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A PLEISTOCENE GIANT RIVER OTTER FROM ARGENTINA: REMARKS ON THE FOSSIL RECORD AND PHYLOGENETIC ANALYSIS

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ABSTRACT—The fossil record of Neotropical Lutrinae is very incomplete, with a few specimens of *Lontra* and three records of *Pteronura*. The published records of *Pteronura* correspond to remains of *Pteronura* sp. from Lujanian beds in Entre Ríos province (Argentina) and *P. brasiliensis* found in the "Late Pleistocene" of Brazil, but they lack stratigraphic context and their age could range from at least 380–0.9 Ka. *P. brasiliensis*, the giant river otter, inhabits rivers and lakes of northern central South America, and has been related to the North American fossil otter *Satherium*. In this work we describe and compare a very complete specimen of *Pteronura* found in Entre Ríos province using classical morphological descriptive and multivariate analyses, discuss the importance of this specimen for the fossil record of the taxon, and perform a preliminary phylogenetic analysis. The specimen agrees in morphometric and qualitative characters with the recent species *P. brasiliensis*, but is slightly larger and presents some minor differences in skull and dental morphology. These differences are interpreted as intraspecific variation, thus the fossil is interpreted as *P. brasiliensis*. In the phylogenetic analysis, the studied specimen clusters with *P. brasiliensis*, corroborating the taxonomic determination and supporting a relationship between *Satherium* and *Pteronura*. The specimen is the first fossil record of the genus for Argentina, and the oldest corroborated record, with a 130–125 Ka tentative age.

INTRODUCTION

The lutrines are currently represented by seven genera and 13 species that occur in nearly all continents, from southern South America to northern North America, Europe, Asia, and Africa (Wilson and Reeder, 2005). The fossil record of this subfamily begins in the lower Miocene of Europe, Asia, and North America, where several taxa have been recovered (Van Zyll de Jong, 1972; Willemsen, 1992; Baskin, 1998; Werdelin and Lewis, 2005). These continents have also yielded several Pliocene and Pleistocene records. The group also has late Miocene, Pliocene, and Pleistocene reports in Africa (e.g. Van Zyll de Jong, 1972; Hendey, 1974). In contrast, the lutrine fossil record in South America begins in the Pleistocene, but is very scarce during that period (Berta and Marshall, 1978; Marshall et al., 1984; Berman, 1994; Cartelle and Hirooka, 2005; Soibelzon and Prevosti, in press).

Two genera of lutrines live in South America: Lontra (American otter), with three species (L. longicaudis, L. felina, and L. provocax), and the monotypic Pteronura brasiliensis (giant river otter) (Wilson and Reeder, 2005), both represented in the fossil record of this continent. The oldest lutrine record is L. longicaudis from the Ensenadan of Buenos Aires province in Argentina (Rusconi, 1932; Berta and Marshall, 1978; Berman, 1994), found in levels that could be dated between 1.8 and 0.98 Ma (Soibelzon et al., 2005). Other Pleistocene records of this species come from the Lujanian (late Pleistocene-early Holocene) of Buenos Aires province and northern Uruguay, and from the late Pleistocene of Minas Gerais and Bahia in Brazil (Ameghino, 1889; Lessa et al., 1998; Cartelle, 1999; Ubilla et al., 2004; Cartelle and Hirooka, 2005). The Argentinean fossil has been found in Lujanian beds potentially between 130 and 8.5 Ka (Cione and Tonni 1999, 2005), whereas the Uruguayan record comes from beds dated between 58 and 43 Ka (Ubilla et al., 2004). The age of the Brazilian remains is problematic because of the lack of clear stratigraphy in these caves and the complex taphonomic history of these sites (see Auler et al., 2006). Fossils from these caves have been dated from 30 Ka to the Holocene (Auler et al., 2006).

The record of Pteronura is even poorer, and until a few years ago some authors (e.g., Hunt, 1996) deemed it as nonexistent. Some have considered that the "Lutra aff. brasiliensis" of Lund (1842) corresponded to Pteronura brasiliensis (e.g. Paula Couto, 1940; Paula Couto in Lund, 1950; Berta and Marshall, 1978), but Winge (1895), who studied the specimens, stated that they belonged to Lontra longicaudis (see Cartelle and Hirooka, 2005). Cartelle (1999) listed P. brasiliensis from the late Pleistocene of Bahia (Brazil), but without any specification or support for this mention. Later, Carlini et al. (2002), Carlini el at. (2004), and Noriega et al. (2004) mentioned a very complete specimen from the Lujanian of Entre Ríos province (Argentina), which was found in a layer assigned to the last interglacial (≈130 Ka). These authors noted that this locality is outside the recent distribution range of P. brasiliensis. Though Carlini et al. (2002) did not publish a detailed description of the fossil, they mentioned that the skeleton was larger than the recent species, and suggested that the specimen could represent a new species of Pteronura. More recently, Cartelle and Hirooka (2005) described some remains from the Pleistocene of Mato Grosso (Brazil), and Penini et al. (2006) cited this species for the same age and region. In both cases the age is loosely referred to the late Pleistocene, but this must be verified in the future.

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SPECIMEN	CBL	LOO	BW	PW	RWC1	WBC	WPC	IOW	LM	HCP	HHR	WHR	LC1	WC1
CICYTTP-PV-M-1-21	174.50	154.60	111.10	57.65	43.35	85.75	19.95	22.95	117.45	52.30	23.40	10.85	10.05	8.35
Х	152.73	135.77	95.79	50.99	34.59	73.36	16.40	18.01	97.15	43.22	20.16	9.04	8.79	6.88
SD	7.19	5.49	5.05	2.31	1.98	2.35	1.43	1.67	4.51	1.89	1.38	0.47	0.51	0.47
CV	4.71	4.05	5.27	4.53	5.72	3.21	8.73	9.28	4.64	4.38	6.85	5.21	5.84	6.78
CV*	5.44	4.87	6.13	5.16	7.60	4.68	9.56	10.60	6.51	6.20	7.48	6.63	6.40	7.91

TABLE 1. Measurements (in mm) of fossil (CICYTTP-PV-M-1-21) and recent specimens of Pteronura brasiliensis.

The monotypic genus that includes the giant river otter (*Ptero-nura*) shows some morphological affinities with *Satherium*, a genus occurring in Pliocene-early Pleistocene beds of USA (Van Zyll de Jong, 1972; Kurtén and Anderson, 1980; Baskin, 1998). However, no detailed comparisons between these genera, or a phylogenetic analysis of *Satherium*, are available at present.

In this paper we describe the *Pteronura* specimen mentioned by Carlini et al. (2002) and compare it with several lutrines to test their hypothesis that it represents a new species. We also discuss the fossil record of *Pteronura* and the phylogenetic arrangement of the Lutrinae based on a preliminary cladistic analysis of craniodental characters (plus one postcranial character).

MATERIALS AND METHODS

Cranial anatomical nomenclature is in accordance with Evans (1993), while cusp terminology follows Wang et al. (1999), with some modifications to adapt it to the orientation nomenclature proposed by Smith and Dodson (2003) (e.g., posterior accessory cusp was changed to distal accessory cusp). We follow the biostratigraphic/chronostratigraphic scheme of Cione and Tonni (2005). Measurements were taken using dial and digital callipers with 0.05 mm precision; they are listed in Table 1 and Supplementary Data 1 (www.vertpaleo.org/publications/JVPContents .cfm) and illustrated in Figure 1.

The principal components analyses were performed from the variance-covariance matrix obtained from the \log_{10} -transformed measurements of Table 1. We did several independent analyses with different combinations of measurementes, but present only those based on cranial, mandibular, lower and upper dentition measurements, since the others yielded similar results. The size factor was corrected with the multivariate extension of the Lleonart et al. (2000) methodology (see Marroig and Cheverud, 2004).

The recent distribution of *Pteronura brasiliensis* (Fig. 2) was taken from Cabrera (1958), Massoia (1976), Eisenberg (1989), Redford and Eisenberg (1992), Linares (1998), Eisenberg and Redford (1999), Beccaceci and Waller (2000), Wilson and Reeder (2005), Barquez et al. (2006), and dos Reis et al. (2006).

The phylogenetic analysis (maximum parsimony) was performed with the program TNT (Goloboff et al., 2003a), using equal weight and unordered states for all characters (see Appendices 1-2). We conducted an exact search (implicit enumeration), and used rule number 1 for collapsing trees (see Coddington and Scharff, 1994). Branch supports were measured with symmetrical resampling (1000 resamplings and implicit enumeration), estimating absolute frequencies and frequency differences (see Goloboff et al., 2003b). We included all the living genera of Lutrinae, plus Satherium, and several mustelines, mephitids, and procyonids as outgroups (14 total taxa). The 69 parsimoniously informative craniodental and postcranial characters were scored from specimens deposited in museums, with the exception of some states of Satherium piscinarium, where we followed Gazin (1934), Barbour and Schultz (1937), and Bjork (1970, 1973). The majority of the characters were modified from Van Zyll de Jong (1972), de Muizon (1982), Berta and Morgan (1985), Willemsen (1992), Bryant et al. (1993), and Wolsan (1993) (see Appendix 1). We were able to study UF 95088, a cast of a mandibular fragment with the p4-m1 of Satherium piscinarium.

Anatomical and Metric Abbreviations—BW, bizygomatic width; CBL, condylobasal length; HCP, height of coronoid process; HHR, height of horizontal ramus below distal border of m1; IOW, minimum interorbital width; LM, length of mandible, from condyle to mesial border of c1; LOO, distance between occipital condyles and anterior margin of premaxillaries; PW, maximum palatal breadth; RWC1, rostrum width at C1; WBC, maximum width of braincase, taken above temporal crests; WHR, width of horizontal ramus below distal border of m1; WPC, minimum width of postorbital constriction.

Dental Terminology—C/c, upper/lower canine; **L**, mesiodistal length of dental elements; **LM1**, labial length of M1; **Ltrm1**, length of m1 trigonid; **M/m**, upper/lower molar; **P/p**, upper/lower premolar; **W**, labiolingual distance of dental elements; **Wm1**, width of m1 at talonid; (see Fig. 1).

Institutional Abbreviations—AMNH M, American Museum of Natural History, Mammalogy, USA; CEMyF, Colección Elio Massoia y familia; CICYTTP-PV-M, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante, Argentina. Laboratorio de Paleontología de Vertebrados; EBRG, Estación Biológica Rancho Grande, Venezuela; FMNH, Field Museum of Natural History, Department of Mammalogy, USA; MACN Ma, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Departamento Mastozoología, Argentina; MLP Ma, Museo de La Plata, Departamento Científico Zoología Vertebrados, Argentina; MUSM Ma, Museo de la Universidad de San Marcos, Mastozoología, Perú; UF, Florida Museum of Natural History, Vertebrate Paleontology, University of Florida, USA.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821 Suborder CANIFORMIA Kretzoi, 1938 Family MUSTELIDAE Fischer, 1817 Subfamily LUTRINAE Bonaparte, 1838 Genus PTERONURA Gray, 1837 PTERONURA BRASILIENSIS (Gmelin in Linnaeus, 1788) (Fig. 3, Table 1)

Emended Diagnosis—very large lutrine (CBL > 135 mm); skull long and narrow; postorbital constriction very long and narrow; rostrum short (anterior border of orbit above P2); postorbital process not enlarged; anterior opening of palatine channel at level of P1–2 contact; sphenopalatine foramen rounded; posterior carotideal foramen located at level of scar for longus capitis muscle; two small foramina present over foramen magnum; lateral borders of basiooccipital expanded ventrally; subangular lobule well developed; horizontal ramus lower than in *Satherium piscinarium*; dentition sharp; P3 with well developed distolingual cingulum; parastyle of P4 well expanded mesially; m1 without metastylid.

Studied Material—CICYTTP-PV-M-1-21, skull and mandible with most of dentition; incomplete vertebrae; fragments of ribs; incomplete left scapula; right humerus; fragments of left humerus; fragments of right radius; distal fragment of left radius; left ulna; left metacarpals 2–5; some carpal elements; fragment of the pelvis; proximal fragment of left femur; left tibia and fibula;

SPECIMEN	LP3	WP3	LP4	WP4	LM1	WM1	Lp3	Wp3	Lp4	Wp4	Lm1	Ltrm1	Wm1	Lm2	Wm2
CICYTTP-PV-M-1-21	10.40	7.85	19.65	16.6	14.25	19.15	9.15	6.30	13.05	8.85	22.2	13.15	12.55	8.60	8.30
Х	9.46	6.73	17.64	13.66	10.66	16.21	8.21	4.96	11.36	6.82	19.14	11.78	9.58	6.87	6.80
SD	0.72	0.55	0.90	0.741	0.98	0.61	0.53	0.33	0.64	0.44	1.02	0.51	0.49	0.52	0.60
CV	7.66	8.11	5.11	5.43	9.16	3.73	6.51	6.64	5.63	6.46	5.37	4.33	4.79	7.56	8.10
CV*	7.72	8.56	5.46	6.73	11.00	5.06	6.77	8.58	6.25	8.67	6.11	4.83	7.77	9.03	9.10

TABLE 1. (Extended)

Abbreviations: X, mean of recent specimens; SD, standard deviation of Recent specimens; CV, coefficient of variation of recent specimens plus CICYTTP-PV-M-1-21

*Approximate measure. See text for other abbreviations.

incomplete right tibia; nearly complete left and right posterior autopodium; isolated phalanges.

Description

Horizon, Age, and Locality-The fossiliferous locality is located on the south bank of Ensenada Creek (32° 7' 43" S, 60° 26' 12" W), Department of Diamante, Entre Ríos province, Argentina (Fig. 2). The fossil material comes from the Arroyo Feliciano Formation (Carlini et al., 2002), a unit composed of fine sands and clayey greenish silts which crops out as the highest terrace along the major rivers and streams of Entre Ríos province (Iriondo et al., 1985; Iriondo, 1996). This geologic unit is assigned to the Lujanian Stage/Age (130-8.5 Ka, late Pleistocene; Cione and Tonni, 1999, 2005) based on the biochronology of the mammals it bears (Noriega et al., 2004). Noriega et al. (2004) have suggested that this level could correspond in age to the last interglacial due to the presence of fauna associated with warm and humid climatic conditions (e.g. Tapirus). This information suggests that the age of the fossil giant otter could be 130-120 Ka.

Skull—The specimen is a well preserved complete skull, with most of the basicranium flattened and broken. The occipital condyles and part of lateral occipitals are also well preserved. All sutures are obliterated. The dorsal and lateral bones of the cranium and rostrum are practically intact, whereas the parietal region is compressed. Cranial measurements are given in Table 1 and show that the specimen corresponds to a very large lutrine. The skull is very flat and low in lateral profile, with a shallow sagittal crest that begins near the postorbital processes and reaches the lambdoideal crests. It is proportionally long and narrow. The rostrum has a steep slope. The anterior border of the orbits is above P2. The facial region is nearly level with the cranium. The infraorbital foramen is very large and elliptical. In lateral view, the preorbital processes are visible as small rounded swellings. Platelike ossifications are present at the anterionternal



FIGURE 1. Schematics showing the measurements taken in this study. **A**, skull in dorsal view; **B**, skull in ventral view; **C**, mandible in lateral view; **D**, c1-m2 in occlusal view; **E**, C1-M1 in occlusal view. Modified from Van Zyll de Jong (1972).



FIGURE 2. Map of the Recent distribution of *Pteronura brasiliensis* and *Pteronura* fossil localities. **Circle**, Gruta do Curupira (Cartelle and Hirooka, 2005); **Square**, Serra da Bodoquena (Penini et al., 2006); **Star**, Arroyo Ensenada (Carlini et al., 2002).



FIGURE 3. Skull and mandible of the new specimen of *Pteronura brasiliensis* (CICYTTP-PV-M-1-21). **A**, skull in dorsal view; **B**, skull in ventral view; **C**, skull in lateral view; **D**, mandible in lateral view; **E**, mandible in medial view, **F**, mandible in dorsal view. Scale bar equals 50 mm.

parts of the orbits, and cover part of the anterior section of the zygomatic arches and the lacrimals laterally. In dorsal view, the left ossification develops a conspicuous process in the same horizontal plane as the frontals, hardly higher than the nasals. The nasals have a V-shaped contact with the frontals. In dorsal view, the cranium shows a long, narrow postorbital constriction, with smoothly concave lateral margins; this constriction is narrowest near the postorbital processes. The lambdoideal crests are poorly developed and well separated, forming an angle of 140° and projecting backwards to end just before to condyles. The ventral region of the skull is well preserved, except for the basicranium;

it shows a complete zygomatic arch, premaxilla and maxilla with well preserved toothrow. Palate length is at least 26 mm behind M1. The palatines are robust and their posterior margins are broken. The vomer, presphenoids, pterygoids, and basisphenoids are missing. The postglenoid processes are broken and both mastoid processes are intact, robust, and greatly expanded anteroventrally. The left glenoid fossa is incomplete. Broken and compressed pieces of bone from the ventral floor of the braincase are found inside the skull. The tympanic bullae are flattened by compression and strongly displaced into the cranial cavity. Their size and morphology is very difficult to discern, but it is clear that they are not inflated and that a large external auditory meatus is present. Most of the foramina and other anatomical details of the tympanic basicranial region have been destroyed by strong compression. The paraoccipital processes are platelike, with a broad triangular base and backward orientation. In anterior view, the premaxilla shows bony rounded excrescences between the third incisor and the canine, and around the lateral border of C1 alveolus. These excrescences are better preserved on the right side. The supraoccipital is poorly preserved and represented by a smoothly concave edge. The nuchal region is broken. The ascending process of the supraoccipital is represented by a lateral expansion, visible in dorsal view. The occipital condyles are well preserved. One foramen opens above the upper border of the foramen magnum on the left side, while two smaller foramina are in the right side.

Mandibles—The jaw is well preserved, although it shows significant damage. The articular processes are broken. The left hemimandible is severely damaged at the level of masseteric fossa, both the coronoid and condylar processes are well preserved. The right hemimandible shows a relatively deep masseteric fossa. The coronoid processes are relatively low and with a rectangular shape. The condyle is laterally broad, well rounded, and positioned level with the tooth row. The height of the horizontal ramus is slightly greater than the length of m1. The mandibular symphysis is long and low, and extends distally to below the mesial border of p4. Three mentonian foramina are present on the right mandible, one below p3, another below the mesial border of p2, and the last one below the distal border of c1.

Dentition—All upper incisors are well preserved and unworn or with very little wear, as can be seen in the labial face of m1. The I1-2 are small and possess a single labiolingually compressed cusp. The size of I3 is twice that of I1-2 and it presents a more conical cusp with notable mesiolingual cingulum. The incisor series is nearly straight, with a diastema separating it from C1. The upper canines are strong, with crowns more laterally compressed on the lingual than on the labial side, with the cones slightly curving caudally. The axis of the canine forms an angle close to 90° with respect to the tooth row. The single-rooted P1 has a small, single, conical cusp located immediately behind the canine. The single-rooted P2 possesses a laterally compressed cusp, larger than that of P1. The P3 is double-rooted and laterally compressed. The paracone is placed higher than the metacone in the upper carnassial. The outline of the P4 talon is much expanded and forms a shelf (the "medial," "protoconal," or "internal" shelf of different authors) that is nearly semicircular and reaches the distal part of the metastyle. The wider part of this shelf is at the level of the paracone, with a central depression. The P4 shows a strong parastyle, a somewhat elevated ridgelike protocone, and a small cusp between paracone and protocone. The protocone is located at the mesiolingual border of the talon and the parastyle is well expanded mesially. The M1 bears all the typical cusps (parastyle, paracone, metacone, protocone, metaconule, and hypocone), but it is relatively short and wide and rectangular in outline. The right M1 has a smooth edge between the protocone and hypocone; this feature is absent in the left molar.

The crowns of i1–2 are conical and very small. These teeth are not preserved in the right mandible. The i3 is larger than i1–2 and has a strong distolingual cingulum. Both c1 are well preserved, although the right cusp is broken. The c1 are strong and similar in size to the upper canines, but with more curved axes. The p2 is not preserved in the right mandible; the right p3 is broken and the left lacks some parts of the tooth. The p2 is double-rooted and has a single main cusp. The right p3 has a well-developed cingulum. The p4 has an accessory cusp, very conspicuous in lateral view, located behind the main cusp. The metaconid of m1 is smaller than that of the other trigonid cusps and is located distolingually. The labial cingulum of the trigonid is well developed. The talonid is shorter than the trigonid, and its distal portion is acute. The labial portion of the talonid bears a well developed hypoconid and a small hypoconulid. In lateral view, a well developed W-shaped labial cingulum is present, with a strong, high edge at the level of the protoconid. The m2 shows a tall crestlike labial cusp (protoconid) and a strong lingual cusp (metaconid).

Postcranium—The preserved postcranial elements are morphologically very similar to recent specimens of *P. brasiliensis*. The epiphyses are not completely fused in some elements (e.g., tibia, fibula, humerus).

Morphometric Analyses

The analyses of cranial and dental measurements show that, with the exception of LM1 and Lp3, CICYTTP-PV-M-1-21 is larger than the studied recent specimens of *P. brasiliensis* (Table 1). The metric differences between CICYTTP-PV-M-1-21 and the largest *P. brasiliensis* are <10 %, with the exception of, HCP, IOW, RWC1, LM1, Lm2, Wp4, and Wm1, all of which are 11.5–17% (Table 1). On the other hand, the inclusion of CICYTTP-PV-M-1-21 in the sample of recent *P. brasiliensis* slightly increased the values of the coefficient of variation, but this increase only exceeded 10% in the case of LM1.

All PCAs performed agreed in the separation of the fossil specimen along the first component, but not along other components (Fig. 4A). The first three components explain almost all the variance of the sample (Table 2). The first component appears to be a "size vector," because it explains a large portion of the variance and all variables load with the same sign and similar weight. Size correction resulted in CICYTTP-PV-M-1-21 falling within the range of recent *P. brasiliensis* (Fig. 4G–I).

Phylogenetic Analysis

The analysis results in a single most parsimonious tree of 151 steps (Fig. 5A). In the cladogram, the Mustelidae (including mephitids; Node 18), Mustelinae (Node 16) and Lutrinae (Node 23) are monophyletic. The Lutrinae clade assumes a pectinate shape, with *Enhydra* as the basal taxon, followed by *Aonyx*, Recent *Pteronura brasiliensis* + specimen CICYTTP-PV-M-1-21, and finally a group that includes *Satherium*, *Amblonyx*, *Lontra*, *Lutra*, and *Lutrogale*. In this tree, *Amblonyx* is the sister taxon of *Satherium* and *Lutra* + *Lontra* + *Lutrogale* form a clade.

In this phylogeny, Mustelidae (Fig. 5A: Node 18) is supported by the following morphological transformations: mastoid process directed anteroventrally; external auditory meatum forming a complete ring; P4 without carnassial notch or hypocone; and reduction of the parastyle in the P4. Lutrinae (Node 23) is supported by four derived states: large infraorbital foramen; anteroventral portion of the zygomatic arch platelike; paraoccipital process laminar; presence of a flat surface posterior to the mastoid process and external auditory meatus. Specimen CICYTTP-PV-M-1-21 shares several synapomorphies with Recent specimens of *P. brasiliensis*, such as a long and narrow skull, long postorbitary constriction, anterior border of the orbits above P2, lateral borders of the basioccipital projected ventrally, parastyle of P4 expanded mesially, presence of foramina above the foramen magnum, and posterior carotid foramen at the level of the scar for the capitis longus muscle. On the other hand, Satherium is included as the sister taxon of Amblonyx because the masseteric fossa is expanded anteriorly below m2 and the anterior



FIGURE 4. Principal components analyses including CICYTTP-PV-M-1-21 (diamond) and Recent *Pteronura brasiliensis* (filled circles). A and B, cranial measurements; C and D, upper dentition; E and F, mandible plus lower dentition. Principal components analyses with size correction. G, cranial measurements; H, upper dentition; I, mandible plus lower dentition. Abbreviations: PC, principal components; %, percentage of variation explained.

margins of the orbits are placed above the mesial portion of P3. Other character transformations occurring in this tree are listed in Appendix 3.

Branch support values are quite strong for Mustelidae (Node 18), Mustelinae + Lutrinae (Node 17), Mustelinae (Node 16), and Recent + fossil *Pteronura* (Node 26). In contrast, the Lutrinae (Node 23), Node 22, and Node 24 possess low values, but positive differences of frequencies (GCs); Nodes 19–21 and 25 have negative GCs.

DISCUSSION AND CONCLUSIONS

Systematics

Some features of the skull and dentition, like the fused cranial sutures and the little-worn permanent dentition, indicate that CICYTTP-PV-M-1-21 is an adult specimen; the presence of some non-obliterated sutures in the postcranium, however, shows that it is a young adult. Indeed, this latter characteristic was mentioned by Carlini et. al (2002).

The large size and general configuration of the skull of

CICYTTP-PV-M-1-21 (e.g., long and narrow with very large and compressed postorbital constriction) constitute a combination of characters that only occurs in Pteronura (see Van Zyll de Jong, 1972). The other genus that is similar in these aspects is the fossil Satherium, but several features separate it from CICYTTP-PV-M-1-21 and Pteronura, such as the presence of a longer rostrum, orbits located at the distal border of the P3, wider postorbital constriction, parastyle of P4 not mesially expanded, m1 with metastylid, mandibular condyle situated lower with respect to m1, and a stronger horizontal ramus of the mandible (cf. Bjork, 1970; see also Gazin, 1934; Bjork, 1973). Some authors (e.g. Gazin, 1934; Van Zyll de Jong, 1972; Bjork, 1973) have mentioned the presence of a cuspule between the protocone and the mesial part of the metacone in P4 as a distinctive character of Satherium. However, Bjork (1970) showed that this structure is variable and absent in the P4 figured by Gazin (1934:fig. 3), where it is replaced by a transverse crest. The presence and development of this structure is variable in P. brasiliensis and Aonyx. Other characters that associate CICYTTP-PV-M-1-21 with P. brasiliensis and exclude Satherium are the above

TABLE 2.	Factor loadings and additional data for principal component
analyses.	

Skull			
	PC 1	PC 2	PC 3
CBL	0.28	-0.24	0.04
LOO	0.26	-0.22	-0.02
BW	0.26	-0.42	0.02
PW	0.24	-0.25	0.13
RWC1	0.36	-0.22	0.54
WBC	0.21	-0.24	0.01
WPC	0.42	0.71	0.45
IOW	0.61	0.21	-0.71
Eigenvalue	0.005	0.001	0.0005
% Total variance	63.78	20.64	7.17
Upper Dentition			
	PC 1	PC 2	PC 3
LC1	-0.31	-0.12	0.39
WC1	-0.37	0.04	0.01
LP3	-0.31	0.61	0.30
WP3	-0.41	0.40	-0.15
LP4	-0.27	0.01	0.29
WP4	-0.29	0.13	-0.75
LM1	-0.55	-0.65	0.05
WM1	-0.22	-0.12	-0.29
Eigenvalue	0.007	0.001	0.0006
% Total variance	72.11	13.13	6.10
Lower Dentition and Mandible			
	PC 1	PC 2	PC 3

LM	-0.25	0.2	-0.07
HCP	-0.23	0.13	0.14
HHR	-0.26	0.51	0.23
WHR	-0.26	0.17	0.22
Lp3	-0.24	0.18	-0.61
Ŵp3	-0.36	-0.07	-0.17
Lp4	-0.25	-0.06	-0.34
Ŵp4	-0.36	-0.1	0.18
Lm1	-0.24	0.01	0.10
Ltrm1	-0.17	0.15	0.12
Wm1	-0.3	0.13	0.22
Lm2	-0.29	-0.67	0.35
Wm2	-0.32	-0.33	-0.37
Eigenvalue	0.009	0.001	0.0008
% Total variance	66.06	10.09	5.90

Abbreviations: PC, principal component. See the text and Fig 4 for additional details.

mentioned synapomorphies corresponding to Node 26 (Fig. 5A).

The morphology of CICYTTP-PV-M-1-21 is very similar to that of *P. brasiliensis*, with only minor differences. Some of them, like the platelike ossification present at the anterointernal part of the orbit (see description) appear to be a pathological structure; we failed to find such a structure in any of the studied carnivore skulls. Other differences can be accounted for by the degree of development of dental characters, such as the labial cingulum in m1, the accessory cusp of P4 between the protocone and the metacone, and the metaconid of m2. These last two characters are variable in *P. brasiliensis*. These differences are not very marked and could be interpreted as intraspecific variation. Thus, specimen CICYTTP-PV-M-1-21 could be assigned to the Recent species *P. brasiliensis*.

The morphometric analyses show that CICYTTP-PV-M-1-21 is larger than Recent *P. brasiliensis* (vide supra; Table 1). However, the size difference is small and several factors weaken its taxonomic value. First, the sample of Recent specimens is relatively small (<30), and second, most skulls come from northern South America (e.g., Peru, Venezuela, Ecuador) and only two from Argentina. These could introduce some bias into the sample in the form of a sub-estimation of the variation range,

Α



FIGURE 5. Most parsimonious tree resulting from the cladistic analysis. **A**, including fossil specimen (CICYTTP-PV-M-1-21); **B**, excluding fossil specimen. Nodes are numbered above branches, whereas branch support values and group frequencies/frequencies differences, respectively, are included below branches. Negative values are shown in parentheses. See text for details.

and obscure possible geographical patterns of size variation. Furthermore, the PCA failed to find shape differences between fossil and Recent specimens (Fig. 4; Table 2).

The quantitative and qualitative analyses agree that the differences between the fossil and living specimens are small, and that they could be interpreted as intraspecific variation. Another possibility is to consider the fossil as representing a new species of *Pteronura*, as Carlini et al. (2002) claimed, but we think that these differences are insufficient to support this hypothesis.

Phylogeny

The phylogenetic analysis (Fig. 5A) corroborates the relationship of CICYTTP-PV-M-1-21 with *P. brasiliensis* and supports the inclusion of skunks within Mustelidae, contrasting with DNA phylogenies (e.g., Flynn et al., 2006), but agreeing with older morphological studies (e.g. Wozencraft, 1989; Bryant, et al., 1993; Wyss and Flynn, 1993); skunks are not positioned as the sister taxon of otters (Lutrinae), however.

In these trees (Fig. 5), the relationships of otters are highly incongruent with the Wagner tree (based on cranial measurements) of Van Zyll de Jong (1987) and recent DNA phylogenies (e.g., Koepfli and Wayne, 1998; see also Flynn et al., 2006). In the analysis of Koepfli and Wayne (1998), *Pteronura* is the most basal taxon, and the other species are grouped in two clades: one of them composed of the species of *Lontra*, the other including the remaining genera. It must be noted that several nodes of our phylogeny have negative or low branch support, thus the incongruence could be caused by spurious branch resolution. Other factors, such as taxon sampling, choice of outgroups, and sources of characters, could be related to this incongruence. The phylogenetic analysis presented herein is preliminary, and must be expanded to include most of the Recent and fossil species, as well as other sources of characters (e.g., DNA, soft anatomy).

The position of *Satherium* in the most parsimonious tree (Fig. 5A) is noteworthy; it appears as the sister taxon of Amblonyx, contradicting the supposed sister relationship of the former with Pteronura (Bjork, 1970; Van Zyll de Jong, 1972; Kurtén and Anderson, 1980). However, there is no branch support for the clade Satherium + Amblonyx (negative GC values), and when CICYTTP-PV-M-1-21 is excluded from the analysis (Fig. 5B), it results in a most parsimonious tree of 149 steps, that only differs from the former in that Satherium becomes the sister taxon of Pteronura (with a low but positive GC value of 33), both sharing the presence of a long postorbital constriction. This change is caused by the combined effects of missing data and polymorphic character states. The entries for CICYTTP-PV-M-1-21 differ from those of *P. brasiliensis* in the presence of more missing data and the absence of polymorphic cells. The inclusion of CICYTTP-PV-M-1-21, together with the contributions of missing cells from Satherium (and other taxa), changes the optimization of some characters (e.g., extension of the masseteric fossa), giving support to the relationship between Satherium and Pteronura. However, this hypothesis must be corroborated with more data in the future.

Fossil Record

As mentioned above, the fossil record of *Pteronura* and other Neotropical Lutrinae is extremely incomplete, and the known records consist of a few specimens found in Brazilian caves (Fig. 2) that lack good stratigraphic context. In a recent paper, Auler et al. (2006) show that several Brazilian caves have a large timeaveraging, ranging between 380–0.9 Ka. Therefore, based on the published information about the Brazilian fossil specimens of *Pteronura*, it is not possible to constrain their antiquity. In this context, CICYTTP-PV-M-1-21 constitutes the first fossil record of *P. brasiliensis* with accurate stratigraphic provenance, with a 130-120 Ka tentative age

Specimen CICYTTP-PV-M-1-21 also represents the first paleontological report of P. brasiliensis in Argentina. The fossiliferous locality is located outside the Recent distribution of P. brasiliensis. At present, P. brasiliensis is practically extinct in Argentina due to anthropogenic activities, but it could still be present in the northeast borders of the country (Misiones province) from whence came the last records twenty years ago (Chebez, 1994). Historical records and old museum specimens show that this species inhabited Corrientes province in the past, and that the southernmost records in Argentina occured along the Paraná river in northernmost Entre Ríos province, and in Uruguay across the river from central Entre Ríos (Fig. 2; Chebez, 1994). The presence of P. brasiliensis south of its present and historical distribution range could be explained by a warmer and more humid climate during the last interglacial, but we cannot dismiss the possibility that the absence of younger records in southern Entre Ríos province could be due to the lack of thorough sampling during historical times.

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APPENDIX 1. Description of characters used in phylogenetic analyses. Unordered states for all characters.

- (0) Skull shape: long and narrow, bizygomatic width smaller than distance between occipital condyles and distal border of M1 (0); short, bizygomatic width larger than distance between occipital condyles and distal border of M1 (1).
- Position of orbits: over medial portion of P4 (0); at mesial border of P4 (1); above distal portion of P3 (2); above mesial border of P3 (3); above P2 (4).
- (2) Development of postorbital process: very reduced (0); moderately developed, as a sharp but small tip (1); expanded laterally, as a large triangular process (3).
- (3) Extension of postorbital constriction: similar or shorter than its wider section (0); clearly longer than its wider section (1) (cf. character 1 of Wolsan, 1993).
- (4) Development of sagittal crest: absent (0); present as a single crest (1) (cf. character 2 of Wolsan, 1993).
- (5) Position of anterior opening of palatine canal: between M1 and M2 (0); between P4 and M1 (1); at anterior half of P4 or between P4 and P3 (2); at P3 (3); between P1 and P2 (4) (cf. Pocock, 1921; character 1 of Wozencraft, 1989; and character 1 of Bryant et al., 1993).
- (6) Infraorbital foramen: small, clearly less than 1/3 of orbital width (0); large, around or more than 1/3 of orbital width (1) (cf. characters 4 and 5 of Bryant et al., 1993).
- (7) Position of anterior opening of infraorbital canal: anterior to nasolacrimal foramen (0); at level of nasolacrimal foramen or posterior to it (1) (character 5 of Wozencraft, 1989).
- (8) Contact of rostral process of premaxilla with nasal bone: wide (0); narrow (1) (character 6 of Wozencraft, 1989).
- (9) Caudal extension of nasals: far beyond frontomaxillary suture (0); near position of frontomaxillary suture (1); anterior to frontomaxillary suture (2) (cf. van Zyll de Jong, 1972).
- (10) Shape of ventral margin of anterior portion of jugal: smooth and rounded (0); as a platelike process, and expanded ventrally (1).
- (11) Preorbital process: absent (0); present (1).
- (12) Size of preorbital process: small (0); very large (1).
- (13) Position of sphenopalatine foramen: anterior to posterior palatine foramen (0); displaced caudally (1).
- (14) Shape of sphenopalatine foramen: round (0); elliptical (1).
- (15) Separation between rotundum and anterior laceratum foramina: well developed, extended to or near to outer border of anterior laceratum foramen (0); separation absent (1).
- (16) Position of oval foramen with respect to Eustachian tube: separated by a bony shelf shorter than maximum diameter of oval foramen (0); distance similar to diameter of oval foramen (1); separated by a clearly larger distance (2) (cf. Pocock, 1921).
- (17) Position of posterior carotid foramen: posterior to anterior border of scar for longus capitis muscle (0); at or anterior to this scar (1) (cf. character 8 of Bryant et al., 1993).
- (18) Position of stylomastoid foramen and tympanohyal-bulla articulation: in a common depression (0); separated by a bony bridge (1) (character 47 of Wozencraft, 1989; character 9 of Bryant et al., 1993).
- (19) Size of posterior laceratum foramen: not enlarged, smaller than opening of external auditory meatus (0); enlarged, similar to exter-

nal auditory meatus (1) (cf. character 22 of Wozencraft, 1989 and character 6 of Wolsan, 1993).

- (20) Development of dorsal wall of external auditory meatus: scarcely developed, not covering suprameatal fossa (0); extensively developed, forming a complete tube (1).
- (21) Auditory bulla inflation: flattened (0); medial portion moderately inflated and rounded (1); very inflated (2) (cf. character 15 of de Muizon, 1982 and character 31 of Bryant et al., 1993).
- (22) Lateral borders of basiccipital with respect to its ventral surface: at same level as ventral face (0); lateral borders expanded ventrally (1).
- (23) Orientation of mastoid process: expanded ventrally (0); greatly expanded anteriorly (1) (cf. Willemsen, 1992).
- (24) Development of lambdoidal crest: scarcely expanded behind cranial cavity (0); greatly expanded behind cranial cavity (1).
- (25) A wide flat horizontal area between mastoid process, paraoccipital process and tympanic bulla: absent (0); present (1).
- (26) Development of postglenoid foramen: foramen large (0); reduced or vestigial (1) (cf. character 14 of de Muizon, 1982).
- (27) Preglenoid process: absent (0); present (1).
- (28) Position of paraoccipital process: in contact with tympanic bulla (0); caudally displaced, separated from main body of bulla (1) (cf. character 23 of de Muizon, 1982 and character 11 of Bryant et al., 1993).
- (29) Shape of paraoccipital process: tubercle-like (0); bladelike, oriented ventromedially (1) (cf. character 23 of de Muizon, 1982 and character 11 of Bryant et al., 1993).
- (30) Small foramina on upper margin of foramen magnum: absent (0); present (1).
- (31) Depth of mandibular ramus below m1: less than length of m1 (0); clearly greater than length of m1 (1) (cf. Berta and Morgan, 1985; Willemsen, 1992).
- (32) Mandibular subangular lobule: smooth (0); sharp (1) (cf. Berta and Morgan, 1985).
- (33) Anterior extension of masseteric fossa: not extended below m2 (0); extended below m2.
- (34) Angular process, shape of inferior ramus of medial pterigoid muscle fossa: dorsoventrally expanded with triangular outline (0); long and dorsoventrally narrowed (1).
- (35) P1: present (0); absent (1) (cf. Berta and Morgan, 1985; Willemsen, 1992; character 12 of Wolsan, 1993; characters 15 of Bryant et al., 1993).
- (36) Development of P3 lingual cingulum: reduced (0); well expanded, developing a shelf (1).
- (37) Carnassial notch of P4: present (0); absent (1) (character 13 of Wolsan, 1993).
- (38) Development of protocone on P4: not differentiated, crestlike or crescentic (0); conical (1) (character 14 of Wolsan, 1993; character 20 of Bryant et al., 1993).
- (39) Hypocone of P4: absent (0); present (1) (cf. Willemsen, 1992; cf. character 15 of Wolsan, 1993; character 21 of Bryant et al., 1993).
- (40) Mesial expansion of P4 parastyle: short, scarcely expanded beyond mesial border of lingual shelf (0); expanded, with well developed constriction separating it from lingual shelf (1).
- (41) Size of P4 parastyle with respect to paracone-metastyle: small (0); large and very high (1).
- (42) Morphology of M1: "square-shaped," with labial length similar to transverse length (0); rectangular, with labial length much smaller than transverse length (1) (cf. de Muizon, 1982; character 17 of Wolsan, 1993; character 24 of Bryant et al., 1993).
- (43) Development of M1 metacone: well developed and separated from paracone (0); reduced and connected to paracone (1); forming continuous ridge with paracone (2) (cf. de Muizon, 1982; character 17 of Wolsan, 1993; character 24 of Bryant et al., 1993).
- (44) Distal constriction between labial and lingual "halves" of M1: absent (0); present (1) (cf. character 17 of Wolsan, 1993).
- (45) Mesial and distolingual cingula of M1: separated (0); forming continuous structure surrounding protocone (1) (character 18 of Wolsan, 1993).
- (46) Shape of M1 hypocone: well developed as a cusp (0); well developed as a sharp crest (1); well developed as a broad crest or shelf (2); reduced (3).
- (47) M1 labial cingulum: reduced (0); developed as a platform (1).
- (48) Postprotocrista of M1: present and long (0); absent or scarcely developed (1) (cf. character 25 of Bryant et al., 1993).

- (49) M1 paraconule: absent (0); present (1).
- (50) Shape of M1 paraconule: crestlike, formed by an interrupted preprotocrist (0); cusplike (1).
- (51) M1 maximum mesiodistal length: < P4 maximum mesiodistal length (0); $\ge P4$ maximum mesiodistal length (1).
- (52) M2: present (0); absent (1) (cf. character 20 of Wolsan, 1993).
- (53) Position of lower premolars: in tandem with diastema (0); without diastema, some premolars in oblique position (1) (Berta and Morgan, 1985).
- (54) p1: present (0); absent (1) (cf. Berta and Morgan, 1985, Willemsen, 1992; character 16 of Bryant et al., 1993; character 21 of Wolsan, 1993; cf. character 12 of Wolsan, 1993).
- (55) Accessory distal cusp of p4: absent (0); present (1) (character 23 of Bryant et al., 1993).
- (56) Metaconid of m1: present (0); absent (1).
- (57) Development of m1 metaconid: larger than paraconid (0); subequal to paraconid in height (1); clearly smaller (2) (cf. character 23 of Wolsan, 1993).
- (58) Length of m1 talonid relative to trigonid: conspicuously smaller (0); subequal (1); clearly greater (2) (character 28 of Bryant et al., 1993).

- (59) Labial cingulum in m1 talonid: scarcely developed (0); moderately expanded (1); strongly developed (2).
- (60) Development of m1 entoconid: reduced to a thin, low cingulum (0); as a strong cingulum expanded lingually and moderately elevated but lower than the hypoconid (1); similar to state 1 but subequal in height to hypoconid (2); cusplike (3) (cf. character 24 of Wolsan, 1993).
- (61) Metastylid of m1: absent (0); present (1) (Willemsen, 1992; cf. character 24 of Wolsan, 1993).
- (62) Strong protostylid on m1: absent (0); present (1) (cf. Berta and Morgan, 1985).
- (63) m1 hypoconulid: absent (0); present (1) (cf. Willemsen, 1992).
- (64) Lingual cingulum of m1 trigonid: scarcely developed (0); well developed (1) (cf. Willemsen, 1992).
- (65) Development of m2: reduced, with circular outline and a single root(0); well developed with rectangular outline and several roots (1).
- (66) Shape of m2 protoconid: cusplike (0); crestlike (1).
- (67) Metaconid of m2: present (0); absent (1).
- (68) Entepidondylar foramen of humerus: present (0); absent (1) (character 35 of Bryant et al., 1993).

APPENDIX 2. Character-taxon matrix used for phylogenetic analysis. "A" indicates character state 0 or 1; "B" indicates character state 1 or 2.

	0	10		20		30		40		50		60		
	1	1		1		1		I.		I		I		
Procyon cancrivorus	11100	10000	10?00	01000	02000	00000	01100	01011	01000	130?1	110A0	10000	30100	0000
Nasua nasua	10201	00002	00?00	01000	02001	00000	01100	01011	01000	00000	?1000	10020	30000	0000
Mustela putorius	02201	301??	01011	12010	10011	00100	00000	10110	10111	13010	?0101	01?00	00000	110?
Galictis cuja	02200	40112	01011	12010	10010	01100	01011	00101	10111	13010	?0111	01?00	00000	11A0
Conepatus chinga	10001	300??	00?00	11001	11010	01010	01100	10100	00021	01100	11111	A0120	21100	1111
Amblonyx cinerea	13101	3111?	11111	01011	10010	10111	00011	11100	00101	12110	?0111	1011B	101A1	11A0
Enhydra lutris	13A01	11110	11110	02011	10011	11111	00101	11010	??100	10011	11111	00000	10000	1100
Lutra lutra	02200	311?1	A1111	02011	10010	10111	00001	00100	00101	A21A0	?0111	10111	101A1	1110
Lutrogale perspicillata	04200	3111?	11111	01011	10010	10111	00111	00100	00101	12111	00111	10111	101?1	1110
Lontra provocax	12200	211??	11111	01011	10010	11111	00001	A1100	00101	12110	?0111	00112	10111	110?
Pteronura brasiliensis	04111	41110	11110	11111	10110	10111	1A1A1	01100	10101	12110	?0111	A0111	101A1	11A0
CICYTTP-PV-M-1-21	04111	?11??	111??	??1??	?0110	1?111	10101	01100	10101	12110	?0111	10111	10101	1110
Satherium piscinarium	13111	311??	?????	?1?1?	?0?1?	10111	?111?	01100	00101	12110	?0111	10111	11111	111?
Aonyx capensis	12101	311??	11110	01011	10011	10111	01111	01100	00121	12100	?0101	10111	10101	110?

APPENDIX 3. Recent specimens used in the phylogenetic analysis.

Procyon cancrivorus: CEMyF 4566; MLP Ma 27.XI.01.1; MLP Ma 5.X.99.8; MLP Ma 1.IX.00.63. Nasua nasua: CEMyF 3803; MLP Ma 27-X-97-11; MLP Ma 1009; MLP Ma187. Mustela putorius: MLP Ma 6.III.36.35; MLP S/N°. Galictis cuja: CEMyF 4375; MLP Ma 1706; MLP Ma 674; MLP Ma 23.X.98.3. Conepatus chinga: MLP Ma 1.II.95.1; MLP Ma 19.XII.02.2; MLP Ma 8.IX.98.3. Amblonyx cinerea: FMNH 88612; FMNH 88611; FMNH 62869; FMNH 121229. Enhydra lutris: FMNH 78761; FMNH 129314; FMNH 78760. Lutra lutra: FMNH 88660; FMNH 81491; FMNH 75862; FMNH 97838. Lutrogale perspicillata: FMNH 38010; FMNH 63799. Lontra provocax: FMNH 24224; FMNH 24222; MLP 1282. Pteronura brasiliensis: FMNH 41223, FMNH 2015, FMNH 70768, FMNH 41210, FMNH 98078, FMNH 98077; MLP Ma 18-XI-99-3. Aonyx capensis: AMNH 165148; MLP Ma 1542.

APPENDIX 4. Characters state transformations at nodes on the most parsimonious tree (Fig. 5A).

- Node 16: Char. 0: 1 > 0; Char. 14: 0 > 1; Char. 32: 1 > 0; Char. 40: 0 > 1; Char. 43: 0 > 1; Char. 56: 0 > 1.
- Node 17: Char. 1: 0 > 2; Char. 7: 0 > 1; Char. 11: 0 > 1; Char. 13: 0 > 1; Char. 18: 0 > 1; Char. 27: 0 > 1; Char. 42: 0 > 1; Char. 48: 0 > 1.
- Node 18: Char. 20: 0 > 1; Char. 23: 0 > 1; Char. 37: 0 > 1; Char. 39: 1
- > 0; Char. 41: 1 > 0; Char. 44: 0 > 1; Char. 52: 0 > 1; Char. 54: 0 > 1; Char. 65: 0 > 1; Char. 66: 0 > 1.
 - Node 19: Char. 1: 2 > 3; Char. 33: 0 > 1.
 - Node 20: Char. 14: 0 > 1; Char. 63: 0 > 1.
 - Node 21: Char. 67: 0 > 1.
 - Node 22: Char. 47: 0 > 1; Char. 58: 0 > 1; Char. 59: 0 > 1; Char. 64: 0 > 1.
 - Node 23: Char. 6: 0 > 1; Char. 10: 0 > 1; Char. 25: 0 > 1; Char. 29: 0 > 1.
 - Node 24: Char. 0: 1 > 0; Char. 36: 1 > 0.
- Node 25: Char. 2: 1 > 2; Char. 4: 1 > 0
- Node 26: Char. 0: 1 >0; Char. 1: 2 > 4; Char. 3: 0 > 1; Char. 17: 0 > 1;
- Char. 22: 0 > 1; Char. 30: 0 > 1; Char. 40: 0 > 1.