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Original article

New material of Pleistocene cats (Carnivora, Felidae) from Southern South America, with comments on biogeography and the fossil record

Nouveaux matériels de chats pléistocènes (Carnivora, Felidae) dans le sud de l'Amérique du Sud, commentaires sur la biogéographie et le registre fossile

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Abstract

In this paper the systematic position and age of several Pleistocene cat remains found in southern South American are studied, in an attempt to more fully document the scarce record of the group and clear up their obscure Quaternary history. The fossils are compared with a large sample of recent specimens by means of qualitative and quantitative characters, as well as multivariate methods (discriminant analysis). The age of previous records is restricted using recent chronostratigraphic and biostratigraphic studies. *Ly. colocolo* is recorded in the late Ensenadan (0.78–0.5 Ma BP) and Bonaerian/Lujanian (0.5 Ma–8.5 Ka BP) ages of the Pampean Region (Argentina) and in the late Pleistocene or Holocene of Tierra del Fuego (Chile). An incomplete hemimandible found in the Bonaerian of the Pampean Region is referred to cf. *Herpailurus* and could be the earliest record of this lineage. Two other remains could belong to *On. geoffroyi*, but their incompleteness and some differences prevent their assignation to this recent species. The age of "*Felis*" *vorohuensis* is restricted to the late Ensenadan. The fossil record of the Ocelot Lineage is very fragmentary, but it is at least as old as late Ensenadan. Taphonomic biases are responsible for this poor fossil record and this fact could partially explain the hiatus with respect to the timing estimated by molecular divergence. The combination of data suggests that *Ly. colocolo, On. guigna, On. geoffroyi* and *Oreailurus jacobita* speciated in South America, supporting previous opinions. If the molecular divergence dates are right the recent diversity of this group could be explained by a minimum of five to six immigrations.

Résumé

La position systématique et l'âge de plusieurs restes de chats pléistocènes retrouvés dans le sud de l'Amérique du Sud sont étudiés, dans le but de compléter partiellement le pauvre registre fossile du groupe et d'éclaircir son histoire quaternaire, lacunaire. Les fossiles sont comparés avec un grand échantillon de spécimens récents, en utilisant la morphologie, la morphométrie et des méthodes d'analyse multivariée (Analyse Discriminante). Les âges proposés antérieurement sont rectifiés à l'aide de nouvelles études chronostratigraphiques et biostratigraphiques. *Ly. colocolo* est signalé dans l'Ensénadéen tardif (0,78–0,5 Ma AP) et le Bonaëréen/Lujanéen (0,5 Ma–8,5 Ka AP) de la Région Pampéenne (Argentine) et dans le Pléistocène tardif ou l'Holocène de la Terre de Feu (Chili). Une mandibule incomplète retrouvée dans le Bonaëréen de la Région Pampéenne est assignée à cf. *Herpailurus* et pourrait être le fossile le plus ancien de cette lignée. Deux autres restes pourraient correspondre à *On. geoffroyi*, mais leur incomplétude et quelques différences avec le matériel type empêchent de les assigner à cette espèce récente. L'âge de « *Felis* » *vorohuensis* est restreint à l'Ensénadéen tardif. Le registre fossile de la lignée de l'ocelot est très fragmentaire et commence certainement dans l'Ensénadéen tardif. Plusieurs biais taphonomiques sont responsables de la pauvreté du registre fossile et pourraient expliquer partiellement

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l’écart avec les âges proposés par divergence moléculaire. Les résultats suggèrent que *Ly. colocolo, On. guigna, On. geoffroyi* et *Oreailurus jacobita* ont leur origine en Amérique du Sud, ce qui étaye les opinions antérieures. Si les dates de la divergence moléculaire sont correctes, la diversité récente de ce groupe peut être expliquée par un minimum de 5–6 immigrations.

Keywords: Felidae; Pleistocene; Systematics; South America; Biogeography

Mots clés : Felidae ; Pléistocène ; Systématique ; Amérique du Sud ; Biogéographie

1. Introduction

The recent small felids of South America are diverse with eight species known (Wozencraft, 1993). Several species (e.g. *Le. pardalis*, *Le. wiedii*, *On. tigrina*; see Cabrera, 1958, 1961; Nowell and Jackson, 1996) inhabit forest and scrublands of the northern part of South America (i.e. northern Argentina and Uruguay, Bolivia, Brazil and northern countries), as well as Central America and southern North America (De Oliveira, 1997, 1998a, 1998b). Other cats (*On. geoffroyi*, *Ly. colocolo*) are found mainly in open environments of the southern part of South America (i.e. Uruguay, Chile, Argentina; Cabrera, 1961; Garcia Perea, 1994), whereas *Or. jacobita* and *On. guigna* are restricted to the high mountains of the Andes (Argentina, Chile, Bolivia and Peru) and to the Patagonian forest of Chile and Argentina, respectively (Nowell and Jackson, 1996; Yensen and Seymour, 2000; Quintana et al., 2000). The remaining species, *Herpailurus yagouaroundi*, is widely distributed from northern Patagonia to southern North America (De Oliveira, 1998b).

The Neotropical cat species are a monophyletic group (the Ocelot Lineage; e.g. Collier and O’Brien, 1985; Pecon Slattery et al., 1994), with the exception of *H. yagouaroundi* that is more closely related to *Puma* and other felids (Salles, 1992; Eizirik et al., 1998; Johnson et al., 1999; Seymour, 1999; Mattern and Mclennan, 2000). The time of divergence of this clade was calculated at 3–4 Ma BP (Wayne et al., 1989; Bininda Emmons et al., 1999) or 5–6 Ma BP (Pecon Slattery et al., 1994; Pecon Slattery and O’Brien, 1998; Johnson et al., 1999). The first date is coincident with the rise of the Panama bridge at 2.8–3.1 Ma AP (Coates and Obando, 1996), which connects Central and South America, but the second one predates this event.

Contrasting with their rich recent diversity and their early age of divergence and radiation as estimated by molecular methods, the fossil record of this group is scarce and relatively young. The oldest records correspond to “*Felis*” *vorohuensis* and “*Felis*” sp. from the Ensenadan (late Pliocene to early middle Pleistocene, sensu Cione and Tonni, 1999), and “*H. yagouaroundi*” from the “Ensenadan” of Bolivia (Hoffstetter 1963, 1986; Berta, 1983; Deschamps and Borromei, 1992; Berman, 1994; but see below). *On. tigrina, H. yagouaroundi, Le. pardalis, Le. wiedii*, have been found at paleontological sites in Brazil (late Pleistocene–Holocene; (Winge, 1895; Lund, 1950; Guérin et al., 1996; Lessa et al., 1998; Seymour, 1999). Seymour (1999) described several bones of *Le.* cf. *Le. wiedii* and of *Oncifelis* sp. or *Leopardus* sp. from the latest Pleistocene (≈ 13 Ka BP, see Marshall et al., 1984) site of Talara (Peru). *Le. wiedii amnicola, Le. pardalis* and *Leopardus* sp. reached southern North America during the last interglacial and glacial periods (Sangamon and Wisconsin, respectively; Werdelin, 1985; Hulbert and Pratt, 1998). “*Felis*” *geoffroyi* was mentioned for the late Pleistocene of the Buenos Aires province (Argentina; Berman, 1994; but see below) and “*Felis lujanensis*” for the Lujanian of Buenos Aires province. The latter may be a synonym of *Ly. colocolo*, but the holotype has been lost and the original description is confusing (Seymour, 1999). Fossils of *Or. jacobita* and *On. guigna* have not yet been found. Several specimens of “*Felis*” sp. have been mentioned in faunal lists of Pleistocene sites of Argentina (e.g. Deschamps and Borromei, 1992; Tonni and Scillato-

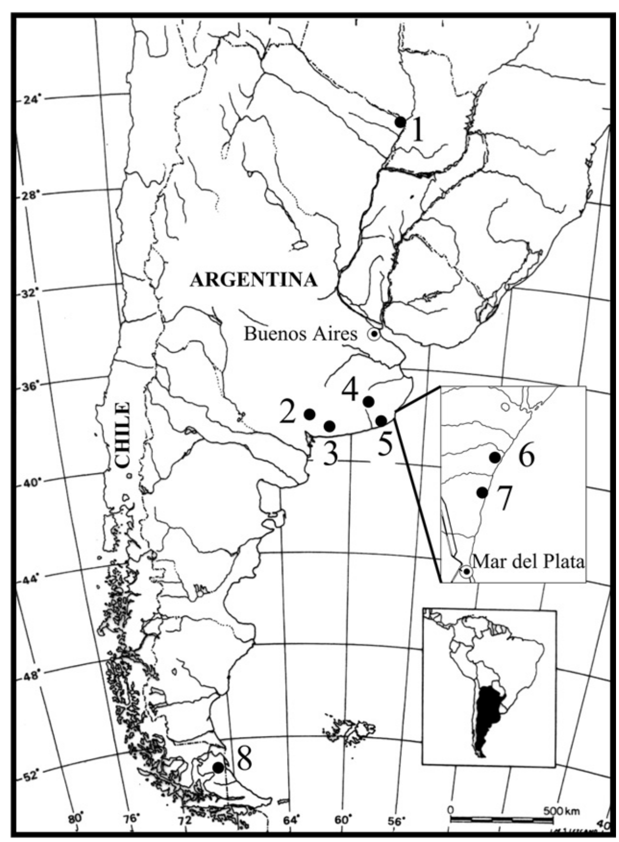

Fig. 1. Map of fossil localities. **1**: Río Pilcomayo; **2**: Bajo San José; **3**: Arroyo Indio Rico; **4**: Lobería; **5**: Centinela del Mar; **6**: Camet Norte; **7**: Regimiento 601; **8**: Alero Tres Arroyos 1.

Fig. 1. Carte schématique indiquant les localités fossilifères. **1** : Río Pilcomayo ; **2** : Bajo San José ; **3** : Arroyo Indio Rico ; **4** : Lobería ; **5** : Centinela del Mar ; **6** : Camet Norte ; **7** : Regimiento 601 ; **8** : Alero Tres Arroyos 1.

Yané, 1997; Fig. 1), but without descriptions or figures. This situation is more common in the Holocene archeological and paleontological faunal lists (e.g. Goñi et al., 1996; Quintana, 2001; Tonni et al., 2002).

The objectives of this work are, the description of new and undescribed specimens of Pleistocene cats from the southern cone of South America, and a review the systematic status of other previously published specimens, using “classic” systematic methods, discriminant analysis and assessing the intraspecific variation of qualitative characters in the recent species. Second, the age of previous records is restricted with the aid of new paleomagnetic and biostratigraphic data (e.g. Bidegain et al., 1998, 2003; Cione and Tonni, 1999, 2001). Finally, a discussion of the history of the Ocelot Lineage in the light of fossil and molecular evidences is included.

2. Materials and methods

The specimens described here were compared with recent and fossil individuals from several institutions (see Institutional Abbreviations). As the size of these specimens is small than that of *Le. pardalis*, and their morphology is clearly different (see Seymour, 1999: 227), only the smaller Neotropical cats (i.e. *Or. jacobita, Le. wiedii, On. tigrina, On. geoffroyi, On. guigna, Ly. colocolo*, *H. yagouaroundi*) and *Felis catus* were used for comparison. Of the recent specimens, only those with fully erupted permanent dentition were selected. A further distinction of older specimens with obliterated basioccipital–basisphenoid suture could be made; however, this procedure caused an excessive reduction of group size, and it was preferred to pool all specimens in a single group. Only a cast of the dentary series of “*F.*” *vorohuensis* deposited at Museo de La Plata was available for examination, because the holotype (MMP 1047) is on load from MMP. The measurements were taken using dial and digital calipers with 0.05 and 0.01 mm precision, respectively (see Tables 1 and 2). The statistical analyses were carried out with the software package Statistica 6.0 (Statsoft Inc., 2001), using the “Direct Method” of the Discriminant Functions Analysis (DA) with the purpose of identifying the South American fossil cat specimens studied. The recent species were the a priori groups for the discriminant analysis functions and equal probabilities were assigned to all groups. Only complete specimens were included in the multivariate analysis, and their measurements were $\log_{10}$-transformed. Following Seymour (1999: 226), I ignored the sex variable because, on the one hand, all samples include both male and female specimens, and on the other hand, the number of sexed recent felid specimens is low.

The fossil and recent specimens studied are deposited in the following repositories: American Museum of Natural History, Mammalogy. New York, USA (AMNHMa); Museo Nacional de Historia Natural, Mastozoología, Colección Boliviana de Fauna, La Paz, Bolivia (CBF); Collection of the Grupo de Ecología Comportamental de Mamíferos, Universidad Nacional del Sur, Bahía Blanca, Argentina (CGECM); Collection Daniel Ibañez, Maipú 7283, Mar del Plata, Argentina (CI); Instituto Miguel Lillo, Tucumán, Argentina (CML); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Departamento de Paleontología, Buenos Aires, Argentina (MACN-Pv); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Departamento Mastozoología. Buenos Aires, Argentina (MACN-Ma); Museo de La Plata, Departamento Científico Paleontología Vertebrados, Argentina (MLP); Museo de La Plata, Departamento Científico Zoología Vertebrados, Argentina (MLPMa); Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Sección Paleontología, Argentina (MMP); Museo Municipal de Ciencias Naturales de Mar del Plata “Lorenzo Scaglia”, Sección Mastozoología, Argentina (MMPMa); Museu de Zoologia da Universidad de São Paulo, Brasil (MZUSP); Collection of the Proyecto Gato del Monte, Buenos Aires, Argentina (PGM); Collection of the Cátedra de Geología Histórica de la Universidad Nacional del Sur, Bahía Blanca, Argentina (UNSGH); Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile (IPUM). The generic nomenclature of the South American cats follows Seymour (1999), except *Lynchailurus* and *Oreailurus* are retained for the pampas cat (*Ly. colocolo*) and the Andean cat (*Or. jacobita*).

The cusp terminology follows Salles (1992), modified in order to adapt it to the orientation nomenclature proposed by Smith and Dodson (2003) (e.g. posterior accessory cusp was changed to distal accessory cusp).

I follow the biostratigraphic/chronostratigraphic scheme of Cione and Tonni (2001).

The color of the sediments from the stratigraphic profiles studied has been identified with Munsell Soil Color Charts.

A modification of the “Manhattan Stratigraphic Measure” index (MSM*; Pol et al., 2004) was used to contrast the current phylogenetic hypothesis of the Ocelot Lineage clade (e.g. Johnson et al., 1999; plus “*F.*” *vorohuensis* as a basal taxon) with its fossil record. MSM* was calculated with the SPA (Goloboff, 1996) and PAUP* (Swofford, 1999) software packages.

Measurements and anatomical abbreviations: I: upper incisor; C/c: upper/lower canine; P/p: upper/lower premolar; m: lower molar; L: mesiodistal length; W: labiolingual width; LP4-C1: length of the upper dental series, from the distal border of the P4 to the mesial border of the C1; Lm1-c1: length of the lower dental series, from the distal border of the m1 to the mesial border of the c1; LM: mandible length, from the condyle to the mesial border of the i1 alveolus; MHDBm1: height of the mandible ramus at the distal border of the m1; MWDBm1: width of the ramus at the distal border of the m1; MHm1-p4: height of the mandible ramus between m1-p4; MWm1-p4: width of the ramus between the m1-p4; MHp4-p3; height of the mandible ramus between p4-p3; MWp4-p3: width of the ramus between the p4-p3; MHMBp3: height of the mandible ramus at the mesial border of the p3; MWMBp3: width of the ramus at the mesial border of the p3; WDHu: maximum width of the distal epiphysis of the humerus; APLDHu: maximum anteroposterior length of the distal epiphysis of the humerus; WOlec: width of the ulna olecranon; LOlec: length of the ulna olecranon; APUln: anteroposterior

Table 1
Cranial, mandibular and dental measurements of southern South American fossil cats. See text for abbreviations
Tableau 1 Mensurations crâniennes, mandibulaires et dentaires des chats fossiles du sud de l'Amérique du Sud. Voir le texte pour les abréviations

	"*F.*" *vorohuensis* (MMP 1047)	*Ly. colocolo* (MLP 90-XII-10-1)	*Ly. colocolo* (CI S/N°)	*Ly. colocolo* (IPUM 6872)	*F. catus* (MLP 89-XI-10-7)	cf. *Herpailurus* (UNSGH 464)	*Felidae* sp. (MLP 91-IV-15-1)	*Felidae* sp. (MLP 96-V-10-11)
LP4-C1	28.80	29.95						
LP4	11.40	13.05						
WP4	5.20	6.10						
LP3	7.40	7.50						
WP3	4.10	4.30						
LC1	5.30	6.11						
WC1	3.90	4.75						
LM				71.85	57.25			
MHDBm1				13.20	10.55	11.15		
MWDBm1			6.20	6.65	5.40	5.10		
MHm1-p4			13.55	13.45	10.70	10.50		12.95
MWm1-p4			7.05	6.90	5.75	5.85		6.70
MHp4-p3			12.65	12.95	9.70	8.25		11.80
MWp4-p3			6.10	6.80	5.90	5.25		5.70
MHMBp3			12.80	12.95	10.10	8.70		12.35
MWMBp3			6.65	6.95	5.40	5.25		6.10
Lm1-c1	32.7				31.95			
Lm1	8.90			9.20	8.60	9.10	9.40	
Wm1	4.40			4.10	3.50	4.35	3.90	
Lp4	7.30		8.55	7.35	7.20	7.70	8.10	8.45
Wp4	3.90		4.40	3.90	3.15	3.50	3.30	3.95
Lp3	5.50		6.90	5.80	4.50	5.80	6.70	6.75
Wp3	3.15		3.55	3.35	2.60	3.70	2.80	3.20
Lc1	5.05		5.90		4.00			
Wc1	3.95		4.45		3.30			

length of the ulna at the medial coronoid process; PEWRad: width of the proximal epiphysis of the radius; PEAPLRad: length of the proximal epiphysis of the radius, perpendicular to PEWRad.

Statistical abbreviations: DA: Discriminant Functions Analysis; PP: posterior probability; CC: percentage of correct reclassification: F: Fisher value associated with the respective Wilks' Lambda.

3. Systematics

Order CARNIVORA Bowdich, 1821.
Family FELIDAE Fischer, 1817.
Subfamily FELINAE Fischer, 1817.
Genus ***Lynchailurus*** Severtzow, 1858.

Lynchailurus colocolo (Molina, 1782)

Material examined: MLP 90-XII-10-1 (Fig. 2(A, B) and Table 1): left fragmentary maxilla with the C and P3-P4; CI S/N° (cast MLP 01-V-20-1; Fig. 2(C, D), Table 1): left incomplete mandibular ramus with i2-p4 and a incomplete m1; IPUM 6872 (Fig. 2(E, F), Table 1): right hemimandible with p3-m1.

Geographic and stratigraphic distribution: The MLP 90-XII-10-1 and CI S/N° were found in the costal cliffs of Camet Norte (38°00′S, 57°33′W; Buenos Aires, Argentina; Fig. 1), near the Arroyo Seco stream. The CI S/N° comes from the lowest stratigraphic level, a brown (7.5 YR 4/3) sandy silt layer, 50 m north of the Arroyo Seco stream. *Mesotherium cristatum* and other Ensenadan mammals were found in this layer (Pardiñas et al., 1998: 258), and this level can be correlated with the Upper Ensenadan (0.78–ca. 0.5 Ma BP) levels situated some kms south that were described by Cione et al. (2002: 16–17) and Bidegain et al. (2003: 1–10). MLP 90-XII-10-1 was found 500 m south of the Arroyo Seco stream, in the lower portion of the profile but in the layer above the bearing level of CI S/N°. This layer is composed of a very pale brown (10YR 7/3) sandy silt and contains late Pleistocene (Bonaerian-Lujanian) mammals; it underlies the levels dated in 24.550 ± 600 ^{14}C years old (Pardiñas et al., 1998: 259) and 21.000 ± 7.000 (fission tracks on volcanic glass) years BP (Bigazzi et al., 1995: 112). The two stratigraphic levels are included in the Santa Clara Formation, where remains of *Equus* sp. have been found (Schnack et al., 1982: 146–147). This taxon is known to be restricted to the Lujanian in the Pampean Region, but unfortunately these authors did not specify the level of the *Equus* remains within the Formation. Thus, the age of MLP 90-XII-10-1 could be Bonaerian or Lujanian (0.5 Ma–8.5 Ka BP). IPUM 6872 was found at the IV stratigraphic level (late Holocene, ≈ 1.34 Ka BP) of the archeological site Alero Tres Arroyos 1 (53°23′S, 68°47′W; Tierra del Fuego, Chile; Fig. 1; Latorre, 1998: 81; Borrero, 2003: 87). The site had been disturbed by rodents or rabbits, and some bones from Holocene levels (e.g. level III dated in ≈ 0.7 Ka BP) were dated as late Pleistocene by AMS (accelerator mass spectrometry) ^{14}C (Latorre, 1998: 78; Borrero, 2003: 91–92). Therefore, there is a possibility that IPUM 6872 could be late Pleistocene in age.

Table 2
Postcranial measurements of the MLP 94-II-1-148 (cf. *Ly. colocolo*) compared with recent species. X: mean; S.D.: standard deviation; *N*: sample size; OR: observed range
Tableau 2 Mensurations postcrâniennes de MLP 94-II-1-148 (cf. *Ly. colocolo*) comparées à des espèces récentes. X : moyenne ; DS : déviation standard ; *N* : dimension de l'échantillon ; OR : étendue

	cf. *Ly. colocolo*	*On. geoffroyi*
	MLP 94-II-1-148	X ± S.D. (*N*) OR
WDHu	24.2	21.89 ± 2.43 (13) 18.25–25.00
APLDHu	13.8	12.21 ± 1.11 (13) 10.50–14.70
WOlec	8.8	7.46 ± 1.64 (12) 6.30–9.30
LOlec	29.65	26.70 ± 1.02 (10) 21.75–29.35
APUln	13.85	14.14 ± 2.52 (13) 11.20–15.95
PEWRad	10.95	8.93 ± 0.85 (11) 7.40–9.90
PEAPLRad	7.5	4.99 ± 0.75 (11) 3.70–6.40
	H. yagouaroundi	*Ly. colocolo*
	X ± S.D. (N) OR	X ± S.D. (N) OR
WDHu	21.83 ± 2.44 (4) 20.05–25.45	20.00 ± 1.82 (4) 17.63–21.80
APLDHu	12.98 ± 2.00 (4) 11.15–15.83	11.59 ± 1.47 (4) 9.89–13.40
WOlec	7.58 ± 0.83 (4) 6.70–8.70	7.47 ± 0.77 (4) 6.60–8.45
LOlec	26.81 ± 3.33 (3) 23.59–30.25	23.10 ± 2.11 (3) 21.47–25.50
APUln	14.89 ± 1.78 (4) 13.44–17.34	11.91 ± 1.36 (4) 11.07–13.95
PEWRad	9.25 ± 0.79 (3) 8.34–9.76	6.82 ± 0.12 (3) 6.70–6.95
PEAPLRad	4.71 ± 0.22 (3) 4.49–4.94	3.5 ± 0.39 (3) 3.05–3.80
	On. tigrina	*Le. wiedii*
	X ± S.D. (*N*) OR	MZUSP 28311/MZUSP 9998
WDHu	16.10 ± 0.46 (4) 15.72–16.68	20.61/20.01
APLDHu	9.21 ± 0.86 (4) 8.46–10.23	10.66/10.60
WOlec	5.54 ± 0.44 (4) 5.00–5.94	5.83/6.48
LOlec	18.46 ± 1.25 (4) 16.75–19.49	22.89/22.49
APUln	9.92 ± 0.84 (4) 9.32–11.16	12.14/11.94
PEWRad	5.93 ± 0.47 (4) 5.48–6.58	7.12/7.53
PEAPLRad	3.24 ± 0.54 (4) 2.75–4.02	4.23/3.56

Description: MLP 90-XII-10-1: The P4 is large and has a reduced protocone. The parastyle is small, conical and pointed. P3 and P4 are aligned and crowded, with the distal portion of P3 lingual to the parastyle of P4. The P3 has a tall and robust paracone (morphotype 1 of García Perea, 1994: 13–14), with a shallow vertical ridge on its lingual surface, and reduced but differentiated metastyle and distal cingulum. The C1 is well developed, with two vertical ridges on the lingual surface. The P2 is absent.

CI S/N°: The masseteric fossa nearly reaches the level of the distal border of m1. The diastema between c1 and p3 is relatively short. The symphysis is high and anteroposteriorly narrow. The protocone of m1 is broken and the lingual constriction is poorly developed. The p4 has a sharp protoconid, with straight mesial and distal cristids. The paraconid is larger than the first distal accessory cusp, well separated from the protoconid, but transversally compressed. The p3 is short but with a pointed protoconid and a reduced first distal accessory cusp. The mesial cingulum is also reduced, but it bears a tiny paraconid. The c1 presents a strong vertical groove (lingual cavity) on the lingual surface, mesially to the mesiolingual cristid.

IPMU 6872: The horizontal ramus does not taper in rostral direction. The m1 lacks any trace of talonid, metaconid or distal cingulum. The labial border of the carnassial blade is moderately worn. The lingual constriction is slightly developed at the level of the carnassial notch. The premolars are high and short in proportion to their transversal width. A short diastema is present between the p3 and p4. In this premolar the paraconid is small and pointed, and the first distal accessory cusp is labially coalescent the distal cingulum. The P3 has a high pointed protoconid, which is slightly lower than the p4.

Discussion: Berman (1994: 392) stated that MLP 90-XII-10-1 shared similarities with *Ly. colocolo*, but assigned it to "*Felis*" sp. because its P3-4 are crowded and it has a large and curved C1. The presence of a ridge on the lingual surface of the C1 and P3 are diagnostic features of *Ly. colocolo* within the South American cats (Salles, 1992: 14–16; Seymour, 1999: 148–150; García Perea, 2002: 110–124). The size of the C1 (and other measurements, see Table 1 and Appendix A) fall within the range of the recent specimens of *Ly. colocolo*. In these specimens the position of the P3-4 shows variation, reaching in some cases the condition seen in MLP 90-XII-10-1. The morphological features of MLP 90-XII-10-1: P3 with a large and high paracone (morphotype 1 of García Perea, 1994: 13, 15), the absence of protocone in the P4 and the lack of P2, are common in *Ly. colocolo* (García Perea, 1994: 14–15; García Perea, 2002: 110–124).

The size and morphology of CI S/N° is comparable to *Ly. colocolo* (Table 1, Appendix A and Fig. 2(C, D)). The p3 is short and has a high and sharp protoconid. I have found this p3 morphotype in only some of the *Ly. colocolo* specimens (see also Seymour, 1999: 319), but several specimens of *On. geoffroyi*, *Le. wiedii* and *On. tigrina* exhibit a similar morphology. The p3 morphotype of some specimens of *Ly. colocolo* is very similar to the autapomorphic condition of *Felis nigripes* (Salles, 1992: 17–18). The lingual cavity of c1 is a diagnostic state of *Ly. colocolo* among Neotropical cats (Salles, 1992: 17; Seymour, 1999: 149–150; Yensen and Seymour, 2000: 1). Its size and the abovementioned morphological characters differentiate CI S/N° from other species of Neotropical cats. Seymour (1999: 147–150) found that the lingual ridges of the C1 and P3 and the lingual cavity of the c1 are present in some specimens of other Neotropical cat species, albeit in very low proportion. I have found the c1 lingual cavity in only three specimens of *On. tigrina* (MZUSP 19900; MZUSP 8299; MZUSP 13609) and five *H. yagouaroundi* (MZUSP 13671; MZUSP 13607; MACN-Ma 50-95; MACN-Ma 50-94), but in these cases it is shallower than in CI S/N° and in the studied recent specimens of *Ly. colocolo*. The same is true for the C1 lingual ridges present in two *On. tigrina* (MZUSP 19900; MZUSP 8299), one *H. yagouaroundi* (MZUSP 13671) and one *Le. wiedii* (MZUSP 467). In these specimens the ridges are weaker than in *Ly. colocolo* and MLP 90-XII-10-1.

The size of IPUM 6872 lies within the range of *Ly. colocolo*, *On. geoffroyi*, *H. yagouaroundi* and *Le. wiedii* (Table 1 and Appendix A). Latorre (1998: 81–82) assigned it to cf. "*F.*" *colocolo* because the size is similar and the m1 lacks any vestige of metaconid. However, the development of these structures is highly variable in all recent species, occurring in at least some specimens of every species (Seymour, 1999: 311; Prevosti pers. obs.). Unfortunately this specimen lacks diagnostic features, but the high mesiodistally short premolars make it most similar to *Ly. colocolo* (Fig. 2(E, F); Seymour, 1999: 319, par-

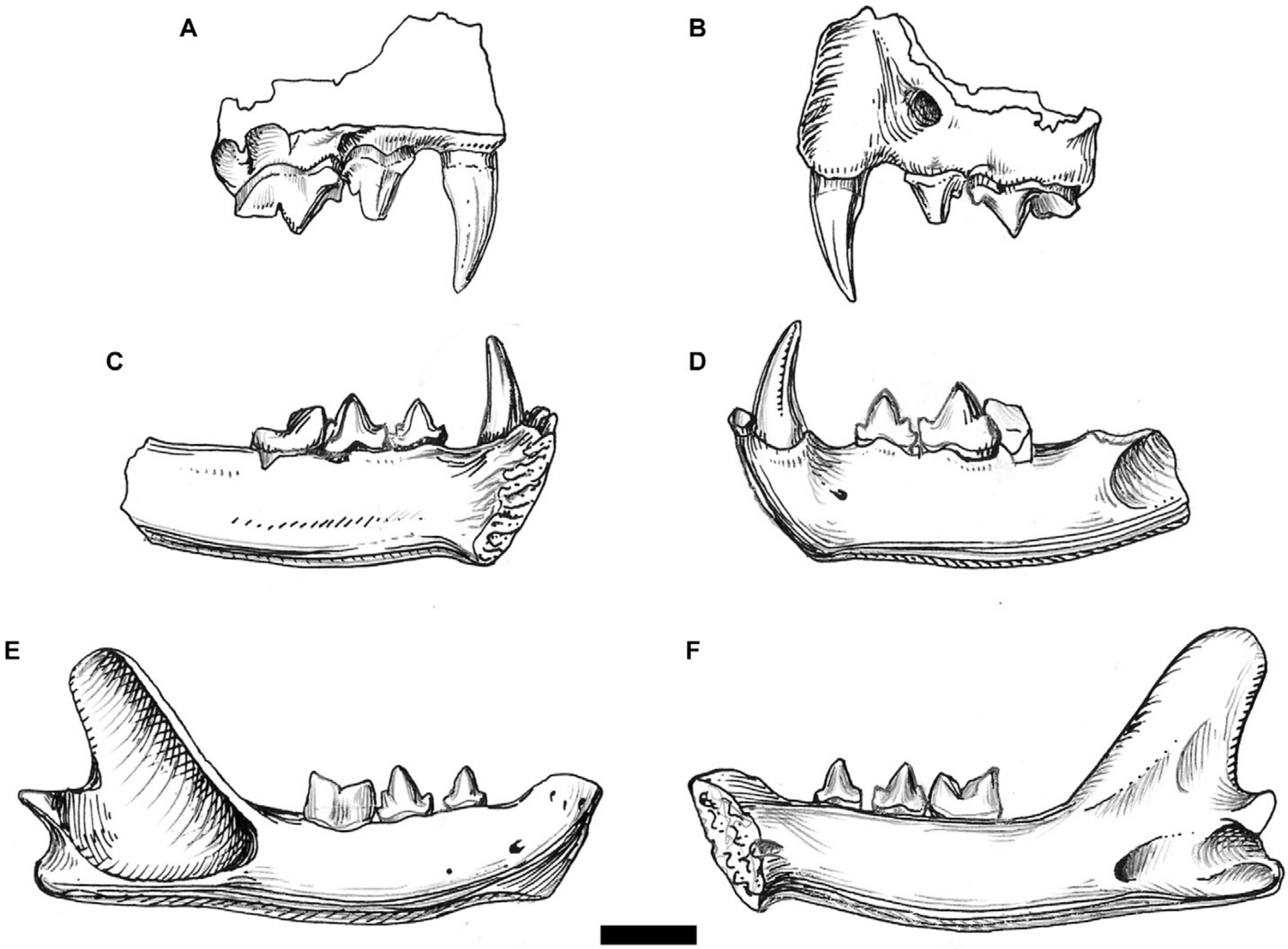

Fig. 2. Fossils of *Ly. colocolo*. Incomplete maxillary MLP 90-XII-10-1 (medial and lateral view, A and B, respectively) and mandibles CI S/N° (medial and lateral view, C and D, respectively), IPUM 6872 (lateral and medial view, E and F, respectively). Scale: 1 cm.

Fig. 2. *Ly. colocolo* fossiles. Vue linguale et labiale du maxillaire MLP 90-XII-10-1 (A et B) et mandibules CI S/N° (C et D), IPUM 6872 (E and F). Échelle : 1 cm.

tim; Prevosti pers. obs.). On the other hand, some *On. geoffroyi* specimens have a proportionally high p3 (see Seymour, 1999: 314; vide supra).

With the aim of identifying these fossil specimens, three independent DA were performed using the four recent species that overlap with the fossils in size (i.e. *Ly. colocolo, On. geoffroyi, H. yagouaroundi, Le. wiedii*. The DA (Wilks' Lambda: 0.28520, approx. F (21.431) = 11.252 $P < 0.0001$; CC: 66.87) constructed for MLP 90-XII-10-1 with a total 170 specimens and seven variables (LP4-C1; LP4; WP4; LP3; WP3; LC1; WC1) assigned it initially to *Ly. colocolo* (PP: 0.628) and secondly to *On. geoffroyi* (PP: 0.240). The low CC and the ambiguous classification of MLP 90-XII-10-1 could be consequences of the low number of variables, but it does not contradict the qualitative morphological assessment of this fossil. The second DA (Wilks' Lambda: 0.1597, 1 approx. F (39.370) = 8.1592 $P < 0.0001$; CC: 82.98) included a total 141 specimens and 13 variables (MWDBm1; MHm1-p4; MWm1-p4; MHp4-p3; MWp4-p3; MHMBp3; MWMBp3; Lp4; Wp4; Lp3; Wp3; Lc1; Wc1) and classify the CI S/N° as *Ly. colocolo* (PP: 0.920). The third DA (Wilks' Lambda: 0.19513, approx. F (39.430) = 8.1221 $P < 0.0001$; CC: 75.77%) constructed with 161 total specimens and 13 variables (LM; MHDBm1; MWDBm1; MHm1-p4; MWm1-p4; MHMBp3; MWMBp3; Lm1; Wm1; Lp4; Wp4; Lp3; Wp3) identified IPUM 6871 as *Ly. colocolo* (PP: 0.961) in agreement with Latorre's (1998) interpretation and the morphology of the premolars (vide supra). Although these two AD have better CC and PP than the first one these values are not exceptionally high but are consistent with the qualitative morphology of these specimens.

Although at present Tierra del Fuego is an island, it was part of the South American continent until late Pleistocene (Clapperton, 1993: 124). At present, felids are absent in the island, and *On. geoffroyi* and *Ly. colocolo* only occur north of the Magellan strait (Cabrera, 1961). The direct dating of IPUM 6872 via AMS ^{14}C could be relevant to establish the possible extinction time of *Ly. colocolo* on the island.

Felidae cf. *Lynchailurus colocolo* (Molina, 1782)

Material examined: MLP 94-II-1-148 (Fig. 3 and Table 2): distal fragment of left humerus, left radius and ulna without the distal portion.

Geographic and stratigraphic distribution: Confluence of Indio Rico creek with the Quequén Salado river (38°09′S, 60° 35′W; Buenos Aires, Argentina; Fig. 1). MLP 94-II-1-148 comes from the Guerrero Member of the Luján Formation, which contains mammals of the *Equus* (*Amerhippus*) *neogeus* Biozone (Lujanian; Alberdi et al., 1989). The ^{14}C dates of the Guerrero Member in Buenos Aires province range between 29.85 ± 1.37 and 10.07 ± 0.13 Ka BP (Tonni et al., 2003) and its faunal association suggests arid climates.

Description: The coronoid and radial fossae of the humerus are deep, but the latter is deeper. There is a small supratrochlear foramen. The anconean process is short and wide. The medial coronoid process is short, blunt and has a subtriangular profile in cranial view. The radial notch is wide because the lateral coronoid process is not well developed. The ulnar tuberosity is clearly visible distal to the sigmoid notch on the medial side of the diaphysis. A slightly convex and narrow surface on the proximal portion of its medial border is the rough attachment for the interosseus ligament.

Discussion: Only a few postcranial skeletons of Neotropical cats are available at the museums visited. I could study only four *Ly. colocolo*, *On. tigrina* and *H. yagouaroundi*, 13 *On. geoffroyi* and two *Le. wiedii* (Table 2). Unfortunately, the postcranial skeleton of *Or. jacobita* is unknown, but this species is slightly larger than the other Neotropical cats (with the exception of *Le. pardalis*). On the other hand, *On. guigna*, which was not available for study, is clearly smaller, according to the measurements given by Seymour (1999: 905–929). The distal fragment of humerus shows overall similarity with *On. geoffroyi* and *Ly. colocolo*, but I only observed a supratrochlear foramen in one specimen of the latter species. In this fossil the medial epicondyle does not expand distally near the level of the distal end of the trochlea as in *H. yagoauroundi* and *On. tigrina*. In this latter species the lateral epicondylar crest is more developed. The trochlea is more developed and expanded in comparison with the capitulum than in *On. tigrina* and *Le. wiedii*. The shaft of the radius and ulna are slender, straight and proportionately longer than in *On. tigrina*, *On. geoffroyi*, *Le. wiedii* and *H. yagouaroundi* and similar in these features to *Ly. colocolo*. The lateral coronoid process of the ulna is larger in *On. tigrina* and *H. yagouaroundi*, while the medial coronoid process is low as in *Ly. colocolo*, *On. tigrina*, *Le. wiedii*, and some *On. geoffroyi* specimens. The anteroposterior diameter of the proximal portion of the shaft is proportionally short as in *Ly. colocolo*, *On. tigrina*, and *Le. wiedii*. The ulna of MLP 94-II-1-148 differs from *H. yagouaroundi* because the anconeus muscle attachment is not distally depressed and the proximal part of the humeral articulation facet is dorsally expanded on the radial side (Seymour, 1999: 364). This last character occurs in *Ly. colocolo*, *On. guigna*, *Le. wiedii* and some specimens of *On. geoffroyi* (Seymour, 1999: 364; Prevosti pers. obs.). MLP 94-II-1-148 shares a low undifferentiated capitular eminence with *Ly. colocolo* (Fig. 3). In *H. yagouaroundi* the articular fovea of the radius is more rounded and the radial tuberosity is larger and elongated. The combination of characters seen on MLP 94-II-1-148 make it appear most similar to *Ly. colocolo*, but an assessment of the intraspecific variation of these characters in a larger series of specimens is still required for a definitive identification. The measurements of MLP 94-II-1-148 are larger than those of *On. tigrina* and slightly larger than those of *Le. wiedii* and *Ly. colocolo*, but they fall within the variation range of *On. geoffroyi* and *H. yagouaroundi*, although the sample sizes are small (Table 2). A similar pattern appears when I compare the measurements given by Seymour (1999: 904–929) for a larger sample, but in this case MLP 94-II-1-148 falls within the range of *Le. wiedii*. Because the sample size of *Ly. colocolo* is also small (nine specimens in Seymour, 1999, and four in the present work), the measurements of MLP 94-II-1-148 could fall within the range of this species if a larger sample were available. The known postcranium of "*F.*" *vorohuensis* is limited to a few vertebrae, a proximal portion of the humerus and a portion of the scapula. The full assignment of this fossil to *Ly. colocolo* is not possible because its dimensions are larger and the stability of the shared characters remains to be checked.

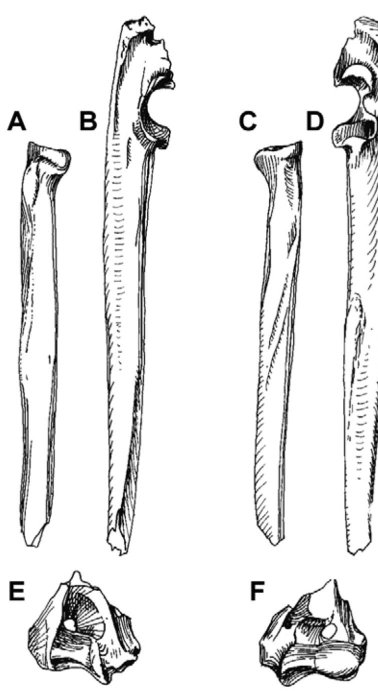

Fig. 3. MLP 94-II-1-148 (cf. *Ly. colocolo*). Lateral and internal view of left radius (A and C, respectively), left ulna (B and D, respectively), and posterior and anterior view of the distal fragment of left humerus (E and F, respectively). Scale: 1 cm.

Fig. 3. MLP 94-II-1-148 (cf. *Ly. colocolo*). Vue latérale et interne du radius gauche (A et C, respectivement), cubitus gauche (B et D), vue postérieure et antérieure du fragment distal de l'humérus gauche (E et F, respectivement). Échelle : 1 cm.

Genus Felis Linnaeus, 1758

Felis catus Linnaeus, 1758

Material examined: MLP 89-XI-10-1 (Fig. 4(A, B) and Table 1): nearly complete right mandible with c-m1, but lacking the angular process.

Geographic and stratigraphic distribution: Lobería (38° 09′S, 58°46′W; Buenos Aires, Argentina; Fig. 1). MLP 89-XI-10-1 comes from the upper section of the La Postrera Formation, a widely distributed aeolic deposit in Buenos Aires province, dated in 0.44 Ka BP (Tonni et al., 1999: 276) but extending to post-Hispanic times (after 1492 AD). It is possible that this specimen was deposited during post-Hispanic age because it is scarcely mineralized and retains a high concentration of organic material (collagen).

Description: The coronoid process is anteroposteriorly expanded and caudally slanted. The coronoid crest is low; the masseteric fossa is shallow and does not reach anteriorly the distal border of the m1. The m1 is small and narrow with respect to the ramus and the premolars. The p4 has a first distal accessory cusp that is completely separated from the labial portion of the distal cingulum. The p3 is mesiodistally short, lacks a paraconid and the first distal accessory cusp is reduced, but has a tall protoconid. The p3 shows an elliptic outline in occlusal view. The c1 is proportionally small and presents a weak vertical groove on its mesiolingual border.

Discussion: MLP 89-XI-10-1 was determined as "*Felis*" cf. "*F.*" *geoffroyi* by Berman (1994: 396) but this author did not provide any description, comparison or discussion. The measures of the mandible are greater than those for *On. guigna* and fall within the range of *Ly. colocolo*, *Le. wiedii*, *On. geoffroyi*, *H. yagouaroundi* and *On. tigrina* (except MHDBm1 and

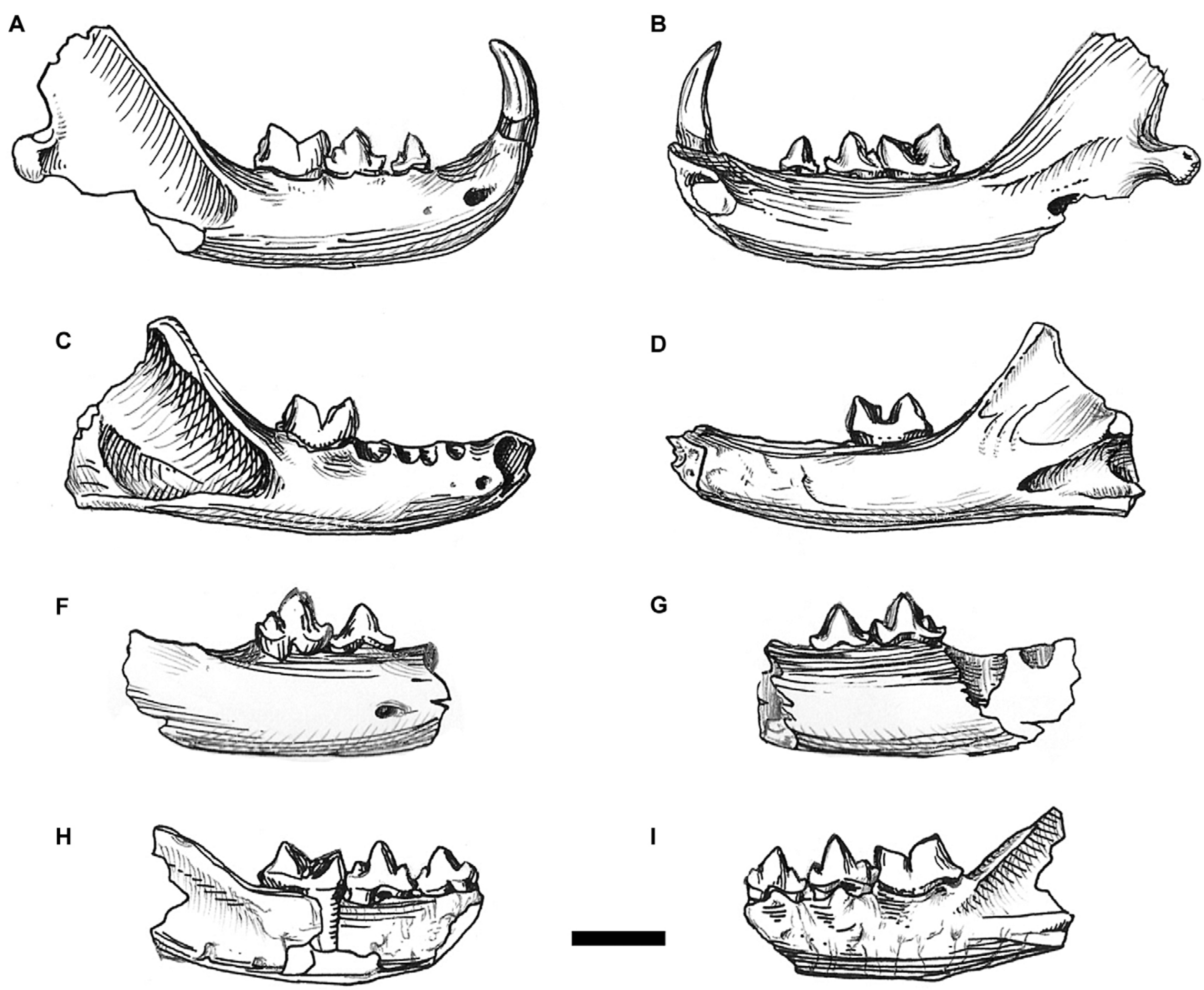

Fig. 4. Southern South American fossil cats. Mandibles MLP 89-XI-10-7 (*F. catus*; lateral and medial view, A and B, respectively), UNSGH 464 (cf. *Herpailurus*; lateral and medial view, C and D, respectively), MLP 96-V-10-11 (Felidae indet.; lateral and medial view, E and F, respectively) and MLP 91-IV-15-1 (Felidae indet.; lateral and medial view, G and H, respectively). Scale: 1 cm.

Fig. 4. Chats fossiles du sud de l'Amérique du sud. Vue linguale et labiale des mandibules MLP 89-XI-10-7 (*F. catus* ; A et B), UNSGH 464 (cf. *Herpailurus* ; C et D), MLP 96-V-10-11 (Felidae indet. ; E et F), MLP 91-IV-15-1 (Felidae indet. ; G et H). Échelle : 1 cm.

MWDBm1) (Table 1 and Appendix A). All the measurements of *Or. jacobita* are greater than those of MLP 89-XI-10-1 (Appendix A). The proportionally short p3 with a large protoconid is similar to some specimens of *Ly. colocolo* and *F. catus* (Fig. 4 (A, B). The mesiolingual groove of the c1 is shallower than in *Ly. colocolo*; furthermore, this feature also presents the same development in other species (vide supra). MLP 89-XI-10-1 shows two characters not present in Neotropical cats: anterior border of the masseteric fossa, behind the coronoid crest, poorly excavated; c1 proportionally small. Both these features occur in *F. catus*. In agreement with the qualitative assessment, the specimen was assigned to *F. catus* (PP: 0.985) in a DA (Wilks' Lambda: 0.04325, approx. F (80.880) = 10.127 $P < 0.0001$; CC = 83.74%) performed using six species (*Ly. colocolo*, *Le. wiedii*, *On. geoffroyi*, *H. yagouaroundi*, *On. tigrina*, *F. catus*), 203 specimens and 16 variables (LM; MHDBm1; MWDBm1; MHm1-p4; MWm1-p4; MHMBp3; MWMBp3; Lm1-c1; Lm1; Wm1; Lp4; Wp4; Lp3; Wp3; Lc1; Wc1).

Felidae cf. *Herpailurus* sp.

Material examined: UNSGH 464 (Fig. 4(C, D) and Table 1): incomplete right mandible with m1.

Geographic and stratigraphic distribution: Bajo San José (38°29′S, 61°47′W; Buenos Aires, Argentina; Fig. 1). UNSGH 464 was found in the lower section of the San José sequence (Deschamps, 2003: 166). This level had been previously assigned to the Ensenadan (Deschamps, 1998: 3) on the basis of its mammalian fauna, but a reanalysis of the fauna has shown it to belong to the younger Bonaerian stage/age (Deschamps, 2003: 245).

Description: The mandible is small (Table 1) but the horizontal ramus is strong with a rounded lateral wall. The horizontal ramus tapers rostrally, and the symphysis is low and triangular. The masseteric fossa is deep and wide, reaching the distal portion of the m1. The angular process is robust, short and not expanded behind the mandibular condyle. The m1 is large with respect to the size of the ramus and very wide, lacking a middle lingual constriction, but with a distal cingulum slightly expanded. The labial faces of the trigonid blade present heavy wear facets.

Discussion: The mandible is similar to *H. yagouaroundi* in several aspects of the ramus: the lateral face is rounded; its height decreases rostrally and the symphysis is low. These similarities may be the reasons for Deschamps' (2003: 165–166) identification of the specimen to "*H.* cf. *yagouaroundi*", but she did not provide descriptions or discuss the characters used for the determination. On the other hand, UNSGH 464 differs from the recent species in other characters. In *H. yagouaroundi* the ventral border of the mandible is narrow and the angular process is expanded posteriorly behind the condyle. The measurements are smaller than those for *Or. jacobita* and fall within the range of *On. geoffroyi*, *H. yagouaroundi*, *Le. wiedii* and *Ly. colocolo* (Table 1 and Appendix A). The measurements of MHp4-p3 are below the observed range of *Ly. colocolo* (Table 1 and Appendix A). The size of the m1 and the width of the horizontal ramus are greater than in *On. guigna* and *On. tigrina*, and allow to separate it from these recent species (Table 1 and Appendix A). *F. vorohuensis* has a shorter and wider m1 (Table 1). The DA (Wilks' Lambda: 0.20574, approx. F (40.822) = 8.9887 $P < 0.0001$; CC = 62.68%) identified UNSGH 464 as *H. yagouaroundi* (PP: 0.923). Six groups (*On. geoffroyi*, *On. guigna*, *On. tigrina*, *H. yagouaroundi*, *Le. wiedii*, *Ly. colocolo*), 201 specimens and eight variables ((MHDBm1 MWDBm1; MHm1-p4; MWm1-p4; MHMBp3; MWMBp3, Lm1; Wm1) were used in this analysis. The full assignment of this specimen to *Herpailurus* is not possible because it shows some morphological differences with respect to the recent species and the CC of the DA is low.

Felidae indet

Material examined: MLP 96-V-10-11 (Fig. 4(E, F) and Table 1): right incomplete ramus, with p3-p4; MLP 91-IV-15-1 (Fig. 4(G, H) and Table 1): incomplete right mandible with m1-p3; MMP S215: fragmentary right maxillary and premaxillary with I2-3 and C1 inside the alveolus.

Geographic and stratigraphic distribution: MLP 96-V-10-11 was collected at the eastern sector of the alluvial fan of the Pilcomayo river downstream from Juntas de Fontana (≈ 25° S, 10°W; Formosa, Argentina; Fig. 1; Tonni and Scillato Yané, 1997: 345). The associated mammalian fauna restricts the age of this bed to the Lujanian (0.13 Ma–8.5 Ka BP; Tonni and Scillato Yané, 1997: 345). MLP 91-IV-15-1 was found in a stratigraphic unit below an aeolian deposit of the last interglacial stage (isotopic substage 5e, 0.125 Ma AP; Isla et al., 2001: 9) at Centinela del Mar (38°25′S, 58°13′W; Buenos Aires, Argentina; Fig. 1). The fossil bearing level could be the coastal lagoon facies of the last interglacial, described by Isla et al. (2001: 7); Schultz et al. (2004: 223). These data suggest that MLP 91-IV-15-1 is close to 0.125 Ma AP (lower Lujanian) in age. An $^{40}Ar/^{39}Ar$ date of 0.23 ± 0.04 Ma was recently published (Schultz et al., 2004) from a lower stratigraphic level (3 m below), which is consistent with this interpretation. The only information concerning the stratigraphic/geographic provenance of MMP S215 is an inscription "Chap" on the fossil. This could be a reference to the locality Chapadmalal (≈38°11′ S, 57°41′W; Buenos Aires, Argentina) or to the Chapadmalal "Formation" (Chapadmalalan, Early Pliocene; Cione and Tonni, 1995, 2001). If MMP S215 comes from Chapadmalal "Formation", it would be the earliest record of Felidae in South America, but I was not able to confirm this supposition.

Description: MLP 96-V-10-11: The premolars are proportionally long, with weakly developed distal cingulums. The main cusps of the premolars are obliquely oriented with respect to the long axis of the ramus. The first distal accessory cusp of the p4 is separated from the distal cingulum. The p3 is proportionally long and has a robust, mesiodistally expanded protoconid, well-developed distal and mesial cingulums, and lacks the paraconid and accessory cusps.

MLP 91-IV-15-1: This specimen is poorly preserved due to the action of humic acid. The m1 is long and has a minute distal cingulum and small wear facets on the trigonid. The p4-3 are long and low with respect to their transverse diameter.

The p4 has a low protoconid, with straight proximal and distal cristids. Its paraconid and first distal accessory cusp are rounded and subequal. The distal cingulum is strong on the lingual border. The p3 is smaller than the p4, but proportionally longer. The paraconid, first distal accessory cusp and distal cingulum are more reduced than in the p4.

Discussion: The size of MLP 96-V-10-11 falls within the range of variability of *H. yagouaroundi*, *On. geoffroyi, Ly. colocolo*, and *Le. wiedii*, but is greater than *On. guigna* and *On. tigrina* (Table 1 and Appendix A). The dental measures are smaller than in *Or. jacobita*, and the mandible ramus is more narrowed transversally. In *H. yagouaroundi* the ramus tapers rostrally and the symphyseal region is lower. Only a few specimens of *Ly. colocolo*, *On. geoffroyi* and *Le. wiedii* have a similar p3 without cingular or accessory cusps and with a mesiodistally elongated protoconid. Both paraconid and first distal accessory cusp are normally present, although reduced, in the p3 of *H. yagouaroundi*; only in one specimen this premolar lacks the paraconid, and the first distal accessory cusp are represented by a minute knot of enamel. "*F.*" *vorohuensis* is smaller and has shorter premolars (Table 1). In addition, the vertical cristid of the p4 protoconid is straighter in the latter species; the first distal accessory cusp and distal cingulum are not separated on the labial side, whereas the P3 presents a small paracone and first distal accessory cusp, with an acute tall protoconid. However, the systematic value of some of these differences (e.g. the undifferentiated first distal accessory cusp and distal cingulum on the labial border) is doubtful. Again, the obliquity of the premolar with respect to the long axis of the ramus is variable in recent specimens (Seymour, 1999: 307; Prevosti pers. obs.; vide supra). I performed a DA (Wilks' Lambda: 0.19813 approx. F $(30.382) = 9.3766$ $P < 0.0001$; CC = 76.92%) using the four recent species that are similar in size to MLP 96-V-10-11 (vide supra), as a priori groups (153 total specimens, 10 variables: MHm1-p4; MWm1-p4; MHp4-p3; MWp4-p3; MHMBp3, MWMBp3; Lp4; Wp4; Lp3; Wp3). This function classified MLP 96-V-10-11 as *On. geoffroyi* (PP: 0.738) and with less probability to *Ly. colocolo* (PP: 0.187).

MLP 91-IV-15-1 was determined by Berman (1994: 395) as "*Felis* cf. *F. colocolo*" because it is "merísticamente semejante" ("meristically similar") and the ramus is high and narrow. The ramus is very deteriorated, which makes it difficult to appreciate its exact morphology. Apparently it is not different from other species (e.g. *On. geoffroyi*). In contrast to "*F.*" *vorohuensis*, *Ly. colocolo* and other recent species, the premolars of MLP 91-IV-15-1 are proportionally low and narrow (Table 1 and Appendix A). Some specimens of *On. geoffroyi* and *On. guigna* have similarly proportioned premolars, but the protoconids are higher and larger in the recent species. The measures are smaller than those of *Or. jacobita* and greater than those of *On. guigna* and *On. tigrina*, but fall within the variation range of the other recent species (Table 1 and Appendix A). The length of the m1 is greater than in *Le. wiedii*, and also than in "*F.*" *vorohuensis* (Table 1 and Appendix A). The DA (Wilks' Lambda: 0.42521 approx. F $(18.453) = 8.8852$ $P < 0.0001$; CC = 65.68) performed with four species (*Ly. colocolo*, *On. geoffroyi*, *H. yagouaroundi*, *Le. wiedii*), 169 specimens and six variables (Lm1; Am1; Lp4; Wp4; Lp3; Wp3) identified MLP 91-IV-15-1 as *On. geoffroyi* (PP: 0.904) in agreement with the proportion of the premolars. A different possibility, namely, that this fossil might correspond to a new species, cannot be assessed due to the fragmentary condition of the specimen and the great intraspecific variation found within the recent species.

The morphology of MMP S215 and the size of its incisors (LI2: 0.1.95, WI2: 2.45, LI3: 3.15, WI3: 3.4) agrees with those of the large species of Neotropical cats (i.e. *Ly. colocolo*, *On. geoffroyi*, *Le. wiedii*, "*F.*" *vorohuensis*), but it was not possible to assign it to any genus or species.

4. Fossil record, molecular divergence dates and the small felid immigrations to South America

The osteological, soft anatomy, chromosomal, and molecular evidence shows that the Ocelot Lineage is a monophyletic group (Collier and O'Brien, 1985; Herrington, 1986; Modi and O'Brien, 1988; Pecon Slattery et al., 1994; Johnson et al., 1996, 1998, 1999; Masuda et al., 1996; Pecon Slattery and O'Brien, 1998; Eizirik et al., 1998; Seymour, 1999; Mattern and McLennan, 2000), and several authors have suggested that this radiation occurred in Central and South America (Glass and Martin, 1978: 85; Werdelin, 1989: 290–291; Berman, 1994: 413).

Prior to this work, "*F.*" *vorohuensis* was the oldest record of the Ocelot Lineage, and its Ensenadan age (2–0.5 Ma BP) has recently been recognized on the basis of new biostratigraphic studies (e.g. Tonni et al., 1992, 1998; Cione and Tonni, 1995; Vucetich et al., 1997; Verzi et al., 2002; see Berman, 1994; Seymour, 1999). Recent field work (with the aid of the collector of MMP 1047, Alejandro Dondas, see Berta, 1983: 721) allowed me to recognize the exact stratigraphic provenance of the holotype of "*F.*" *vorohuensis*. The material has been collected from a very yellowish brown (10YR 5/6) sandy silt bed at the middle section of the profile, at the marine cliffs 800 m south of the northern boundary of the Regimiento 601 (37°52′58″S, 57°31′01″W; Fig. 1). The stratigraphic position, structure, diagenesis and texture of the bearing level suggest its correlation with the upper section of the unit 4 or the unit 3 described by Bidegain et al. (1998: 238; Bidegain et al. (2003: 7) at F.U. Camet (3 km south of the type locality of "*F.*" *vorohuensis*), which belong to the Brunhes Chron. This and the presence of Ensenadan mammals at similar stratigraphic levels (Vucetich et al., 1997: 209; Prevosti et al., 2004), restrict the age between 0.78 and ca. 0.5 Ma BP (Fig. 5). The other oldest record is reported here and corresponds to the presence of *Ly. colocolo* at the early Middle Pleistocene (latest Ensenadan, 0.78–ca. 0.5 Ma BP) of the Pampean Region, too (vide supra). *Ly. colocolo* occurs also in the Bonaerian or Lujanian of this region (vide supra), and *On. tigrina*, *Le. pardalis*, *Le. wiedii* in the Lujanian of Brazil (Seymour, 1999: 393–402; Lessa et al., 1998: 160). The specimens MLP 96-V-10-11 and MLP 91-IV-15-1 present some affinity with *On. geoffroyi*, and could be representatives of this taxon for the Bonaerian and Lujanian in Argentina, but the morphological evidence is not conclusive as discussed. Thus the record of the South American cats starts after the massive record of North American mammals in the Pampean region at the earliest Ensenadan (ca. 2–1.8 Ma AP, Cione and Tonni, 2001: 171). The presence of the Ocelot Lineage in North America begins during the Sangamonian (≈0.13 Ma BP), when *L. pardalis* and *Le. wiedii amnicola* are first recorded (Werdelin, 1985: 198). Some species of the Miocene/Pliocene of North America have been considered as the ancestors of the Ocelot Lineage (e.g. Glass and Martin, 1978: 85; Wayne et al., 1989: 471; Wayne et al., 1991: 312) but the phylogenetic relationships of these Tertiary species have not been tested in a cladistic framework (Werdelin, 1985: 207; Seymour, 1999: 459).

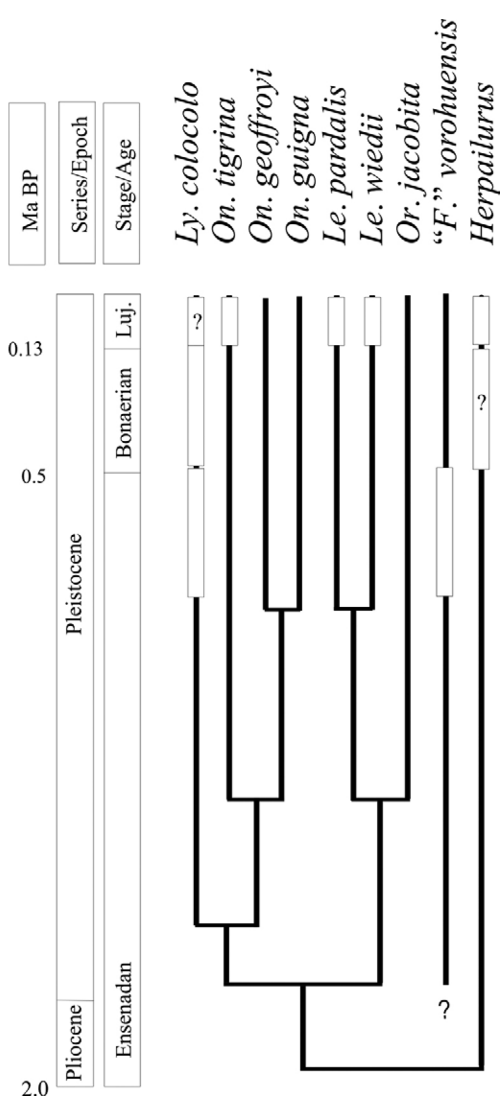

Fig. 5. Phylogenetic hypothesis for South American cats (adapted from Johnson et al., 1998, 1999) and their stratigraphic record in South America. White box: stratigraphic record. Luj.: Lujanian. The splittings do not represent real time of divergence.

Fig. 5. Hypothèse phylogénétique des chats d'Amérique du Sud (modifié de Johnson et al., 1998, 1999) et leur dossier stratigraphique. Boîte blanche : dossier stratigraphique. Luj. : Lujanéen. Les ramifications ne représentent pas le temps réel de la divergence.

Several time divergence dates of the Ocelot Lineage species have been calculated with different molecular methods (e.g. immunological distance; electrophoresis; DNA hybridization; nuclear and mitochondrial gene distance) and compared with the time of the rising of the Panamian Bridge (e.g. Bininda Emonds et al., 1999: 163) for an estimation of their geographical area of origin. The Isthmus of Panama was completely established at 2.8–3.1 Ma BP (Coates and Obando, 1996: 21), but eustatic sea-level changes interrupted it several times until the middle Pleistocene (Beu, 2001: 715). The separation of the ancestor of this clade from other felids is estimated to have occurred between 10 and 4 Ma BP, predating this geological event (Wayne et al., 1989: 470–471; Pecon Slattery et al., 1994: 302; Johnson et al., 1996: 110; Johnson and O'Brien, 1997: S106; Pecon Slattery and O'Brien, 1998: 1252; Johnson et al., 1999: S88). Some authors have estimated that the radiation of the group began at 2–3 Ma BP (Wayne et al., 1989: 470–471; Johnson and O'Brien, 1997: S106) coinciding with the rising of the Panamian bridge, but others have suggested older estimates for the separation of the ancestor of some species (6–3.9 Ma BP; Pecon Slattery et al., 1994: 302; Johnson et al., 1996; Johnson et al., 1999: S88; Bininda Emmons et al., 1999). According to analysis of mitochondrial genes the time of separation of the ancestors of *Ly. colocolo* (5.3 Ma BP), *On. tigrina* (3.9 Ma BP), and *Or. jacobita* (≈5 Ma BP) are older than the Panamian bridge, while the time of separation of the ancestor of *Le. pardalis* (3 Ma BP), *Le. wiedii* (3 Ma BP), *On. guigna* (2.3 Ma BP) and *On. geoffroyi* (2.3 Ma BP) are "synchronic" or younger, respectively (Eizirik et al., 1998: 620; Johnson et al., 1999: S88). On the other hand, the divergence time of the recent mitochondrial lineages of *Ly. colocolo* (1.7 Ma BP; Johnson et al., 1999: S88) agrees with a younger date.

The comparison of the new information of the fossil record of the Ocelot Lineage with the molecular estimation of its dates of divergence and its first fossil representative reveals a large gap, approximately 1 Ma larger than previously thought (Fig. 5). The first fossil appearance usually marks the younger date of origin (speciation), but does not necessarily coincide with the actual time of origin of a taxon, and usually postdates it (see Brochu et al., 2004: 2). Second, the combination of several taphonomic biases and other biological factors, could partially explain this "incongruity". Some potential biological and taphonomic factors could be: (1) Favored bone deposition and preservation at cool and/or dry climates in continental environments (Behrensmeyer et al., 2000: 122; see also Retallack, 1998: 141–142). (2) Taphonomic bias against small mammals (Behrensmeyer, 1978: 160), because small bones are more easily destroyed by transport, scavengers, trampling, weathering and acids (the last two due to the relative high surface/volume ratio; Behrensmeyer, 1978: 160–161; Behrensmeyers, 1991: 300; Retallack, 1998: 141). (3) As predators, the carnivores are relatively less abundant than other mammals (Sunquist and Sunquist, 2001: 399), also the small wild felids are currently scarcer than other carnivores (e.g. canids) in several regions of the Neotropics (Robinson and Redford, 1989: 585–588; Cajal and Bonaventura, 1998: 191–213; Luengos Vidal et al., 2003: 4). On the other hand, the fossil record preserves information about the branching order, and it shows moderate congruence with the current phylogenetic hypothesis of the group (MSM* = 0.50, *P*. 0.024, but turned out non significant if "*F*." *vorohuensis* is excluded, *P*. 0.125). Thus it is possible that several methodological biases in the estimation of the molecular divergence time result in older estimated dates (e.g. Rodríguez Trelles et al., 2002: 8112–8115; Graur and Martin, 2004: 80–83).

The comparison of these dates with the rising of the Panamian bridge can be used to speculate on the number of immigration events to South America, but we cannot identify with certainty the "area" of differentiation of the recent species or exclude the possibility that the ancestors of the recent species reached South America prior to the rise of the bridge, as occurred with the procyonids of the *Cyonasua* "group" (Kraglievich and de Olazabal, 1959; Marshall et al., 1979). This last scenario is not supported by the fossil record (Fig. 5), but the Ocelot Lineage species could have been restricted to northern South America at earlier times and expanded to southern regions during the Pleistocene; in this case, their absence in older rocks could be due to a taphonomic bias of the South American fossil record against tropical regions (Campbell et al., 2000: 97–115).

If the Ocelot Lineage species (or their ancestors) invaded South America after the rise of the Panama Bridge, as recorded in the fossil record, and if the molecular dates (Eizirik et al., 1998; Johnson et al., 1999) are reliable, we can explain the present diversity with a minimum five or six immigrations leading to: *Or. jacobita* (1); *Ly. colocolo* (2); *On. geoffroyi–On. guigna* ancestor (3), *On. tigrina* (4); *Le. pardalis–Le. wiedii* ancestor (5). If *Le. pardalis* and *Le. wiedii* speciated outside South America, or one originated in South America and the other in Central America, an additional immigration event is required. On the other hand the current geographical distribution, habitats (Nowell and Jackson, 1996) and fossil record of *Ly. colocolo* (vide supra) suggest that *Or. jacobita*, *Ly. colocolo*, *On. geoffroyi* and *On. guigna* evolved in South America. Johnson et al. (1999: S88) considered the possibility that *Or. jacobita* and *Ly. colocolo* speciated simultaneously in the Andes after becoming isolated from their ancestors, who occupied lowlands and tropical habits, but we can not reject the southern open habitats as a scenario for the speciation of *Ly. colocolo*. With this scenario the number of immigrations may be reduced to 1 or 2, but implied that the molecular dates are too old. *Le. pardalis*, *Le. wiedii* and *On. tigrina* could have originated in Central America, or even in the southern portion of North America in the case of the first two species, but the phylogeographic patterns of *Le. pardalis* and *Le. wiedii* show that their recent populations in Central America are descended from South American populations (Eizirik et al., 1998: 620). Finally, the Ocelot Lineage radiation beginning earlier than the late Pleistocene (contra Berman, 1994: 413).

H. yagouaroundi is phylogenetically close to the *Puma concolor* "group" (Herrington, 1986; Masuda et al., 1996; Johnson and O'Brien, 1997; Pecon Slattery and O'Brien, 1998; Bininda Emonds et al., 1999; Mattern and McLennan, 2000) and represents another felid invasion into South America. The presence of *H. yagouaroundi* in North American Pleistocene sediments is doubtful (Werdelin, 1985: 194). This species is recorded in Lujanian deposits in Brazil (Seymour, 1999: 402; Cartelle, 1999: 32, Table 4.1), but earlier records of this lineage in South America are conditioned to the determination of cf. *Herpailurus* for the Bonaerian of Argentina (vide supra; Fig. 5). Upon examination, the supposed *H. yagouaroundi* specimen found in Ensenadan beds of Tarija (Bolivia; Hoffstetter, 1963: 199; Hoffstetter, 1986: 225) has been shown to be too fragmentary to be assigned to any living species of Neotropical small cat (Seymour, 1999: 405; Prevosti pers. obs.). On the other hand, the age of this fossil is dubious because it lacks precise stratigraphic and geographic provenance, and the Tarija stratigraphic column comprises a long deposition period, from the Jaramillo event of the Matuyama chron (≈1 Ma BP; MacFadden, 2000: 121–123) to probably late Pleistocene (Takai, 1982: 5; Hoffstetter, 1986: 225).

5. Conclusions

The C/I S/N°, the oldest record of *Ly. colocolo*, was found in late Ensenadan beds (0.78–ca. 0.5 Ma BP) in the Pampean region (Argentina). Other records of this species have occurred in the Bonaerian or Lujanian of the region. I confirm the presence of *Ly. colocolo* in Tierra del Fuego, an island not inhabited by any felids at present, but the age of this fossil could be Holocene or late Pleistocene due the bioturbation of the site.

If the determination of UNSGH 464 as *Herpailurus* is confirmed, this record would represent the earliest fossil of the genus, and expand its range to the Bonaerian (ca. 0.5–0.13 Ma BP).

MLP 96-V-10-11 and MLP 91-IV-15-1 show some similarities to *On. geoffroyi*, but it is not possible to assign them confidently to the latter species. On the other hand, the specimen determined as *On. geoffroyi* by Berman (1994) actually belongs to *F. catus*, and its taphonomic features suggest that it comes from post-Hispanic sediments. The apparent absence of *On. geoffroyi* in the South American fossil record contrasts with its status as the most common South American cat today (e.g. Johnson et al., 1999: S90).

New biostratigraphic/chronostratigraphic schemes (Cione and Tonni, 1999, 2001), paleomagnetic studies (Bidegain et al., 1998, 2003) and the author's field work, permit to restrict the age of "*F*." *vorohuensis* to the late Ensenadan (0.78–ca. 0.5 Ma BP).

The fossil record of the Ocelot Lineage is very fragmentary and begins in the late Ensenadan. Various taphonomic biases clearly affect this record. The molecular divergence times suggest that the radiation of the clade began in the lower Pliocene, but overestimation due to some methodological bias could be partially responsible for these old dates. The age of the oldest records stated in this paper shows that the gap is larger than previously thought. The combination of paleontological and distributional evidence suggests that *Ly. colocolo*, *On. guigna*, *On. geoffroyi* and *Or. jacobita* speciated in South America, thus supporting the opinion of Johnson et al. (1999: S88), but we can not exclude the possibility that *Le. pardalis*, *Le. wiedii* and *On. tigrina* could have originated outside this subcontinent.

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Appendix A

Cranial, mandibular and dental measurements of recent species used for comparison. Abbreviations as in Table 2, see text for other explanations.

	On. geoffroyi X ± S.D. (*N*) OR	*H. yagouaroundi* X ± S.D. (*N*) OR	*On. guigna* X ± S.D. (*N*) OR	*Ly. colocolo* X ± S.D. (*N*) OR
LP4-C1	28.75 ± 2.48 (65) 23.5–35.55	29.04 ± 1.70 (45) 26.40–33.24	24.78 ± 2.25 (8) 22.40–30.00	29.13 ± 1.40 (15) 26.50–31.40
LP4	12.05 ± 0.87 (72) 10.00–13.60	11.70 ± 0.87 (50) 10.20–14.40	9.68 ± 0.38 (8) 9.10–10.20	11.92 ± 0.74 (20) 10.95–13.20
WP4	5.47 ± 0.53 (72) 4.40–7.05	5.31 ± 0.56 (50) 4.50–7.02	4.67 ± 0.53 (8) 3.70–5.60	5.28 ± 0.35 (21) 4.55–6.10
LP3	7.55 ± 0.62 (71) 6.10–9.80	7.40 ± 0.60 (49) 6.20–8.99	6.08 ± 0.40 (8) 5.50–6.80	7.20 ± 0.40 (20) 6.35–8.05
WP3	3.68 ± 0.35 (71) 4.50–7.25	3.71 ± 0.35 (49) 3.20–4.80	2.96 ± 0.20 (8) 2.50–3.20	3.68 ± 0.26 (19) 3.10–4.35
LC1	5.69 ± 0.68 (65) 4.50–7.25	5.06 ± 0.44 (48) 4.15–6.17	4.23 ± 0.30 (8) 3.60–3.67	5.60 ± 0.37 (16) 4.96–6.40
WC1	4.00 ± 0.50 (66) 2.95–5.05	3.63 ± 0.33 (48) 3.00–4.51	3.14 ± 0.30 (8) 2.60–3.67	3.92 ± 0.41 (16) 3.20–4.95
LM	63.41 ± 6.10 (63) 50.50–77.05	58.76 ± 4.58 (44) 51.30–72.57	51.21 ± 2.70 (7) 47.40–54.90	63.09 ± 4.24 (18) 53.65–69.95
MHDBm1	11.89 ± 1.66 (64) 8.10–16.20	11.71 ± 1.26 (45) 8.60–14.72	9.10 ± 0.57 (7) 8.60–10.30	12.20 ± 1.10 (18) 9.76–14.6
MWDBm1	5.55 ± 0.75 (64) 4.05–7.30	5.19 ± 0.52 (45) 4.28–7.05	4.37 ± 0.44 (7) 3.70–4.90	5.57 ± 0.63 (18) 4.31–6.60
MHm1–p4	11.40 ± 1.46 (64) 7.99–15.20	11.15 ± 1.14 (45) 9.20–13.94	8.19 ± 0.88 (7) 7.30–9.49	11.95 ± 1.41 (18) 9.30–14.35
MWm1-p4	5.82 ± 0.75 (64) 4.10–7.65	5.51 ± 0.52 (45) 4.65–7.92	4.36 ± 0.40 (7) 3.90–5.18	5.97 ± 0.59 (18) 5.15–6.90
MHp4-p3	9.46 ± 1.49 (49) 7.70–13.90	9.77 ± 1.08 (45) 7.95–13.24	8.57 ± 0.02 (2) 8.55–8.60	11.48 ± 1.18 (13) 8.56–12.70
MWp4-p3	5.12 ± 0.79 (49) 3.90–6.70	5.00 ± 0.54 (45) 4.00–8.95	4.25 ± 0.30 (2) 3.95–4.55	5.69 ± 0.89 (13) 4.29–7.5
MHMBp3	10.54 ± 1.52 (64) 7.50–14.50	9.39 ± 1.22 (45) 7.60–13.1	7.61 ± 0.74 (7) 6.45–8.95	10.78 ± 1.38 (18) 7.90–12.60
MWMBp3	5.49 ± 0.82 (64) 3.95–7.20	5.17 ± 0.64 (45) 3.80–7.07	4.03 ± 0.41 (7) 3.60–4.90	5.79 ± 0.60 (18) 4.37–7.05
Lm1-c1	33.47 ± 2.70 (61) 27.20–40.10	31.99 ± 1.99 (45) 29.05–37.60	26.98 ± 1.31 (7) 25.10–28.84	33.04 ± 1.70 (18) 29.22–35.90
Lm1	9.07 ± 0.78 (66) 7.40–11.35	8.89 ± 0.66 (47) 8.05–10.92	7.10 ± 0.59 (6) 6.40–8.10	9.21 ± 0.60 (19) 7.71–10.15
Wm1	3.93 ± 0.36 (66) 3.20–4.36	4.02 ± 0.31 (47) 3.30–4.72	3.14 ± 0.29 (7) 2.70–3.70	4.03 ± 0.40 (19) 3.05–4.60
Lp4	7.76 ± 0.62 (66) 6.30–9.00	7.62 ± 0.64 (47) 6.55–9.26	6.49 ± 0.32 (7) 6.00–7.00	7.65 ± 0.59 (18) 6.60–9.35
Wp4	3.50 ± 0.30 (66) 2.90–4.20	3.66 ± 0.37 (47) 2.95–4.64	2.92 ± 0.41 (7) 2.40–3.75	3.82 ± 0.42 (18) 2.90–4.70
Lp3	6.22 ± 0.58 (66) 4.60–7.40	5.97 ± 0.49 (46) 5.15–7.39	5.14 ± 0.28 (7) 4.50–5.50	6.15 ± 0.39 (18) 5.40–6.90
Wp3	2.85 ± 0.29 (66) 2.05–3.45	3.18 ± 0.36 (46) 2.35–4.41	2.36 ± 0.19 (2.10–2.60)	3.30 ± 0.40 (18) 2.70–4.40
Lc1	5.36 ± 0.67 (63) 4.10–7.35	4.96 ± 0.50 (47) 3.80–6.27	4.39 ± 0.38 (7) 3.8–5.1	5.44 ± 0.43 (19) 4.25–6.00
Wc1	4.02 ± 0.41 (62) 3.00–5.25	3.76 ± 0.41 (47) 2.9–4.84	3.05 ± 0.23 (7) 2.7–3.46	4.06 ± 0.79 (19) 3.25–7.20

	Le. wiedii X ± S.D. (*N*) OR	*On. tigrina* X ± S.D. (*N*) OR	*Or. jacobita* CBF 445/CGECM 027	*F. catus* X ± S.D. (*N*) OR
LP4-C1	27.70 ± 1.17 (36) 25.42–30.43	24.49 ± 0.93 (32) 22.48–25.95	34.80/–	–
LP4	10.88 ± 0.64 (40) 9.73–12.01	9.95 ± 0.46 (35) 8.96–11.20	13.60/12.30	–
WP4	5.29 ± 0.45 (40) 4.44–6.35	4.64 ± 0.38 (35) 3.76–5.40	7.10/7.20	–
LP3	6.72 ± 0.41 (40) 6.15–8.26	6.19 0.34 (35) 5.32–6.72	9.90/9.40	–
WP3	3.51 ± 0.27 (40) 3.05–4.12	3.07 ± 0.21 (35) 2.76–3.60	4.20/4.30	–
LC1	5.24 ± 0.44 (39) 4.32–6.15	4.16 ± 0.33 (35) 3.53–4.71	6.40/–	–

	Le. wiedii	*On. tigrina*	*Or. jacobita*	*F. catus*
WC1	3.67 ± 0.33 (39) 2.96–4.40	3.06 ± 0.25 (35) 2.46–3.42	5.20/–	–
LM	58.11 ± 3.36 (37) 51.44–67.90	52.61 ± 2.32 (29) 48.58–56.75	74.40/72.50	62.69 ± 3.67 (22) 56.5–70.90
MHDBm1	10.37 ± 0.81 (37) 8.84–12.2	9.09 ± 0.68 (31) 7.61–10.6	13.80/12.60	11.17 ± 0.82 (21) 9.60–12.70
MWDBm1	4.92 ± 0.51 (37) 4.12–6.05	4.16 ± 0.33 (31) 3.55–5.4	7.50/6.30	5.31 ± 0.87 (21) 2.10–6.20
MHm1-p4	10.05 ± 0.78 (37) 8.40–12.10	8.77 ± 0.67 (31) 7.34–9.93	12.10/12.00	10.71 ± 0.80 (21) 9.50–12.15
MWm1-p4	5.09 ± (37) 4.27–8.08	4.34 ± 0.28 (31) 3.87–4.89	7.20/720	5.66 ± 0.40 (21) 4.70–6.40
MHp4-p3	9.43 ± 0.78 (37) 7.84–11.80	7.84 ± 0.57 (31) 6.84–8.87	–/11.50	10.02 ± 0.86 (22) 7.75–11.60
MWp4-p3	4.60 ± 0.47 (37) 3.78–5.90	3.89 ± 0.27 (31) 3.44–4.48	–/7.10	5.40 ± 0.43 (22) 4.30–6.20
MHMBp3	9.72 ± 0.74 (37) 8.23–11.3	7.95 ± (31) 6.45–9.12	–/12.85	10.16 ± 0.64 (22) 9.25–11.70
MWMBp3	4.82 ± 0.50 (37) 4.05–5.90	4.03 ± 0.32 (31) 3.20–4.72	–/6.80	4.99 ± 0.49 (22) 3.60–5.75
Lm1-c1	31.19 ± 1.45 (37) 28.44–34.2	27.54 ± 1.17 (29) 25.75–29.40	40.00/39.45	32.16 ± 1.81 (17) 29.15–35.70
Lm1	8.17 ± 0.52 (40) 6.88–9.26	7.63 ± 0.37 (34) 6.71–8.24	11.20/11.10	7.60 ± 0.69 (20) 6.60–9.40
Wm1	3.67 ± 0.26 (40) 3.24–4.23	3.30 ± 0.24 (34) 2.90–3.93	4.70/4.98	3.46 ± 0.30 (21) 2.60–4.10
Lp4	7.52 ± 0.41 (40) 6.86–8.60	6.54 ± 0.35 (34) 5.55–7.15	9.20/9.10	6.95 ± 0.67 (20) 5.20–7.70
Wp4	3.39 ± 0.23 (40) 2.96–3.90	2.90 ± 0.15 (34) 2.64–3.25	4.30/4.70	3.03 ± 0.23 (20) 2.55–3.40
Lp3	5.81 ± 0.46 (40) 4.93–7.00	5.14 ± 0.35 (34) 4.38–5.75	7.30/7.80	5.26 ± 0.36 (21) 4.50–5.90
Wp3	2.84 ± 0.38 (40) 2.39–4.89	2.38 ± 0.17 (34) 2.14–2.80	3.80/4.60	2.48 ± 0.79 (21) 2.20–2.80
Lc1	5.23 ± 0.49 (40) 4.01–6.20	4.18 ± 0.34 (34) 3.53–4.80	9.20/7.05	4.46 ± 0.43 (19) 3.50–5.30
Wc1	3.84 ± 0.38 (40) 2.76–4.71	3.15 ± 0.33 (34) 2.25–3.64	4.30/5.00	3.34 ± 0.36 (19) 2.70–4.30

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