	16.8	19	17.6	19.3	20.7	21.3	16.4	17.4	0.21
MACN-Pv-2711 Dm	—	62.4	80.9	54.4	113.3	—	—	43.7	16	14.1	17.8	18.7	18.1	21	19.1	22.7	21	24.6	15.9	19.7	—
MACN-Pv-9181 Dm	23.7	61.2	78.2	55.4	113.8	6.7	16.2	47.1	11.7	9	18.1	17.3	18.5	19.4	18.9	22.9	21.4	22.2	16.5	18.1	0.21
MACN-A-9137 Dm	21.6	63.4	81.8	56.3	117.9	—	—	—	17.6	14.8	17.4	19.3	18.9	20	19.8	22.4	21.6	22.4	17.2	19.5	0.18
MACN-Pv-9208 Dm	21.3	39.8	49.7	35.5	75.1	6.7	—	30.5	9.8	7.7	10.4	11.7	10.3	13.4	11.3	13.4	13.1	13.8	11.6	13.4	0.28
MACN-A-9080 Thm	29.3	49.2	62.4	43.7	92.3	8.4	18.3	36.8	13.5	10.6	13.6	13.5	13.9	16.1	14.9	17.8	16.9	18	14.5	14.8	0.32
MACN-Pv-8001 Ep	—	33.6	46	38.6	71.1	—	—	—	7.1	8.1	10.5	11.6	9.4	14.4	13.9	15.3	15	16.4	14	14.8	—
MACN-Pv-8002 Eo	25.2	49	61.5	37.8	85.4	—	—	—	11.9	11.5	12.7	15.6	13.8	16.7	13	16	13.2	17.5	12.5	17	0.30
MACN-Pv-9026 Am	19.3	44.9	55.5	38.1	81.5	5.9	15	37.6	11.8	11.9	12.4	14.5	13.7	17.8	13.5	16.7	14.6	18.9	12.7	18	0.24
MACN-Pv-5971 Tc	20.1	44.3	56.5	38.2	80.2	—	—	34.3	9.8	10.3	11.4	11	12.7	12.4	13.1	13	13.5	12.8	12.9	10.4	0.25
MACN-Pv-3067 Tl	20.1	38.6	48.8	33.8	71.7	—	—	—	9.7	10.3	10.9	11.9	12.1	13.9	11.4	13.7	12.2	13.9	11.2	11.4	0.28
MACN-Pv-1859 Tl	18	36.4	47.4	32.4	67.6	8.5	16.2	—	9.1	10.6	10	11.4	11.2	12.9	11.3	13.4	12.3	13.3	10.5	12.1	0.27
MACN-Pv-8660 Tl	18.8	40.5	52.2	35.2	74.1	6	14.2	—	9.9	9.6	11.2	12	11.3	14.1	11.8	14.1	12.7	13.5	11.3	12.2	0.25
MACN-Pv-8428 Nm	—	—	—	40.7	72	—	—	—	—	—	—	—	—	—	12.7	13.3	13.3	15.4	13.5	15.4	—
MACN-Pv-8477 Nsp	—	—	—	—	—	7.8	16.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
MACN-Pv-52239 Ps	—	49.4	—	38.2	87.9	—	—	13.1	14.4	14.7	15.8	13.8	19.4	—	—	—	—	—	—	—	—

Taxonomic abbreviations (left column): **Dm**, *Diadiaphorus majusculus*; **Thm**, *Theotherium minusculum*; **Ep**, *Epitherium laterarium*; **Eo**, *Eoauchenia primitiva*; **Am**, *Anisolophus minusculus*; **Tc**, *Tetramerorhinus cingulatus*; **Tm**, *T. mixtum*; **Tl**, *T. lucarius*; **Nm**, *Neobrachytherium morenoi*; **Nsp**, *Neobrachytherium* sp.; **Ps**, *Prollicaphrium specillatum*. **Anatomical abbreviations**: **AP**, *anteropos-terior*; **Bic**, *bicondylar*; **D**, *diastema*; **I**, *incisor*; **L**, *length*; **W**, *width*.

In the Arroyo Malo outcrops of the Sopas Formation, where two upper molars of *N. cf. N. recens* were found (FC-DPV-749; see below), there are many vertebrate taxa, including freshwater fishes, turtles, birds, and predominantly mammals associated with a rich freshwater molluscan fauna (Martínez and Rojas, 2004; Ubilla et al., 2004). In this area, conglomerates, sandy-conglomerates, and sandy and silty limestones in a fining-upwards general pattern can be observed.

The precise stratigraphic level from where the upper molariform MACN-Pv-16603b (see below) comes is not very clear, but the outcrops exposed there are mainly of Bonaerian and Lujanian Stage/Ages (middle Pleistocene to early Holocene): the Timbúes, Puerto San Martín, and Tezanos Pinto formations (see Iriondo and Kröhling, 2009). The material described was associated with several artiodactyls (Tayassuidae and Cervidae), a notoungulate (*Toxodon* sp.) and proboscideans (Gomphotheriidae). Taking into account its uncertain stratigraphic provenance, the age of MACN-Pv-16603 might be Bonaerian or Lujanian.

SYSTEMATIC PALEONTOLOGY

Order LITOPTERNA Ameghino, 1889

Family PROTEROTHERIIDAE Ameghino, 1887

NEOLICAPHRIUM Frenguelli, 1921

Type Species—*Neolicaphrium recens* Frenguelli, 1921.

Included Species—The type, *N. major* Soria, 2001.

Expanded Diagnosis—Small- (*N. recens*) to medium- (*N. major*) sized proterotheriids like *Thoatherium minusculum* and *Eoauchenia primitiva*; dorsal surface of skull almost parallel to the occlusal surface of the cheek teeth series; differing from *E. primitiva* in having an anteriorly convergent dorsal surface; differing from *Diadiaphorus majusculus* and *Epitherium laternarium* in having relatively large orbits and from *Tetramerorhinus* spp. and *Th. minusculum* in having a large diastema; infraorbital foramen located at P4 level (generally located at P3 in all other genera); paraoccipital processes long, differing from shorter processes of *Th. minusculum* and *Tetramerorhinus cingulatum*; very large caniniform upper incisors, longer than in other genera; upper premolars and molars relatively low crowned, comparable to *Ep. laternarium*; P2 nearly quadrangular, uncommon in proterotheriids; differing from *Eoauchenia primitiva* in having an anterolingual cingulum in at least P4–M3; upper molar series anteroposteriorly shorter than *D. majusculus*, *Anisolophus minusculus*, and *Ep. laternarium*, with metaconule reduced to a small transverse crest connecting the hypocone to the metacone, as in *Th. minusculum*; differing from *Eo. primitiva* in having the hypocone nearly absent in M3; M3 subtrapezoidal and below the orbit, differing from *D. majusculus*, *T. minusculum*, and *Ep. laternarium*, in which it is posterior to or near to the posterior border of the orbit.

Diagnostic characters of the mandible were extensively considered by Bond et al. (2001) and are not included here.

NEOLICAPHRIUM cf. *N. RECENS* Frenguelli, 1921
(Fig. 2)

Referred Material—MACN-S-92, an incomplete skull including: dorsal surface with frontals; part of the rostrum with right incisor, diastema, and parts of both premolar and molar series (left P2–3 and M1–3, right P2–M1, and part of M2–3) including the alveolus for P1 (unpreserved); left orbit, partially preserved; incomplete zygomatic arches; left squamosal with glenoid fossa; occipital surface including apex and both occipital condyles; and right paraoccipital process (Fig. 2A–D). FC-DPV-749, fragment of right maxilla with M2–3 (Fig. 2E).

Geographic and Stratigraphic Location—MACN-S-92: Departamento de Salto, Río Arapey Grande, 30°58'39"S, 57°31'26"W, Uruguay; Sopas Formation, late Pleistocene. FC-DPV-749: Arroyo Malo, near Curtina, Departamento de Tacuarembó,

32°03'S, 56°07'W, Uruguay; Sopas Formation, late Pleistocene (Fig. 1).

Description

Skull—MACN-S-92 pertains to a small proterotheriid with the dorsal surface almost parallel to the occlusal surface of the cheek teeth. Sutures and most of foramina are not well preserved and most of the skull has been infilled by sediment. The premaxilla is long, with a convex dorsal border that projects slightly posteriorly; it projects ventrally in a crest that emerges from the posterior border of a large alveolus for the upper incisor to the anterior border of the alveolus of the P1 and mainly straight and parallel to each other. The diastema is large relative to the short cheek teeth series. The orbit is large. The infraorbital foramen is located at the P4 level. The maxillary ramus of the zygomatic arch is horizontally oriented and with its inferior border well above the level of the molariforms. The sagittal crest is preserved only by its posterior portion, which is relatively well developed and slightly convex. The glenoid fossa is shallow, rather round, and with a narrow external opening. The constriction of the occiput is scarcely marked with nearly parallel borders and the lambdaoid crest is quite rounded. The occipital condyle is higher than wide. Paraoccipital process are long and heavy and project below the inferior borders of the occipital condyles.

Description: Dentition—The upper incisor is caniniform, large, and curved; it is the largest among the compared taxa (Table 1), most similar to that of *Epitherium laternarium*. The very worn upper premolars and molars are relatively low crowned, not so brachydont as in *Lophogonodon paranensis* (Huayquerian age according to Soria, 2001) or *Neobrachytherium intermedium*, but more comparable to *Epitherium laternarium* and very different from those of higher crowned specimens attributed to *Eoauchenia primitiva*. Premolars and molars partially preserve cementum in their lateral surfaces and central valleys are filled. The premolar series is nearly equal in length to the molar series (35.6 mm and 35.2 mm, respectively; Table 1). Although p1 is not preserved in mandibles of *N. recens*, this relation seems to be roughly similar (p2–4 length = 32 mm and m1–3 length = 38.3–38.4 mm, respectively; Bond et al., 2001). P2 has the anteroposterior length nearly equal to the buccolingual one. The upper molar series is short anteroposteriorly. Molariforms (at least P4 and M1–3) have very well developed anterolingual cingulae. The central valley forms a shallow but persistent fossa. M1–3 have the metaconule reduced to a small transverse crest connecting the hypocone to the metacone, as is usual in the *Thoatherium* 'series' (see Bianchini and Bianchini, 1971; Soria, 2001), also similar to that observed in *Epitherium laternarium*. The M2 is subquadrangular and the M3 is subtrapezoidal and located well below the orbit. The hypocone is reduced (or nearly absent) in M3 as in *Thoatherium*, *Te. lucarius*, and also *Proterotherium*, differing from that of *Eoauchenia*, which yields hypocone. Posterolingual cingulae are higher than the anterolingual one and are rapidly incorporated into the occlusal surface. The labial surface of the paracone and metacone area very concave and lack any column in those areas.

FC-DPV-749 (M2–3) of the Arroyo Malo are quite similar in shape and size to those of the described material from the Río Arapey Grande (Table 1), and like this exhibit well-developed and persistent anterolingual cingulae (Fig. 2E). These two molars are slightly worn and it is possible to observe that the preserved cementum covers most of the lateral walls, infills the central valleys, and covers at least part of the occlusal surface.

Remarks—MACN-S-92 was collected in the 1970s and was part of the MACN-S until it was by chance 'rediscovered' in the collection more than 35 years later. Despite the fact that *Neolicaphrium recens* is known only by mandibles, and that the skull and upper dental material here studied are not directly associated with mandibular remains, we think the specimen very likely represents *Neolicaphrium recens* rather than

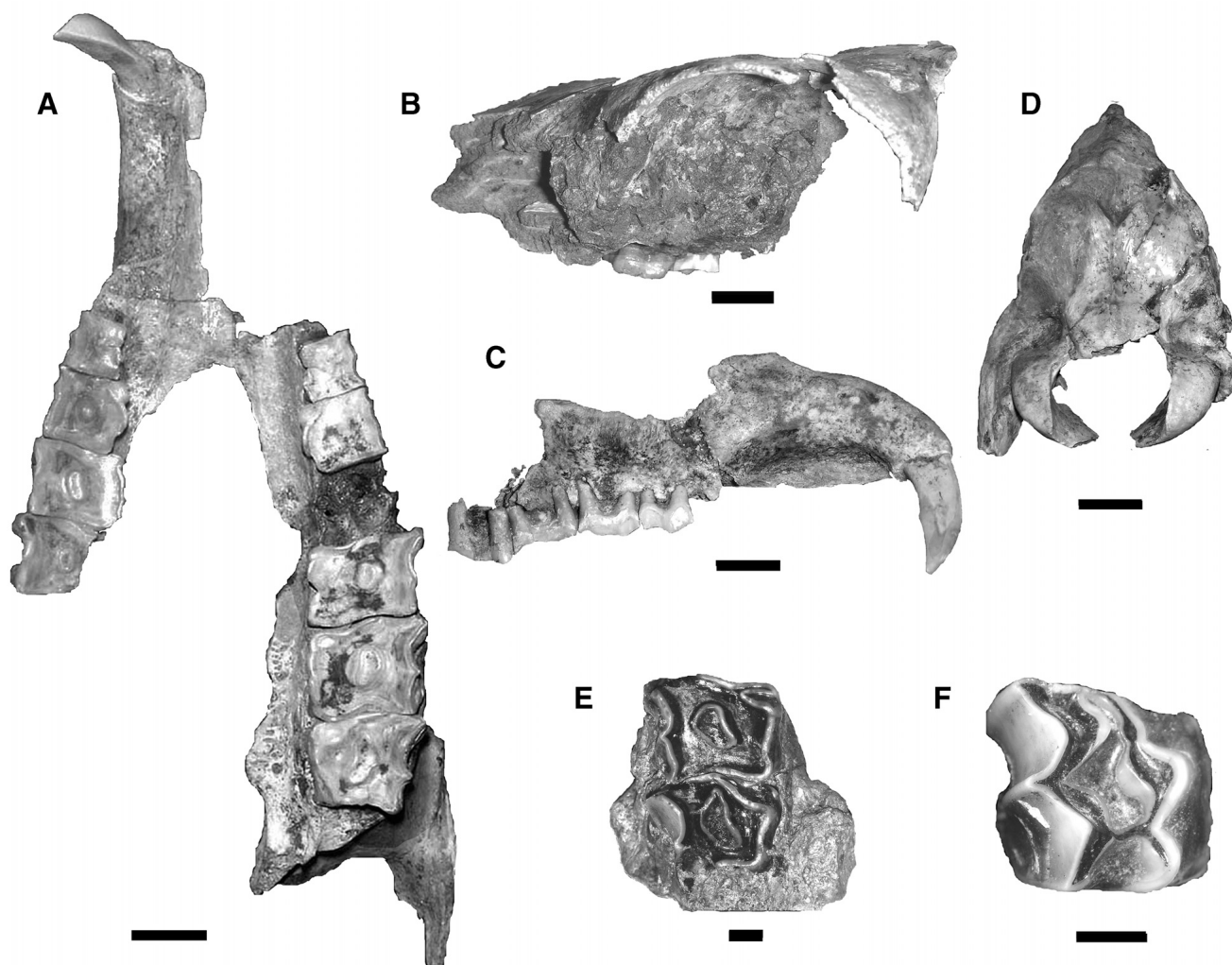


FIGURE 2. *Neolicaphrium* cf. *N. recens*, MACN-S-92 (Río Arapey Grande, Salto, Uruguay): **A**, palatal view; **B**, lateral view; **C**, lateral view of cheek teeth series and diastema; **D**, occipital view. *N. cf. N. recens*, FC-DPV-749 (Arroyo Malo, Tacuarembó, Uruguay): **E**, occlusal view. *Neolicaphrium* sp., MACN-Pv-16603b (Río Coronda, Santa Fé, Argentina): **F**, occlusal view. Scale bars equal 10 mm in **A–D**, 5 mm in **E–F**.

any other described or undefined taxon based on the following reasons: (1) the skull and dental remains belong to a small- to medium-sized protheroitheriid and the measurements of the upper cheek teeth are close to those of the lower cheek teeth of *N. recens* (see Bond et al., 2001); (2) the skull here studied differs significantly from those of the compared genera; and (3) the fossils from Uruguay were found in the same lithostratigraphic unit—the Sopas Formation—that yields mandibles undoubtedly referred to *Neolicaphrium recens* by Bond et al. (2001). The presence of cranial remains of this taxon in this lithostratigraphic unit is to be expected. We believe it unnecessary to describe a new taxon in order to avoid artificially increasing the diversity of Pleistocene protheroitheriid. New and more complete skulls associated with mandibles will confirm or reject this hypothesis.

NEOLICAPHRIUM sp.

Referred Material—MACN-Pv-16603b, right upper molariform (M1?, M2, or P4; Fig. 2F).

Geographic and Stratigraphic Location—Río Coronda, Bajo Hondo, in front of El Encanto island, Provincia de Santa Fe, Argentina; ?middle to late Pleistocene (Fig. 1).

Description—MACN-Pv-16603b, a possible M2 or M1 (although a P4 cannot be ruled out) resembles in morphology the

specimens from Uruguay and, despite its thick cover of cementum, it is less worn than the above described specimens, so some features not observed in those specimens can be seen here. The molariform is somewhat more elongated anteroposteriorly than the specimens referred to *N. cf. N. recens*. The tooth is heavily covered with thick cementum, which nearly conceals the anterolingual cingulum, the internal valley, and the posterolingual cingulum. The cementum surrounds the entire lingual surface and is present on part of the labial surface, especially in the metacone area. A small paraconule is present; it connects posteriorly to the protocone and projects towards the parastylar area. A short and transverse metaconule runs to the small and elongated hypocone and contacts the crest that runs from the posterior part of the protocone to the hypocone. An anterolingual cingulum can be noted as in the Uruguayan specimens but is nearly concealed by cementum; the posterolingual cingulum, also with cementum, is higher and anteroposteriorly shorter than the anterolingual one. The internal valley is elongated and deeply filled with cementum (Fig. 2F).

Remarks—The differences observed between this specimen (MACN 16603b) and the Uruguayan specimens, such as the size and the thick cementum cover that nearly conceals many of the crown features (e.g., the anterolingual cingulum), could be

attributed to wear; MACN 16603b appears to be from a younger individual, whereas those from Uruguay are heavily worn. Nevertheless, we refer here the molariform from Santa Fé only to the same genus as the Uruguayan ones due the scarcity of evidence favoring referral to *N. recens*.

COMPARATIVE MORPHOLOGICAL DISCUSSION

The skull here referred to *Neolicaphrium* cf. *N. recens* has some remarkable characters: the dorsal surface of the skull is quite parallel to the occlusal surface of molariforms (Fig. 2B), as in *Diadiaphorus majusculus* and *Thoatherium minusculum* (and to a lesser degree in *Epitherium laternarium*) and differs from *Eoauchenia primitiva*, which possess a convergent dorsal surface with regard to the occlusal surface (Fig. 3E). The premaxilla in lateral view resembles *Epitherium laternarium* (Figs. 2B, 3C), with a ventrally projected crest, but in ventral view the right and left crests are mostly straight and parallel; in *Ep. laternarium*, they diverge from the midline anteroposteriorly; in *Diadiaphorus* the premaxilla is short with a curved crest that is not ventrally projected (Fig. 3A); and in *Tetramerorhinus* it is also short and curved, and the two crests are quite separated each other. The orbit is large (Fig. 2B) compared to that of *Diadiaphorus majusculus* and *Epitherium laternarium* and resembles that of *Eoauchenia primitiva*, which also is large (Fig. 3). The infraorbital foramen is located at the P4 level, differing from that of compared taxa such as *Diadiaphorus*, *Eoauchenia*, and *Tetramerorhinus* in which this foramen is at the P3 level. The preserved maxillary portion of the zygomatic arch is horizontally oriented as in *Diadiaphorus*, *Epitherium*, *Tetramerorhinus*, and *Thoatherium*, differing from that of *Eoauchenia*, which is posterodorsally oriented; its inferior border, as in *Eoauchenia*, is clearly more dorsally located with respect to the molariform level than in the rest of the compared taxa (Fig. 3). The sagittal crest, represented only by its posterior portion, is relatively well developed and slightly convex as in *Anisolophus* (Fig. 2D; Soria, 2001:117). The glenoid fossa is not so externally open like in *Epitherium* and is less deep than in *Tetramerorhinus*. In occipital view, the occipital constriction is almost not discernable and has the borders almost parallel, whereas in *Anisolophus*, *Tetramerorhinus*, *Diadiaphorus*, and, to a lesser degree, *Epitherium laternarium*, the constriction is variable but well developed; in *Thoatherium* the constriction is also almost absent but the borders diverge from the top of the skull (Fig. 2D; Soria, 2001:fig. 40). The lambdoid crest is quite rounded in its dorsal portion as in some specimens of *Anisolophus* and *Tetramerorhinus* (Fig. 2D; Soria 2001:117). The occipital condyle has an articular surface slightly narrower than *Epitherium laternarium* and *Diadiaphorus* and less high than *E. laternarium* but higher than *Te. cingulatum*. The paraoccipital process is heavy and projects below the inferior borders of the occipital condyles (Fig. 2D), differing from *Thoatherium minusculum* and *Tetramerorhinus cingulatum*, which have shorter processes.

A large, caniniform incisor is the largest in the available comparative sample (Table 1; Fig. 2A, C). Soria (2001) suggested it could be a dimorphic character. An anterolingual cingulum in the molariforms is present in most of the specimens here studied (Fig. 2A, E–F), such as in *Thoatherium minusculum* and *Epitherium laternarium*, but differs noticeably from *Eoauchenia primitiva*, which lacks this character (Fig. 3). The P2 is nearly quadrangular, which is not common in proterotheriids. The M3 is located below the orbit (Fig. 2B), similar to *Eoauchenia primitiva* but differing to *Diadiaphorus majusculus*, *Thoatherium minusculum*, and *Epitherium laternarium*, which have the M3 located behind or near to the posterior border of the orbit (Fig. 3). It differs from *Eoauchenia*, which has hypocone in M3; rather, it is reduced or absent, as occurs in some taxa such as *Thoatherium* and *Te. lucarius*. The molariforms of *Neolicaphrium* are not so brachyodont as some Huayquerian taxa as *Lophogonodon* or *Neobrachytherium*

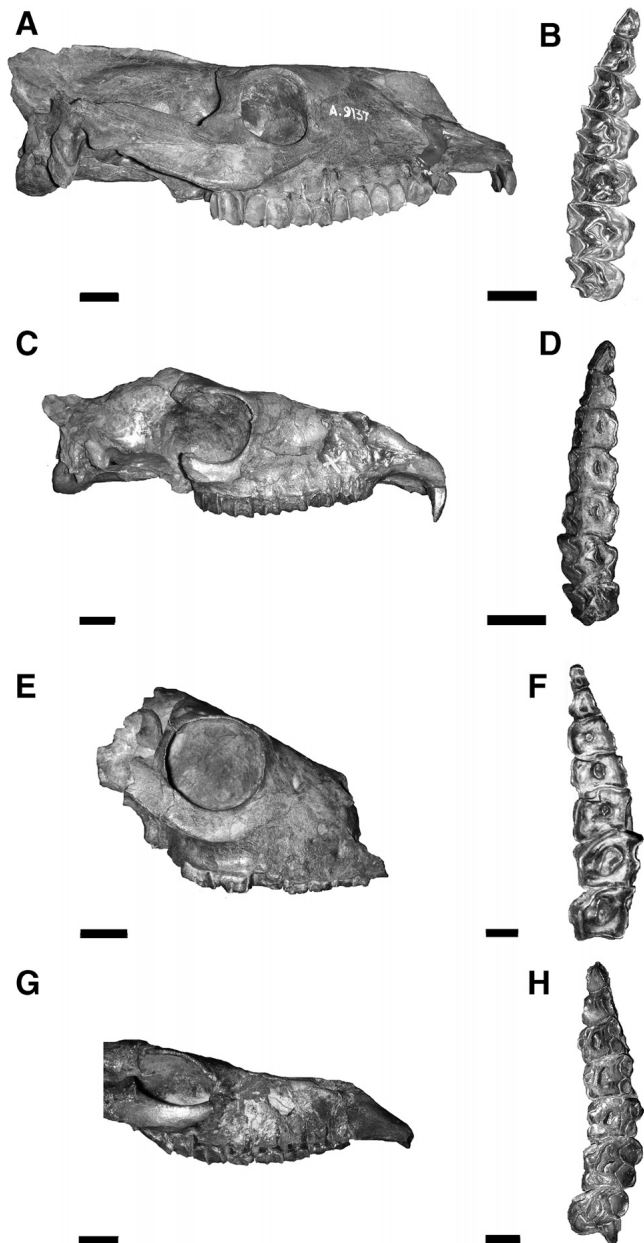


FIGURE 3. Left: skulls in lateral view. Right: occlusal view of upper postcanine series. **A–B**, *Diadiaphorus majusculus* (MACN-A-9137); **C–D**, *Epitherium laternarium* (MACN-Pv-8001); **E–F**, *Eoauchenia primitiva* (MACN-Pv-8002) (inverted image from left); **G–H**, *Thoatherium minusculum* (MACN-A-9080) (inverted image from left). Scale bars equal 2 cm in **A–E** and **G**, 1 cm in **F** and **H**.

but are relatively higher and comparable to forms such as *Epitherium*. The cheek teeth of *Neolicaphrium* cf. *N. recens* also possess cementum, as in *Eoauchenia primitiva*, but differ from this genus in being lower crowned with an anterolingual cingulum and with the central valley not very deep, contrasting with the very deep central fossa of *E. primitiva* (Fig. 3). By the characters mentioned, the upper molariforms of the studied material are more similar to those of *Epitherium laternarium*, differing in their smaller size and the presence of cementum. Nevertheless, the absence of cementum observed in some taxa could be a preservational bias, so this character should be taken with caution. The

TABLE 2. Eigenvalues (E) and % of variation of principal components (PCs).

PC	E	%
1	738.7	93.3
2	16.1	2.03
3	11.4	1.4
4	7.5	0.9
5	7.1	0.9
6	5.5	0.7
7	2.06	0.2

genus *Proterotherium*, represented according to Soria (2001) only by *P. cervioides* and by few comparable material, has columns and labial folds at the paracone and metacone in M1 and at the paracone in M2, which are absent in the material here studied.

A principal component analysis (PCA) was performed on the most complete comparative material (see Table 1). The purpose of this analysis is to compare the taxa based on a set of selected characters in a multidimensional approach that help distinguish the influence of size and shape. Due to the fragmentary condition of specimens FC-DPV-749 and MACN-Pv-16603b, they were not included in the analysis. The data matrix included 19 quantitative characters, and eigenvalues and eigenvectors were obtained using the variance-covariance matrix. The first three principal components (PCs) encompass 96.5% of the total variation (Table 2). Lengths of P1–M3, P1–M1, and P1–4 have the greatest effect on PC 1 and PC 2 and the bicondylar width to PC 3 (Table 3).

The PCA analysis including most complete skulls indicates that the cranial material here studied belongs to a small proterotheriid. The projection of the first and second principal components shows that MACNS-92, here referred to *Neolicaphrium* cf. *N. recens*, is clearly related in multidimensional space to the small proterotheriids (Fig. 4A). PC 1 clearly separates small taxa such as *Eoauchenia primitiva*, *Tetramerorhinus* sp., *Thoatherium minusculum*, and MACNS-92 from the medium to larger taxa such as *Anisolophus*, *Prolicaphrium*, *Epitherium*, and *Diadiaphorus majusculus*. Interestingly, the small species are well separated along the second component, usually related to shape (Fig. 4A). The minimum-length spanning tree (MST) was calculated and

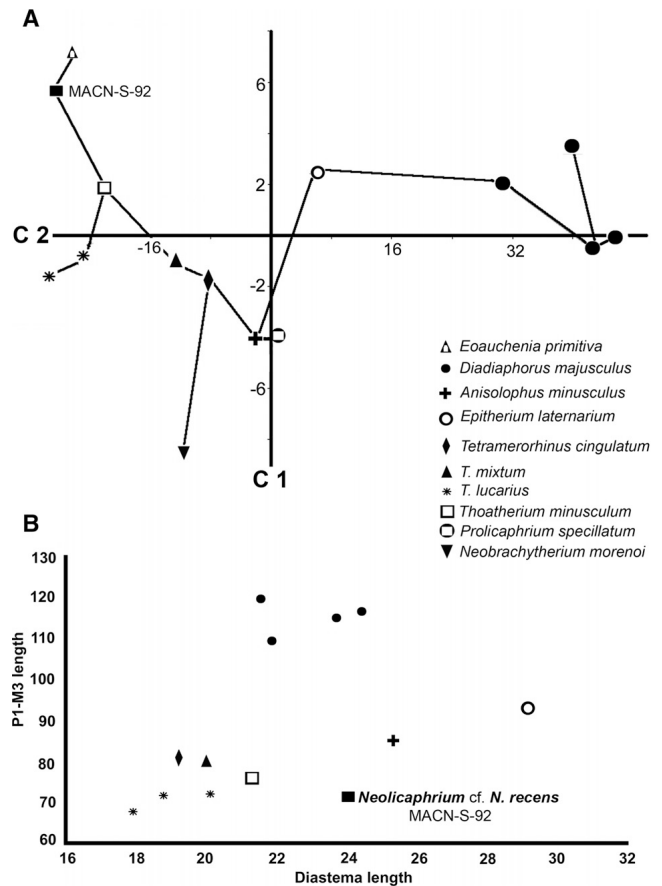


FIGURE 4. **A**, Projection of first two principal components (C 1 and C 2, respectively) based on dental and cranial measurements of some proterotheriids and MACN-S-92 from the Sopas Formation. The black line connecting the points is the minimum-length spanning tree (MST) superimposed. **B**, Bivariate diagram of some proterotheriid species based on diastema and P1–M3 length (measurements from Table 1).

TABLE 3. Loadings for first three principal components (1, 2, and 3) based on dental and cranial characters (see Table 1).

	1	2	3
DL	0.02426	0.1595	-0.1192
P1–4L	0.3568	-0.4458	-0.09117
P1–M1L	0.4659	-0.4278	0.00766
M1–3L	0.3004	0.3069	0.1274
P1–M3L	0.6557	0.4252	-0.2761
APWI	-0.004437	-0.0001641	-0.01677
BicW	0.09509	-0.04425	0.8177
P2L	0.09507	-0.2157	-0.2126
P2W	0.05337	-0.2932	-0.09056
P3L	0.1061	-0.09003	0.1131
P3W	0.1036	-0.1505	0.06127
P4L	0.1086	-0.1391	0.05426
P4W	0.09782	-0.1557	0.1727
M1L	0.1101	0.0863	0.09494
M1W	0.123	0.1916	0.1626
M2L	0.1266	0.2	0.06899
M2W	0.1247	0.1135	0.2067
M3L	0.06801	0.1091	0.01934
M3W	0.08358	-0.006583	0.1734

Abbreviations: AP, anteroposterior; Bic, bicondylar; D, diastema; L, length; W, width. In bold are indicated characters with highest loadings values for each component.

plotted onto the 2D diagram that helps to preclude misinterpretations of the position of points. The ordering of connections is congruent with the expected pattern where the MACNS-92 is spatially connected with the smallest taxa of proterotheriids considered (Fig. 4A).

The postcanine series is quite anteroposteriorly short, similar to that of the small species of *Tetramerorhinus* (particularly *T. lucarius*), *Eoauchenia primitiva*, *Neobrachytherium morenoi*, and also the small *Thoatherium minusculum* (Fig. 4B; Table 1). In contrast, the diastema is large relative to the short cheek teeth series, similar to the large *Diadiaphorus majusculus* and *Anisolophus minusculus* (Fig. 2A, C; Fig. 4B). Moreover, MACNS-92 has the highest diastema/P1-M3 ratio, close only to that of *Epitherium laternarium* and *Anisolophus minusculus* (Table 1). It shows that this taxon had a relatively long snout with a large caniniform.

FC-DPV-749 is similar in size to the material from the Río Arapey Grande and also the molariform of the Río Coronda from Argentina (Table 1). The molariform is subquadrangular and shares a similar size with small species of proterotheriids (Table 1) but relatively more elongated with respect to the material from Uruguay. Soria (2001) identified the material from the Río Coronda as *Neolicaphrium recens* but did not include illustrations of it and considered it as a possible M1 or M2. Due to the scarcity

of evidence available, we consider here the material from Santa Fé province at the generic level only.

CONCLUDING REMARKS

Taking into account that the only known Pleistocene proterotheriid, *N. recens*, was described only based on mandibles, the material here studied is the first known cranial remains of a Pleistocene member of this family. According to the available evidence and the comparisons carried out, its skull yields a unique combination of characters that are enough to differentiate it from the rest of the genera described on the basis of skull characters. It has a relatively large orbit and diastema, the largest caniniform of the sample here considered, an anteroposteriorly short postcanine tooth series, molars with an anterolingual cingulum, and M3 below the orbit with a reduced or absent hypocone. At first glance, it appears that M3 is located below the orbit in those specimens with large orbits (such as *Neolicaphrium* and *Eoauchenia*) and that it is located behind them in those with small orbits (as *Diadiaphorus*), suggesting an ontogenetic constraint on these two characters. The PCA places the specimen identified as *Neolicaphrium* cf. *N. recens* close to the smallest species of Proterotheriidae considered in the analysis.

The fossils of Uruguay were found in the Sopas Formation, which yields mandibular remains undoubtedly described as *N. recens* by Bond et al. (2001); the occurrence of skull remains of this taxon in these beds is to be expected. A taxonomic revision of the Miocene and Pliocene proterotheriids, which is beyond the scope of this paper, should be carried in order to facilitate the elucidation of the phylogenetic relationships of this species.

The material here described reinforces the geographic pattern based on the fossil record of this small Pleistocene proterotheriid that it is restricted to a latitudinal band that includes northeast Argentina (Provincias de Córdoba, Santa Fé and Corrientes) and northern Uruguay (departamentos de Salto and Tacuarembó) (Fig. 1).

It is important to note that some taxa of the Sopas Formation of Uruguay not only are characteristic Pleistocene mammals but also indicate the occurrence of forested to semi-open areas (Bond et al., 2001; Ubilla et al., 2004). *Neolicaphrium recens* could have been part of a relictual lineage of proterotheriids restricted to warmer and more forested areas than Pampean ones (Bond et al., 2001). The mammal association of the Sopas Formation has been related to the last interglacial or last interstadial due to the occurrence of many 'Brazilian' taxa such as *Tapirus*, *Coendou*, *Myocastor*, *Hydrochoerus*, and *Lundomys*, among others (see Ubilla et al., 2004). The relatively high values of mesodonty observed in *N. recens* (Bond et al., 2001), along with the presence of cementum in the molariforms, suggest a likely adaptation to forested, savanna-like habitats, which is in agreement with the information provided by the associated fauna (Ubilla et al., 2004).

Of meaningful significance is the co-occurrence in the Sopas Formation of *Neolicaphrium recens* with an important diversity of deer (five species), its supposed competitors, as well as other Holarctic ungulates (Bond et al., 2001), which are predominant in bone samples (Ubilla and Lorenzo, 2001). *N. recens* was part of mammal communities that included Holarctic ungulates, suggesting that they were apparently not related to its extinction, and that at least this taxon coexisted with them throughout the entire Pleistocene.

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