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On the morphological variation and taxonomy of the Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) (Carnivora, Felidae)

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ABSTRACT

The Geoffroy's cat Leopardus geoffroyi *(d'Orbigny & Gervais, 1844) is a small cat found in the Southern Cone of South America and, depending on the author, four or five subspecies have been usually recognized (*L. g. geoffroyi, L. g. paraguae, L. g. euxanthus, L. g. salinarum *and* L. g. leucobaptus*), mainly based on external morphological characters, such as color pattern of the pelage. In order to clarify the taxonomy of* L. geoffroyi, *I analyzed approximately 200 specimens housed in museums. I have examined the external and craniodental morphology in quantitative and qualitative terms in the search for patterns of congruent characters that would indicate the existence of taxonomic units. Twenty craniodental measurements were taken and tested by univariate and multivariate (MANOVA, PCA and DFA) procedures. In this study I detected a great variation in the morphological characters, and thus it was not possible to determine whether any of these were geographically consistent and could be used to determine any taxonomic unit. Based on this, I do not recognize any subspecific division for* L. geoffroyi. *Along its geographic range, a gradual and subtle change from one color pattern to the next along the latitude was detected, but the morphological characters that were used to define the putative subspecies were also detected in a same population. Furthermore, the present study is congruent with the results obtained by previous molecular data, suggesting that* L. geoffroyi *has a high level of genetic diversity with no geographic structure. This indicates the existence of a large panmictic population with no significant barriers to gene flow and, as a consequence, no subspecies should be recognized.*

Key-Words: *Leopardus geoffroyi;* Taxonomy; Subspecies; Morphology; variation.

INTRODUCTION

The Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) is a small-sized South American felid (4.26 ± 1.03 kg, n = 56) (Lucherini *et al.,* 2006) found from southern Bolivia to the Strait of Magellan, southern Argentina and Chile (Redford & Eisenberg, 1992; Sunquist & Sunquist, 2002, 2009). According to recent phylogenies (Johnson & O'Brien, 1997; Jonhson *et al.,* 1999; Mattern & MacLennan, 2000; Johnson *et al.,* 2006), it is a member of the "ocelot lineage" [= tribe Leopardini (Nascimento & Garbino, *in prep.*)], a group that includes the small and medium-sized spotted Neotropical cats of the

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genus *Leopardus.* Both molecular and morphological data suggests that the Geoffroy's cat and kodkod or huiña *L. guigna* (Molina, 1872) from central Chile and western Argentina are sister species (Johnson & O'Brien, 1997; Johnson *et al.,* 1999; Mattern & MacLennan, 2000; Eizirik & Johnson, 2006; Johnson *et al.,* 2006). Furthermore, recent studies also show the existence of a hybridization zone between Geoffroy's cat and the oncilla, *L. guttulus* (Hensel, 1872) [formerly a subspecies of *L. tigrinus* (Schreber, 1775) (Nascimento, 2010)], in southern Brazil, which is where the extremes of the distribution of the two species are in contact (Eizirik *et al.,* 2006; Trigo *et al.,* 2008).

In the beginning of 19^{th} century, Azara (1802) described in detail a specimen (a female) collected near the border between Uruguay and Brazil ("en la frontera de nuestros Dominios con el Brasil, en los 32 grados y medios de latitud", page 147) (nowadays Departamento de Cerro Largo, Uruguay; Cabrera, 1961), which he named "mbaracayá". According to the description of Azara, "mbaracayá" was clearly an exemplar of Geoffroy's cat, but unfortunately he confused this felid with a "tiger cat" (= *Leopardus wiedii*) (Cabrera & Yepes, 1940; Ximénez, 1971). Four decades later, d'Orbigny & Gervais (1844a) formally described and named this cat as *Felis geoffroyi,* based on three specimens collected on the banks of Rio Negro, Argentina (Figs. 1 and 2). Furthermore, this species was previously associated in a confused way to *Felis himalayana,* described by Jardine in 1834, who proposed the name for a cat from the "Himalaya district of India". The cat was assumed to be a new species of the serval *Leptailurus serval* (Schreber, 1776). Gray (1843) mistakenly associated the name coined by Jardine with the material deposited at the British Museum, and renamed it *Leopardus himalayanus.* Years later, Gray (1867a, b) raised doubts about the locality of the original material that he examined, stating that the specimen probably came from South America. He then renamed it *Pardalina warwickii.* However, Sclater (1870) examined the specimen from the British Museum and found that it belonged to *Felis geoffroyi* d'Orbigny & Gervais collected in Paraguay. In addition, Sclater also pointed out that the animal described and illustrated by Jardine (1834) probably was a specimen of fishing cat *Prionailurus viverrinus* (Bennett, 1833).

In 1903 Thomas described *Felis salinarum* indicating it as a northern representative of *Felis geoffroyi* d'Orbigny & Gervais, 1844 and associating it to *Felis guigna* Molina, 1782: "it is by no means unlikely that *F. guigna* and *F. geoffroyi* will prove to be the same, as in the south the Andes do not present the same faunistic barrier that they do further north". J.A. Allen (1919) followed the opinion of Thomas recognizing *geoffroyi* and *salinarum* as distinct species, but placed both in the genus *Oncifelis.*

Based on British Museum specimens, Pocock (1940) described three subspecies mainly based on color pattern, naming them *Oncifelis geoffroyi euxanthus* (type specimen BM34.9.2.27; Type locality: "Tiragui, Cochabamba, Bolivia"), *O. g. leucobaptus* (type specimen BM28.12.11.2; Type locality: "Salamanca, Chubut, Argentina"), and *O. g. paraguae* (type specimen BM71.3.3.6; Type locality: "Paraguay"); whereas one year later Schwangart (1941) described two additional subspecies, *argentea* and *flava,* based on three specimens from the Muséum National d'Histoire Naturelle, Paris. However, Ximénez (1975) pointed out that the description of *flava* coincided with Pocock's *O. g. paraguae,* and due to the fact that Schwangart based *flava* on the color pattern of one of syntypes of *F. geoffroyi* of d'Orbigny & Gervais, it would be impossible to consider *flava* as a synonym of *paraguae.*

Cabrera (1958) classified the Geoffroy's cat in the genus *Felis* and subgenus *Leopardus,* recognizing five subspecies [*Felis* (*Leopardus*) *geoffroyi geoffroyi, F.* (*L.*) *g. euxantha, F.* (*L.*) *g. leucobapta, F.* (*L.*) *g. paraguae* and *F.* (*L.*) *g. salinarum*]. This is the same taxonomic arrangement present in Wozencraft (2005), except that this last author treated *Leopardus* as a full genus. Before Wozencraft, Ximénez (1971, 1973) also followed this taxonomic arrangement, but he later (Ximénez, 1975) diverged from some of Cabrera's opinions, first regarding the number of subspecies recognized of which Ximénez recognized only four – *F. g. geoffroyi* (including *leucobapta*), *F. g. paraguae, F. g. euxantha* and *F. g. salinarum* – and affirmed that there seemed to be evidence to justify their validities, but the systematic position of *euxantha* was doubtful. The second divergence between Cabrera and Ximénez concerns the geographical distribution of the subspecies *geoffroyi* and *paraguae.* Cabrera (1958, 1961) indicated that *geoffroyi* was distributed from the Pampas district of Argentina (Province of Buenos Aires) to Uruguay and southern Brazil, and that *paraguae* was found in Paraguay and northern Argentina (in the Chaco region). On the other hand, the distribution map present in Ximénez (1975) showed a different pattern, with *geoffroyi* found from the Province of Buenos Aires to the extreme south of the continent, whereas *paraguae* was found in Paraguay, northern and northeastern Argentina, Uruguay and southern Brazil. These facts alone show that there was no consensus regarding a clear definition and delimitation of these putative subspecies. Furthermore, regarding this subject, Ximenéz added that "(t)here is not sufficient information to determine with confidence the marginal areas for the different subspecies, the gaps on the map show this uncertainty rather than the absence of species in these intervening areas".

From a different viewpoint, molecular data suggested that Geoffroy's cat has a high level of genetic diversity with no geographic structure, indicating the existence of a large panmictic population with no significant barriers to gene flow (Johnson *et al.,* 1999; Eizirik & Johnson, 2006); and as consequence no subspecies should be recognized. However, nowadays the taxonomic arrangement of Geoffroy's cat followed by most authorities and conservation institutions and agencies (for example, IUCN – International Union for Conservation of Nature) is the one present in Wozencraft (2005), which put the species in the genus *Leopardus,* recognizing five subspecies: *L. g. geoffroyi, L. g. euxanthus, L. g. leucobaptus, L. g. paraguae* and *L. g. salinarum.*

The main problems in the taxonomy of *L. geoffroyi* – which extends to the other medium and large-sized South American mammals – comprise the identification and delimitation of species and subspecies, which has not been subject to critical

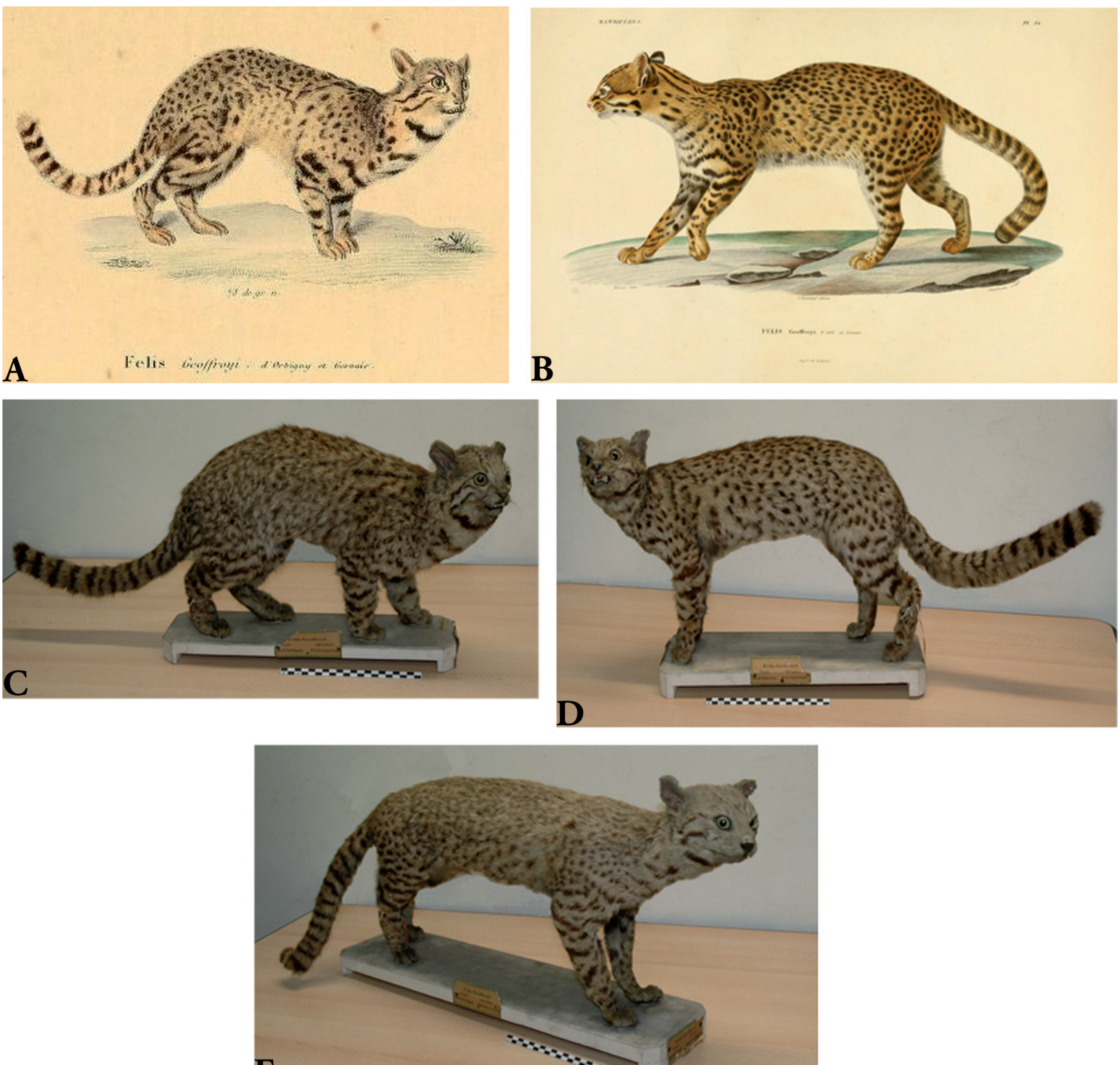

FIGURE 1: Reproduction of the original plates and syntypes of *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844b, 1847): **(A)** overall view of the species (plate published in 1844); **(B)** overall view of the species (plate published in 1847); **(C)** specimen MNHN-ZM-MO-2001-298; **(D)** specimen MNHN-ZM-MO-2001-299; and **(E)** specimen MNHN-ZM-MO-2001-300. Photos of specimens by Cécile Callou (MNHN).

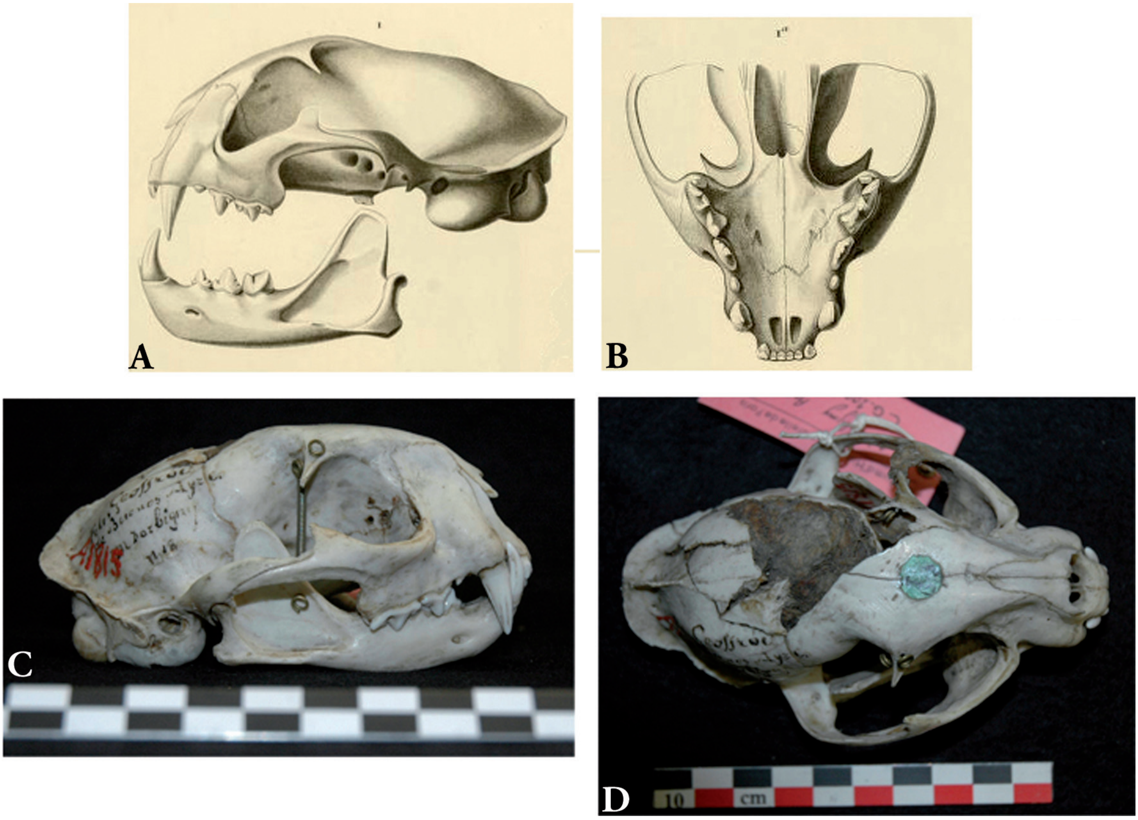

FIGURE 2: (A) lateral and ventral views of the skull (plate published in 1847); **(B)** lateral view from the skull of one of the syntypes, the specimen MNHN-ZM-MO-2001-300; and **(C)** dorsal view from the skull of one of the syntypes, the specimen MNHN-ZM-MO-2001-300. Photo of specimens by Cécile Callou (MNHN).

analysis. In most of the older taxonomic studies on South American mammals, recognition of subspecies was not based on the detection/confirmation of intergradation zones, but on the supposition of their existence (Vivo, 1991, 1996). Although the need for larger, more representative samples is known (Patterson, 2002), nowadays a more conservation-based society established new standards for what is tolerable in terms of collecting specimens. While in the first half of the 20th century it was possible to collect a wide range of animal species (Pinto, 1945), nowadays the collection of large-sized mammals is almost impossible. Thus, most of the samples in scientific collections available today are old. Furthermore, medium and large-sized mammals usually have a small number of specimens housed in scientific collections, covering widely separated geographic areas, which results in a lack of knowledge about the individual and geographic variation of the species and the actual limits of their ranges (Rossi, 2000).

In order to clarify the taxonomy of *L. geoffroyi,* my goals are: (1) to characterize the taxa on morphological and morphometrical terms, and to describe their variation; (2) to estimate its geographic distribution; and (3) to provide a synonymy list and attribute valid names for the recognized taxa. Quantitative and qualitative external and craniodental characters will be employed and considered against the geographical distribution of the species and putative subspecies, aiming at the detection and description of individual, sexual, populational, seasonal and geographic variations. The present work is, in morphological terms, the first one so far to include a large number of samples (around 200 specimens) present along the geographic distribution of the species to investigate the taxonomy of *L. geoffroyi.*

MATERIAL AND METHODS

Samples

I have studied 194 specimens (skins and skulls) of *L. geoffroyi,* as well as specimens of other small and medium sized Neotropical cats [*L. pardalis* (46 specimens), *L. wiedii* (29 specimens), *L. tigrinus* (20 specimens), *L. guigna* (seven specimens), *L. pajeros* (21 specimens), *L. braccatus* (28 specimens), *L. jacobita* (21 specimens) and *Puma yagouaroundi* (29 specimens)], whose collecting localities were within or near the geographical range of *L. geoffroyi,* in order to compare external and craniodental morphology (Appendix 1). All specimens studied are deposited in the following collections: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu Nacional da Universidade Federal do Rio de Janeiro (MN-UFRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museo Nacional de Historia Natural y Antropología, Montevideo, Uruguay (MUNHINA); American Museum of Natural History, New York, USA (AMNH); and Museum of Vertebrate Zoology (MVZ). I also examined photographs of the type series deposited in Muséum National d'Histoire Naturelle, Paris, France (MNHN). A gazetteer is provided in Appendix 2.

Age classes

Following the proposals of Ximénez (1974) and García-Perea (2002) I defined age classes based on dental morphology (sequence of emergence; replacement of deciduous teeth by permanent ones; tooth wear) and fusion of cranial sutures (especially the spheno-occipital suture). Thus, I came up with seven classes: *age class I* (juvenile), with deciduous teeth starting to emerge and spheno-occipital suture not fused; *age class II* (juvenile), with deciduous teeth totally emerged and spheno-occipital suture not fused; *age class III* (juvenile), with deciduous teeth being replaced by permanent ones and spheno-occipital suture not fused; *age class IV* (subadult), with permanent teeth totally emerged and spheno-occipital suture not fused; *age class V* (adult), with permanent teeth having no or very little wear and spheno-occipital suture fused; *age class VI* (adult), with permanent teeth having moderate wear and spheno-occipital suture fused; and *age class VII* (adult), with permanent teeth having excessive wear and spheno-occipital suture fused. In a previous analysis (not shown here), I found that subadult specimens (*age class IV*) and adults (*age classes V* to *VII*) do not differ significantly in overall shape and dimensions of the skull.

Body size

To define the size of the animal, I followed the criterion adopted by Nowell & Jackson (1996), who recognized for felids three size classes: large (35-135 kg), medium (7-20 kg) and small (< 6.5 kg).

Quantitative characters

External measurements were taken from the specimen's tags as follows: (1) head and body length **(HB);** (2) tail length **(T);** (3) fore foot length **(FF);** (4) hind foot length **(HF);** and (5) ear length

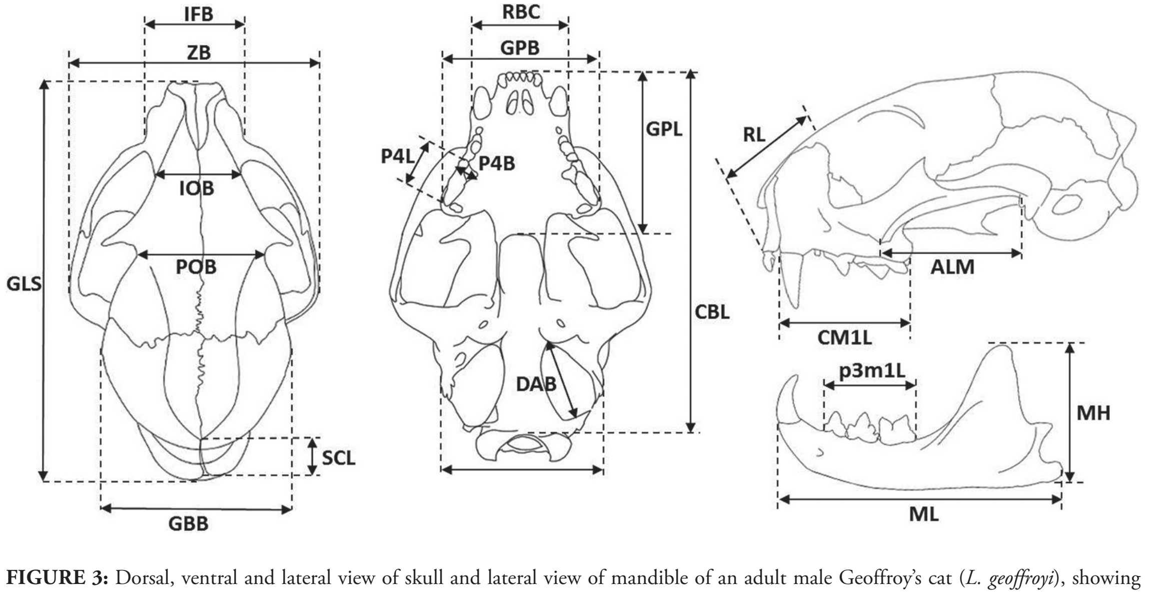

FIGURE 3: Dorsal, ventral and lateral view of skull and lateral view of mandible of an adult male Geoffroy's cat (*L. geoffroyi*), showing 20 craniometrical variables used in the study. The abbreviations assigned to craniometrical variables correspond to those mentioned in the "Materials and methods" section of the text.

(E). When only total length **(TL)** was provided, I subtracted the recorded tail length from total length to obtain the values of the head and body length.

I measured a total of 20 craniodental dimensions from the skull of adults and subadults of both sexes using digital calipers to the nearest 0.01 mm (Fig. 3). Specimens from captivity and/or those with insufficient or missing information about the location of origin were excluded from the analysis. Craniodental dimensions and their respective definitions are as follows: **GLS:** greatest length of the skull; **CBL:** condylobasal length; **RL:** rostral length; **IOB:** interorbital length; **POB:** postorbital breadth; **ZB:** zygomatic breadth; **GBB:** greatest breadth of braincase; **SCL:** length of sagittal crest; **RBC:** rostral breadth across canines; **IFB:** breadth between the infraorbital foramina; **GPB:** greatest palatal breadth; **GPL:** greatest palatal length; **CM1L:** C-M1 length; **P4L:** greatest length of P4; **P4B:** greatest breadth of P4; **DAB:** anteroposterior diameter of the auditory bulla; **ALM:** anteroposterior length of masseter scar on skull; **p3m1L:** p3-m1 length; **MH:** mandible height; and **ML:** mandible length. In addition, nine craniodental indexes [index = (craniodental variable 1 × 100) / craniodental variable 2] were measured: **RL/GLS, IOB/GLS, ZB/GLS, GBB/GLS, GBB/ZB, DBA/CBL, GPL/GPB, P4L/CM1L** and **p3m1L/ML.**

Qualitative characters

External qualitative characters refer to the color and spot pattern of the pelage of the head, body, fore and hind limbs, and tail. For craniodental qualitative characters I have based analysis of morphological variation on the skull of *L. geoffroyi,* mainly on García-Perea (1994) and Yamaguchi *et al.* (2004): degrees of development of temporal lines and sagittal crest; shape of the notch in the postpalatine vein; shape of posterior margin of the palate; depth of the notch on posterior margin of the palate; shape of P3 paracone; presence of parastyle on P3; presence and size of P4 paracone; traces of talonid on m1; shape of auditory bulla in relation to the degree of development of ectotympanic; shape of mastoid process; shape of the anterior end of the nasals; extent of a pit at the posterior end of the nasals; shape of the parietal suture; length of the nasals relative to the maxillae (in line with the posterior portion of the maxilla-frontal suture).

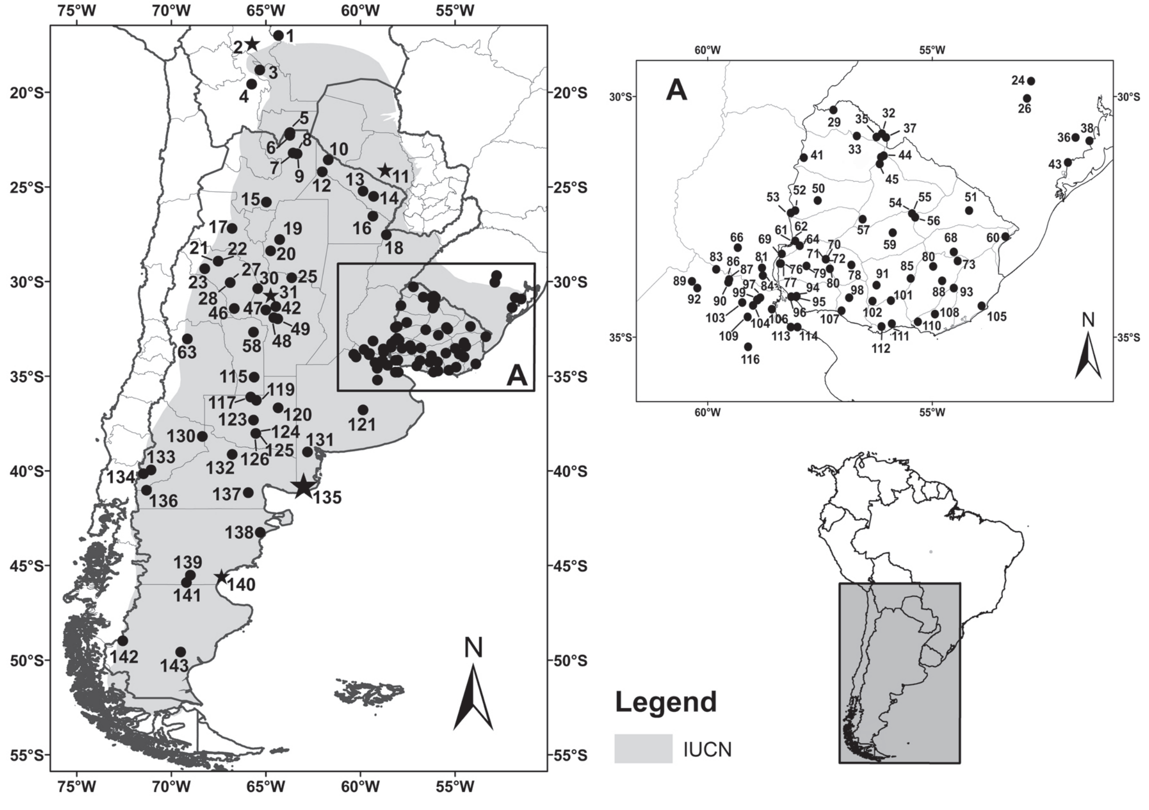

FIGURE 4: Distribution of the specimens of *L. geoffroyi* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 2). Gray shadow corresponds to the geographic range of the species suggested by IUCN.

Distributional data

Geographic data on *L. geoffroyi* (Figs. 4 and 5) were obtained by direct examination of museum specimens. Locality data was obtained from published gazetteers (Paynter Jr. & Traylor Jr., 1991; Vanzolini, 1992; Paynter Jr., 1992, 1994, 1995; Flores *et al.,* 2007) and online ones (Global Gazetteer 2.2, www.fallingrain.com/world/index.html).

Data analysis

To evaluate the existence of sexual dimorphism and to check whether the differences were significant ($p < 0.05$) among the putative subspecies, Student's *t*-test was performed. Due to the small number of specimens with sex determined by sample – either geographical groups or putative subspecies – I realized the analysis of sexual dimorphism only in the larger sample consisting of the Uruguayan population. To test whether I should use pooled sexes on the analyses to be able to increase my sample to include specimens of unknown sex, I employed a two-way multivariate analysis of variance (MANOVA) over the shape variables using *a priori* defined groups and sex as factors (see Machado & Hingst-Zaher, 2009). The *a priori* groups herein recognized are the putative subspecies – *L. g. geoffroyi, L. g. euxanthus, L. g. leucobaptus, L. g. paraguae* and *L. g. salinarum* – based on the definitions proposed, in part, by Ximénez (1975). These putative subspecies respectively correspond to the following geographical areas: (1) central-eastern Argentina; (2) southern Bolivia and northern Argentina; (3) Patagonia south of the Río Negro River; (4) Paraguay, northeast Argentina, Uruguay and southern Brazil; and (5) central-western Argentina (Fig. 5).

For multivariate analysis the specimens with missing values were removed, and from a total of 20 craniodental variables, one was excluded (SCL) because in preliminary analyzes this variable showed a very large individual variation. Thus, the total number of 19 variables was used in the Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA). Moreover, all craniodental variables were $\log_{10}$ transformed. The PCA was extracted from the covariance matrix and it served

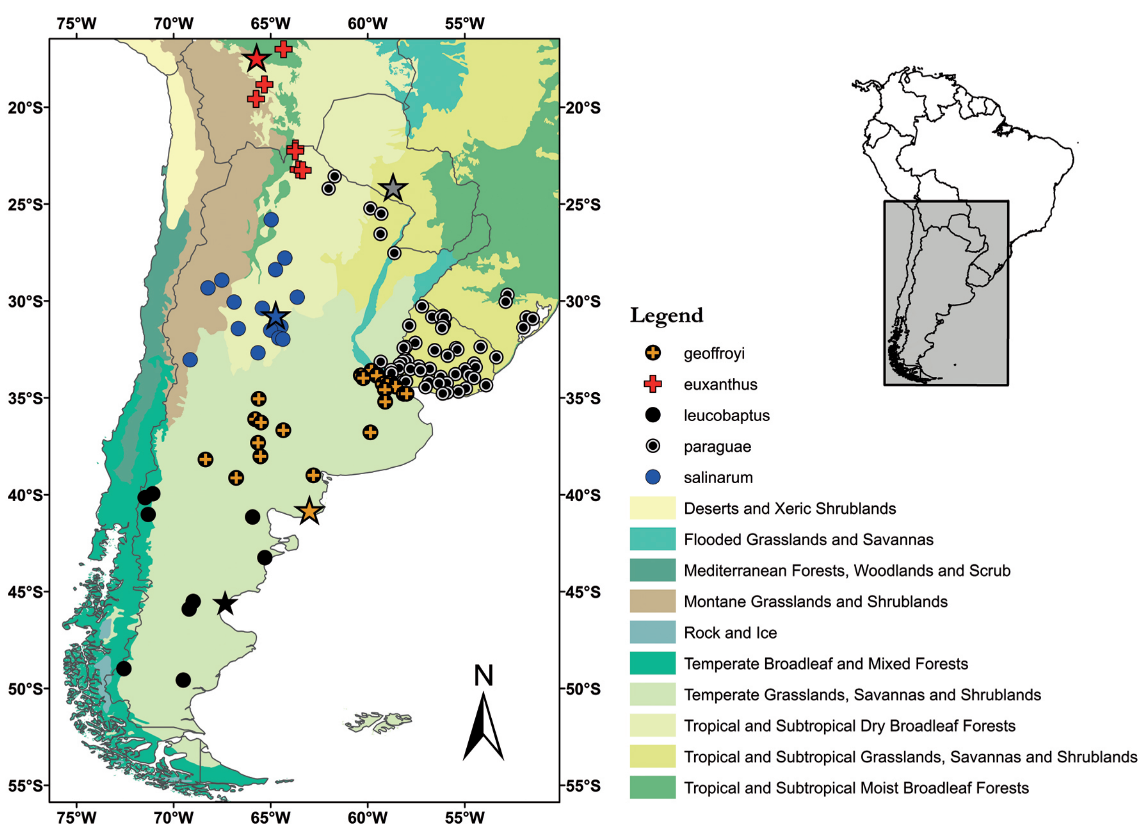

FIGURE 5: Distribution of the putative subspecies of *L. geoffroyi* over the biomes of southern South America (data obtained from WWF – World Wide Fund for Nature). The stars represent the type localities of the putative subspecies.

TABLE 1: Craniodental variables of males and females of *L. geoffroyi.* Legends: M = mean; SD = standard deviation; MIN = minimum; MAX = maximum; and N = number of specimens.

Variables		Males						Females					
		M		SD	MIN		MAX	N	M		SD	MIN		MAX	N
1	GLS	105.64	±	6.72	89.96	–	116.48	35	95.75	±	4.19	84.23	–	112.20	51
2	CBL	98.32	±	7.35	81.48	–	108.95	33	87.97	±	6.52	72.40	–	104.83	53
3	RL	37.13	±	3.01	30.97	–	42.60	37	32.87	±	2.36	25.81	–	41.20	52
4	IOB	19.60	±	1.87	16.91	–	26.95	37	17.41	±	1.34	13.29	–	21.68	53
5	POB	26.39	±	2.12	20.20	–	29.95	37	28.17	±	1.83	24.21	–	35.59	53
6	ZB	70.18	±	5.01	58.31	–	77.49	36	63.53	±	3.40	52.31	–	73.92	52
7	GBB	45.25	±	1.20	42.74	–	49.19	36	44.27	±	1.45	40.06	–	47.25	52
8	SCL	17.08	±	11.47	0.00	–	53.83	35	7.40	±	3.92	0.00	–	15.84	52
9	RBC	24.59	±	1.93	19.79	–	28.05	37	21.44	±	1.30	17.76	–	25.04	53
10	IFB	25.93	±	1.79	21.74	–	28.30	37	23.62	±	1.38	19.91	–	26.58	54
11	GPB	39.34	±	2.07	32.84	–	42.53	36	36.64	±	1.92	30.69	–	41.27	54
12	GPL	39.90	±	2.95	32.83	–	44.97	36	36.21	±	2.22	29.84	–	42.93	53
13	CM1L	31.96	±	1.71	28.66	–	34.97	37	29.37	±	1.38	25.86	–	33.78	53
14	P4L	12.55	±	0.75	10.78	–	13.86	37	11.78	±	0.59	9.85	–	13.11	54
15	P4B	5.79	±	0.48	4.88	–	6.90	37	5.46	±	0.41	4.44	–	6.57	54
16	DAB	21.71	±	1.39	18.48	–	24.47	37	19.76	±	0.95	17.53	–	21.70	53
17	ALM	32.92	±	3.15	26.11	–	39.20	37	28.77	±	2.28	22.12	–	33.38	53
18	p3m1L	23.22	±	1.19	20.48	–	25.04	35	21.62	±	1.11	19.08	–	24.64	51
19	MH	31.47	±	3.29	22.42	–	36.73	36	26.83	±	2.28	20.76	–	33.73	51
20	ML	68.78	±	5.51	52.87	–	77.10	36	61.00	±	3.63	51.69	–	74.13	51

as an exploratory tool for investigating the patterns of variation among the specimens of *L. geoffroyi,* as well as evaluating the degree of separation among them. The first eight principal components were extracted and were afterwards rotated using the varimax criterion. DFA was performed to investigate whether the putative subspecies of *L. geoffroyi* studied could be distinguished based on skull morphology, and also to construct a predictive pattern of different group memberships. The use of PCA scores in DFA was applied to determine whether grouping patterns existed within Geoffroy's cat skulls without *a priori* classification (Yamaguchi *et al.,* 2004; Mazák, 2010), and herein I used the first two component scores in DFA. Both PCA and DFA were performed with males and females separately and with the combination of the sexes with individuals of unknown sex.

I organized the geographic analysis as follows: (1) Northern specimens equivalent to putative *euxanthus* subspecies; (2) Northeast I, specimens of the putative *paraguae* subspecies and occurring in the Argentinean Provinces of Formosa, Chaco and Corrientes; (3) Northeast II specimens of the putative *paraguae* subspecies occurring in the Argentinean Province of Entre Rios, Uruguay and southern Brazil (State of Rio Grande do Sul); (4) Northwest, specimens of the putative *salinarum* subspecies; (5) Center, specimens of the putative *geoffroyi* subspecies; and (6) South, specimens of the putative *leucobaptus* subspecies. These geographic groups were plotted with the scores of the first component obtained from PCA, and males and females were analyzed separately and in combination with individuals of unknown sex.

All statistical analyses were performed using the SPSS 17.0 software.

RESULTS AND DISCUSSION

The updated geographic distribution of *L. geoffroyi* is found in Fig. 4, which shows the localities of the studied specimens and the geographic range suggested by the IUCN Red List (IUCN, 2012), while the distribution of the putative subspecies over the southern South American biomes is shown in the Fig. 5. The craniodental and external variables (mean, standard deviation, minimum and maximum values, and number of specimens) are available respectively in the Tables 1 and 2, whereas the craniodental indexes are available in Table 3. Results of morphological variation of the skull are available in Table 4. The results of Student's *t*-test indicated the existence of sexual dimorphism for all craniodental variables, except for FB (Table 5). The results of the two-way MANOVA for putative subspecies versus sex effects (Table 6) indicated that both subspecies and sexes

TABLE 2: External variables and body mass of males and females of *L. geoffroyi.* Legends: M = mean; SD = standard deviation; MIN = minimum; MAX = maximum; and N = number of specimens.

Variables		Males			Females			Total		
		M SD	MIN MAX	N	M SD	MIN MAX	N	M SD	MIN MAX	N
1	BL	958.46 ± 85.07	810 – 1160	13	728.33 ± 62.52	665 – 790	3	915.31 ± 122.13	665 – 1160	16
2	HB	615.69 ± 76.67	498 – 785	13	456.67 ± 62.92	390 – 515	3	585.88 ± 96.64	390 – 785	16
3	TL	342.77 ± 34.12	270 – 410	13	271.67 ± 5.77	265 – 275	3	329.44 ± 41.92	265 – 410	16
4	FF	–	–	–	145 ± 0	145	1	145 ± 0	145	1
5	HF	130.00 ± 12.78	105 – 150	12	140.33 ± 65.58	100 – 216	3	132.07 ± 27.58	100 – 216	15
6	E	53.73 ± 4.67	45 – 62	11	51.33 ± 5.13	47 – 57	3	53.21 ± 4.68	45 – 62	14
7	M (g)	5205 ± 949.08	3590 – 5900	6	2500 ± 707.11	2000 – 3000	2	4528.75 ± 1510.88	2000 – 5900	8

TABLE 3: Craniodental indexes of males and females of *L. geoffroyi.* Legends: M = mean; SD = standard deviation; MIN = minimum; MAX = maximum; and N = number of specimens (%).

Indexes		Males			Females		
		M ± SD	MIN – MAX	N	M ± SD	MIN – MAX	N
1	RL/GLS	35.09 ± 1.41	32.29 – 37.99	35	34.49 ± 1.49	29.71 – 37.06	49
2	IOB/GLS	18.52 ± 1.69	15.47 – 24.20	35	18.26 ± 1.05	15.78 – 20.33	50
3	ZB/GLS	66.35 ± 2.20	62.39 – 71.21	35	66.45 ± 2.15	62.10 – 71.13	50
4	GBB/GLS	43.01 ± 2.47	39.44 – 47.51	34	46.21 ± 1.83	41.69 – 50.01	50
5	GBB/ZB	64.89 ± 4.30	56.92 – 73.30	34	69.65 ± 3.07	63.28 – 79.16	51
6	GPL/GPB	101.24 ± 5.12	91.28 – 110.56	35	99.07 ± 4.57	85.93 – 110.41	53
7	P4L/CM1L	39.29 ± 1.61	36.75 – 42.56	37	40.10 ± 1.56	36.57 – 43.80	53
8	p3m1L/ML	33.94 ± 1.99	29.55 – 39.00	35	35.49 ± 1.54	33.10 – 41.21	51

were to be statistically different, but the interaction between factors was not significant, therefore allowing the use of males, females, and individuals of unknown sex in subsequent analysis.

The PCA was performed in three different modes: the first with only males, the second with only females, and a third with the combination of both sexes plus unknown sex specimens. For PCA and DFA, a total of 27 specimens with no missing values were selected in the male group (two *L. g. geoffroyi,* two *L. g. euxanthus,* one *L. g. salinarum,* one *L. g. leucobaptus* and 21 *L. g. paraguae*), while for the female group 41 specimens were used (seven *L. g. geoffroyi,* one *L. g. euxanthus,* two *L. g. salinarum,* one *L. g. leucobaptus* and 30 *L. g. paraguae*), and for all specimens combined 88 individuals were included (17 *L. g. geoffroyi,* three *L. g. euxanthus,* seven *L. g. salinarum,* four *L. g. leucobaptus* and 57 *L. g. paraguae*). Eight first components resulting from the PCA and their respective coefficients, eingevalues, and variances are shown in Tables 7, 8 and 9. The first and second components are respectively responsible for 71.41 and 6.99% of variance in the male group (both contributing to about 78.40% of total variance), for 63.09 and 8.97% of variance in the female group (72.06% of total variance), and for 71.60 and 6.01% of variance in all specimens in the combined group (77.61% of total variance). In all groups, all coefficients of the first component (except POB) showed positive signals, indicating a positive correlation to each other, and it can be interpreted as a component usually associated to the overall size of the skull (Jolicoeur & Mosimann, 1960). The variable POB showed a negative signal, indicating a negative correlation to other variables. The greatest coefficient is associated to the variable GLS in each group analysis, indicating it as the dominant craniodental measurement in the first component, but the following six variables in decreasing order, which also contributed in a similar way to each other for the first component, are different in the three groups: ML, ZB, IFB, CM1L, RBC and CBL in the male group (Table 7); ML, GPL, RBC, MH, ZB and GPB in the female group (Table 8); and ML, RBC, ZB, IFB, CM1L, and GPL in all specimens combined (Table 9). Regarding the second component, which is related to form and size, the greatest coefficient in the male group is shown by variable p3m1L and followed in decreasing order by GBB, IOB, P4B, P4L, POB and ALM (Table 7); whereas in the female group POB was the variable with the greatest coefficient, followed in decreasing order by GBB, CBL, GPB, ZB and IOB (Table 8). In all specimens from the combined group the variables that contributed to the second component were, in decreasing order, POB, GBB, P4B, GPB, MH, DAB and CBL (Table 9). In principal component plots for

TABLE 4: Craniodental qualitative characters of males, females, unknown sex specimesn and all specimens combined for five geographical groups.

Craniodental Qualitative Characters		All geographic groups combined					
		males		females		unknown sex	
		%	N	%	N	%	N
I. Degrees of development of temporal lines and sagittal crest							
1. temporal lines present, sagittal crest absent		5.88	2	15.69	8	6.06	2
2. sagittal crest poorly developed, restrict to interparietal region		50.00	17	82.35	42	66.67	22
3. sagittal crest moderately developed		35.29	12	1.96	1	24.24	8
4. sagittal crest well developed		8.83	3	0.00	0	3.03	1
	Total	100.00	34	100.00	51	100.00	33
II. Shape of the notch in the postpalatine vein							
1. broad and comparatively shallow		85.29	29	75.00	39	55.56	20
2. narrow and deep		14.71	5	25.00	13	44.44	16
	Total	100.00	34	100.00	52	100.00	36
III. Shape of posterior margin of the palate							
1. absent		12.12	4	26.00	13	8.33	3
2. present		87.88	29	74.00	37	91.67	33
	Total	100.00	33	100.00	50	100.00	36
IV. Depth of the notch of posterior margin of the palate							
1. shallow		78.13	25	86.05	37	76.47	26
2. deep		21.87	7	13.95	6	23.53	8
	Total	100.00	32	100.00	43	100.00	34
V. Shape of P3 paracone							
1. narrow and long		75.86	22	63.82979	30	67.65	23
2. short and broad		24.14	7	36.17021	17	32.35	11
	Total	100.00	29	100	47	100.00	34
VI. Parastyle on P3							
1. absent		100.00	31	100.00	50	91.43	32
2. present		0.00	0	0.00	0	8.57	3
	Total	100.00	31	100.00	50	100.00	35
VII. P4 paracone							
1. absent		0.00	0	3.85	2	8.57	3
2. present		100.00	31	96.15	50	91.43	32
	Total	100.00	31	100.00	52	100.00	35
VIII. Traces of talonid on m1							
1. absent		83.87	26	91.67	44	83.87	26
2. present		16.13	5	8.33	4	16.13	5
	Total	100.00	31	100.00	48	100.00	31
IX. Shape of auditory bulla in relation to the degree of development of ectotympanic							
1. ectotympanic > entotympanic		0.00	0	0.00	0	0.00	0
2. ectotympanic moderately developed		6.06	2	14.00	7	13.33	4
3. ectotympanic < entotympanic		93.94	31	86.00	43	86.67	26
	Total	100.00	33	100.00	50	100.00	30
X. Shape of mastoid process							
1. poorly developed and posteriorly separated from the process paraoccipital		96.97	32	83.67	41	90.00	27
2. well developed posteriorly and covering the bulla		3.03	1	16.33	8	10.00	3
	Total	100.00	33	100.00	49	100.00	30
XI. Shape of the anterior end of the nasals							
1. curved		80.65	25	64.58	31	66.67	24
2. moderately curved		19.35	6	33.34	16	30.56	11
3. little or no curved		0.00	0	2.08	1	2.78	1
	Total	100.00	31	100.00	48	100.00	36
XII. Extent of a pit at the posterior end of the nasals							
1. deep		9.37	3	22.45	11	2.86	1
2. moderate		37.50	12	53.06	26	42.86	15
3. shallow		53.13	17	24.49	12	54.29	19
	Total	100.00	32	100.00	49	100.00	35
XIII. Shape of the parietal suture							
1. straight		58.07	18	12.50	6	28.57	10
2. moderately sinuous		22.58	7	60.42	29	37.14	13
3. very sinuous		19.35	6	27.08	13	34.29	12
	Total	100.00	31	100.00	48	100.00	35
XIV. length of the nasals relative to the maxilla-frontal suture							
1. anterior		48.49	16	52.00	26	38.89	14
2. equal		45.45	15	44.00	22	52.78	19
3. posterior		6.06	2	4.00	2	8.33	3
	Total	100.00	33	100.00	50	100.00	36

TABLE 5: Levene's test and Student *t*-test to evaluate the existence of sexual dimorphism in a geographical sample (all specimens from Uruguay). Values in bold represent statistical difference at 5% in *t*-test.

Variables	Levene's Test		*t*-test		
	F	p	t	df	p
GLS	5.233	0.026	7.684	39.731	**0.000**
CBL	4.275	0.043	7.306	37.148	**0.000**
RL	3.89	0.053	6.707	57.000	**0.000**
LLR	0.554	0.46	7.364	59.000	**0.000**
GLN	0.002	0.964	2.705	56.000	**0.009**
NB	1.859	0.178	6.43	54.000	**0.000**
MLN	3.027	0.087	5.103	56.000	**0.000**
IOB	3.249	0.077	5.105	58.000	**0.000**
FB	1.102	0.299	1.945	53.000	0.057
POB	2.07	0.156	-3.986	58.000	**0.000**
ZB	7.783	0.007	6.453	39.567	**0.000**
GBB	2.268	0.138	2.478	57.000	**0.016**
SCL	11.31	0.001	4.406	27.169	**0.000**
RBC	6.085	0.017	8.209	41.728	**0.000**
CH	0.083	0.774	4.357	49.000	**0.000**
IFB	3.2	0.079	6.846	59.000	**0.000**
GPB	0.876	0.353	6.496	58.000	**0.000**
GPL	7.994	0.006	6.228	42.605	**0.000**
CM1L	1.123	0.294	7.12	59.000	**0.000**
P4L	2.199	0.143	5.222	59.000	**0.000**
P4B	3.48	0.067	3.234	59.000	**0.002**
DAB	4.199	0.045	6.439	40.252	**0.000**
MB	0.022	0.882	6.907	54.000	**0.000**
DLT	1.458	0.232	2.437	58.000	**0.018**
ALT	7.573	0.008	7.575	36.535	**0.000**
ALM	12.09	0.001	5.678	39.533	**0.000**
p3m1L	0.191	0.664	6.744	56.000	**0.000**
MH	2.688	0.107	7.618	57.000	**0.000**
ML	2.509	0.119	8.181	57.000	**0.000**

all groups (Figs. 6, 7 and 8), all specimens of the five putative subspecies are widely mixed, indicating a huge overlap among them and it is impossible to observe a separation of samples. In other words, the specimens from the putative subspecies have similar size and shape, not differing significantly from each other. However, it is important to draw attention to the PCA of the male group and female groups, of which some putative subspecies had a very small sample.

The DFA, based on two first principal components, created two canonical variables from the original craniodental variables used in the analysis. In the male group, the first canonical variable is responsible for 84.9% of the total variance, and the second for 15.1% (Table 10); while in the female group the first canonical variable is responsible for 84.5% of the total variance, and the second by 15.5% (Table 10). In the group with all specimens combined, the first canonical variable is responsible for 75.5% of the total variance, and the second for 24.5% (Table 10). In all these groups the first and second canonical variables showed a discriminatory power of 100%. Discriminant analysis shows in all groups the existence of overlap among the putative *L. geoffroyi* subspecies (Figs. 9, 10 and 11), but it is possible to observe in the males a small trend of *euxanthus* and *salinarum* specimens separating themselves from the others in relation to the first function. However, this conclusion should be taken carefully since the sample from these groups is greatly reduced, and this separation trend may be an artifact. A predict group membership (Table 11) shows in the male group that 63.0% of original grouped cases are correctly classified, with *geoffroyi, salinarum* and *leucobaptus* being 100% correctly classified, whereas 61.9% of *paraguae* and none *euxanthus* are correctly classified. Among females, the predict group membership (Table 12) shows that 51.2% of the original grouped cases are correctly classified, with *euxanthus* and *leucobaptus* being 100% correctly classified; whereas 60.0% of *paraguae,* 50.0% of *salinarum* and none of *geoffroyi* are correctly classified. For all specimens combined, the predict group membership (Table 13) shows that 37.8% of original grouped cases are correctly classified, with only *leucobaptus* being 100% correctly classified; whereas *geoffroyi, paraguae,* and *salinarum* are 5.6%, 40.7% and 42.9% correctly classified, respectively. In the cross-validated cases (Table 11), for the male group 51.9% of cross-validated grouped cases are correctly classified, with 100% of *geoffroyi,* 57.1% of *paraguae,* and none of *salinarum, leucobaptus* and *euxanthus* being correctly classified. For the female group, 39.0% of cross-validated grouped cases are correctly classified, with 50.0% of *salinarum* and *paraguae* and none *geoffroyi, euxanthus* and *leucobaptus* being correctly classified (Table 12). For the group with all specimens combined, 32.2% of cross-validated grouped cases are correctly classified, with 66.7% of *leucobaptus,* 42.9% of *salinarum,* 40.7% of *paraguae,* 5.6% of *geoffroyi* and none of *euxanthus* being correctly classified (Table 13).

Geographical Analysis

Overlap of values among different geographic groups was observed, especially in the graphs containing only one of the sexes (Figs. 12a and 12b). In the graph showing sexes combining more individuals of unknown sex, there is also overlap in the values of different groups, but it is possible to notice a slight trend in the southern sample having values higher than the others (Fig. 12c).

TABLE 6: Results for the multivariate analysis of variance (MANOVA) performed for the fixed effects of *a priori* groups (putative subspecies), sex, and the interaction between them, on *L. geoffroyi* specimens.

	Value	F	Hypothesis df	Error df	Sig.	Partial Eta Squared	Noncent. Parameter	Observed Power
Sex	0.243	1.188	52	60	0.259	0.507	61.763	0.919
Subspecies	0.011	2.445	104	121.569	0	0.674	250.774	1
Sex vs Subspecies	0.165	0.960	78.000	90.578	0.572	0.451	74.559	0.937

TABLE 7: Factor loadings, eingevalues and percentage of variance of PCA for males using 19 craniodental variables.

Variables		Components							
		1	2	3	4	5	6	7	8
1	**GLS**	0.981	-0.066	-0.071	0.046	-0.049	0.100	-0.011	0.042
2	**CBL**	0.907	-0.003	0.048	-0.106	0.055	0.221	0.237	0.073
3	**RL**	0.853	-0.166	-0.093	-0.040	-0.046	0.280	-0.347	-0.069
4	**IOB**	0.514	-0.413	0.576	0.294	0.351	0.035	-0.094	-0.064
5	**POB**	-0.742	0.339	0.038	0.480	0.061	0.113	0.053	0.273
6	**ZB**	0.958	-0.047	-0.042	0.169	0.013	-0.161	0.038	-0.082
7	**GBB**	0.579	0.453	-0.519	0.267	0.169	0.178	0.009	-0.204
8	**RBC**	0.911	0.176	-0.022	0.081	-0.046	-0.295	-0.123	0.050
9	**IFB**	0.944	-0.097	0.085	0.102	-0.159	-0.098	-0.027	0.033
10	**GPB**	0.872	0.262	0.021	0.128	-0.165	-0.276	-0.005	-0.028
11	**GPL**	0.894	-0.119	-0.087	0.015	-0.245	0.180	-0.140	0.143
12	**CM1L**	0.934	0.001	0.130	0.014	-0.045	-0.017	-0.053	0.107
13	**P4L**	0.827	0.349	0.200	-0.082	0.228	-0.031	-0.038	-0.058
14	**P4B**	0.721	0.402	0.378	-0.202	-0.045	0.160	0.178	0.007
15	**DAB**	0.718	-0.108	-0.384	-0.272	0.418	-0.149	-0.034	0.200
16	**ALM**	0.865	-0.316	-0.046	0.045	-0.078	-0.031	0.293	-0.104
17	**p3m1L**	0.785	0.465	0.230	-0.147	0.018	0.024	-0.083	0.007
18	**MH**	0.900	-0.228	-0.164	0.103	0.056	0.041	0.167	0.052
19	**ML**	0.969	-0.127	-0.102	0.061	-0.068	0.025	0.045	0.042
Eingevalues		13.567	1.327	1.076	0.624	0.523	0.467	0.386	0.234
Variance (%)		71.407	6.986	3.286	3.286	2.754	2.456	2.030	1.231

TABLE 8: Factor loadings, eingevalues and percentage of variance of PCA for females using 19 craniodental variables.

Variables		Components							
		1	2	3	4	5	6	7	8
1	**GLS**	0.955	-0.059	-0.114	0.115	-0.037	0.113	-0.047	0.055
2	**CBL**	0.827	-0.370	0.110	-0.057	0.141	-0.002	-0.061	0.274
3	**RL**	0.748	0.027	-0.221	0.370	-0.334	0.131	0.269	0.120
4	**IOB**	0.748	0.214	-0.296	-0.390	-0.182	0.012	0.241	-0.067
5	**POB**	-0.089	0.934	0.142	-0.091	-0.159	0.053	-0.106	0.157
6	**ZB**	0.854	0.249	-0.327	-0.005	-0.089	-0.037	0.029	-0.115
7	**GBB**	0.520	0.554	-0.072	0.308	0.505	0.095	0.137	0.041
8	**RBC**	0.917	0.062	-0.015	-0.056	-0.024	-0.018	-0.267	0.094
9	**IFB**	0.840	0.144	-0.007	-0.360	0.079	-0.249	-0.029	-0.071
10	**GPB**	0.836	0.307	-0.086	0.180	-0.020	-0.091	-0.245	-0.169
11	**GPL**	0.921	-0.033	-0.056	-0.197	-0.018	-0.011	-0.040	0.173
12	**CM1L**	0.807	-0.172	0.308	-0.120	-0.138	0.267	0.044	-0.129
13	**P4L**	0.579	0.125	0.700	0.031	0.048	-0.189	0.235	-0.188
14	**P4B**	0.794	-0.048	0.325	0.134	-0.110	-0.328	0.096	0.272
15	**DAB**	0.784	0.014	0.310	-0.243	0.140	0.328	0.010	0.029
16	**ALM**	0.805	-0.200	-0.287	-0.064	0.342	0.011	0.101	-0.015
17	**p3m1L**	0.799	-0.081	0.372	0.243	-0.085	0.126	-0.166	-0.131
18	**MH**	0.869	-0.195	-0.203	0.138	-0.003	-0.244	-0.046	-0.142
19	**ML**	0.947	-0.159	-0.177	0.075	-0.055	0.091	-0.047	-0.061
Eingevalues		11.986	1.705	1.385	0.792	0.642	0.519	0.410	0.377
Variance (%)		63.087	8.975	7.290	4.170	3.379	2.734	2.160	1.985

TABLE 9: Factor loadings, eingevalues and percentage of variance of the principal component analysis (PCA) for males, females and unknown sex specimens using 19 craniodental variables.

	Variables	Components							
		1	2	3	4	5	6	7	8
1	**GLS**	0.980	-0.001	-0.060	0.043	-0.041	0.048	-0.016	0.051
2	**CBL**	0.877	-0.127	-0.016	-0.075	-0.017	0.220	-0.290	0.117
3	**RL**	0.900	-0.008	-0.075	0.120	-0.053	-0.010	-0.058	-0.063
4	**IOB**	0.753	0.099	-0.143	0.365	0.468	-0.030	0.008	-0.146
5	**POB**	-0.558	0.744	-0.156	-0.046	0.143	-0.062	0.027	0.251
6	**ZB**	0.937	0.079	-0.068	0.096	-0.094	-0.114	0.096	-0.025
7	**GBB**	0.625	0.602	-0.241	-0.072	-0.274	0.204	-0.009	-0.219
8	**RBC**	0.946	0.018	-0.055	-0.033	0.035	-0.079	0.111	0.032
9	**IFB**	0.933	0.052	-0.084	0.069	0.076	-0.076	-0.034	-0.021
10	**GPB**	0.908	0.162	0.039	-0.049	-0.129	-0.257	0.112	0.046
11	**GPL**	0.926	0.024	-0.108	0.044	0.020	0.059	-0.192	0.127
12	**CM1L**	0.928	-0.021	-0.015	-0.099	0.161	-0.022	-0.058	0.035
13	**P4L**	0.771	0.083	0.249	-0.457	0.148	-0.074	-0.067	-0.232
14	**P4B**	0.398	0.306	0.799	0.301	-0.030	0.125	0.005	0.019
15	**DAB**	0.795	-0.130	-0.019	-0.176	0.124	0.362	0.401	0.078
16	**ALM**	0.891	-0.125	-0.069	0.173	-0.136	0.072	-0.019	0.029
17	**p3m1L**	0.845	0.032	0.192	-0.340	0.068	-0.096	-0.059	0.122
18	**MH**	0.873	-0.156	0.049	0.086	-0.165	-0.231	0.135	0.039
19	**ML**	0.977	-0.067	-0.053	0.065	-0.061	0.018	-0.019	0.060
Eingevalues		13.603	1.142	0.888	0.679	0.470	0.413	0.352	0.255
Variance (%)		71.597	6.009	4.672	3.573	2.476	2.171	1.853	1.342

TABLE 10: Discriminant function analysis (DFA) for males, females and all specimens combined (males + females + unknown sex specimens) using two first componet scores.

Variables	Male group Functions		Female group Functions		All specimens combined Functions	
	1	2	1	2	1	2
Principal Component 1	0.331	0.953	0.933	-0.380	0.335	0.943
Principal Component 2	0.989	-0.200	0.493	0.879	0.955	-0.298
Eingevalues	1.027	0.182	0.505	0.093	0.220	0.071
Variance (%)	84.9	15.1	84.5	15.5	75.5	24.5
Canonical Correlation	0.712	0.393	0.579	0.291	0.424	0.258

Taxonomy

Leopardus geoffroyi (d'Orbigny & Gervais, 1844)

Geoffroy's cat

Leopardus himalayanus Gray, 1843: 44 (non Jardine, 1834) (*nomem nudum*).

Felis geoffroyi d'Orbigny & Gervais, 1844a: 40; 1844b: plate LVII; 1847: 21, plate XIII, plate XIV. Type locality: "des rives Du Rio Negro, Patagonie".

Felis (*Oncifelis*) *geoffroyi:* Severtzov, 1858: 386 (name combination).

Pardalina warnickii: Gray, 1867a: 267; plate 24.

Felis pardoides Gray, 1867b: 403 (non *Felis pardoides* Owen, 1846) (preoccupied name).

Felis guigna: Mivart, 1881: 410 (non *Felis guigna* Molina, 1782) (preoccupied name).

Felis (*Oncoides*) *geoffroyi:* Lahille, 1899: 178 (name combination).

Felis salinarum Thomas, 1903: 239.

Oncoides geoffroyi: Allen, 1905: 180 (name combination).

Felis melas Bertoni, 1914 (non Cuvier, 1809) (preoccupied name).

Herpailurus geoffroyi: Pocock, 1917: 347 (name combination).

Oncifelis geoffroyi Allen, 1919: 366, figs. 5a, 7b, 13a and 23.

Oncifelis salinarum Allen, 1919: 367 (name combination).

Felis geoffroyi mac-donaldi Marelli, 1932: 38.

Oncifelis geoffroyi paraguae Pocock, 1940: 351.

Oncifelis geoffroyi leucobaptus Pocock, 1940: 351.

Oncifelis geoffroyi euxanthus Pocock, 1940: 352.

Oncifelis geoffroyi argentea Schwangart, 1941: 16.

Oncifelis geoffroyi flava Schwangart, 1941: 16.
Felis (*Leopardus*) *geoffroyi geoffroyi:* Cabrera, 1958: 280 (name combination).
Felis (*Leopardus*) *geoffroyi leucobapta:* Cabrera, 1958: 280 (name combination).
Felis (*Leopardus*) *geoffroyi paraguae:* Cabrera, 1958: 280 (name combination).
Felis (*Leopardus*) *geoffroyi salinarum:* Cabrera, 1958: 281 (name combination).
Felis (*Leopardus*) *geoffroyi geoffroyi:* Ximénez, 1975: 1 (name combination).
Felis (*Leopardus*) *geoffroyi salinarum:* Ximénez, 1975: 1 (name combination).
Felis (*Leopardus*) *geoffroyi paraguae:* Ximénez, 1975: 1 (name combination).
Felis (*Leopardus*) *geoffroyi euxantha:* Ximénez, 1975: 1 (name combination).
Felis colocolo geoffroyi: Hershkovitz, 1987: 73, fig. 19 (name combination; probable misspelling).
Leopardus geoffroyi geoffroyi: Wozencraft, 2005: 538 (name combination).
Leopardus geoffroyi euxanthus: Wozencraft, 2005: 538 (name combination).
Leopardus geoffroyi leucobaptus: Wozencraft, 2005: 538 (name combination).
Leopardus geoffroyi paraguae: Wozencraft, 2005: 538 (name combination).
Leopardus geoffroyi salinarum: Wozencraft, 2005: 538 (name combination).

Type locality: "des rives Du Rio Negro, Patagonie" (= riverbanks of Rio Negro, Buenos Aires Province, Argentina) (d'Orbigny & Gervais, 1844a). "Elle habite les Pampas de Buenos-Ayres jusqu'au 44°. degree de latitude sud" (d'Orbigny, 1847).

Type material: d'Orbigny & Gervais (1844a) described the species based on three specimens collected by Alcides d'Orbigny in the lower Río Negro, at the southern end of the Province of Buenos Aires, that are deposited in the collection of the Museum National d'Histoire Naturelle, Paris, France ("Trois exemplaires recueillis par M. d'Orbigny sont depuis longtemps exposés dans les galleries du Muséum"), under the numbers MNHN-ZM-MO-2001-298 (= "number 90") (mounted skin, skull in the skin; "Rives du Rio Negro, Patagonie, Argentine"; February, 1831), MNHN-ZM-MO-2001-299 (= "number 92") (mounted skin, skull in the skin; "Rives du Rio Negro, Patagonie, Argentine"; February, 1831; individual featured in "l'Atlas mammalogique du voyage de M. d'Orbigny, plate XIV") and MNHN-ZM-MO-2001-300 (= "number 91") (mounted skin, skull extracted; "Buenos Aires, Argentine"; July, 1829) (Figs. 1b, 1d and 2). However, d'Orbigny & Gervais (1844a, b) did not indicate which specimens was indeed the holotype (Schwangart, 1941; Cabrera, 1961; Ximénez, 1971, 1975). From information provided to Schwangart (1941, page 15) by Dr. P. Rhodes (MNHN), this author stated that specimen number 92 was the holotype and both this one and specimen number 90 were from Patagonia, each showing yellowish white ground color, while specimen number 91 came from [the Province of] Buenos Aires and had a deep yellow ground color. Cabrera (1961) commented, based on the information from Dr. Jean Dorst (MNHN), that one of the three specimens of the type series is labeled "un des types", and he concluded that this specimen should

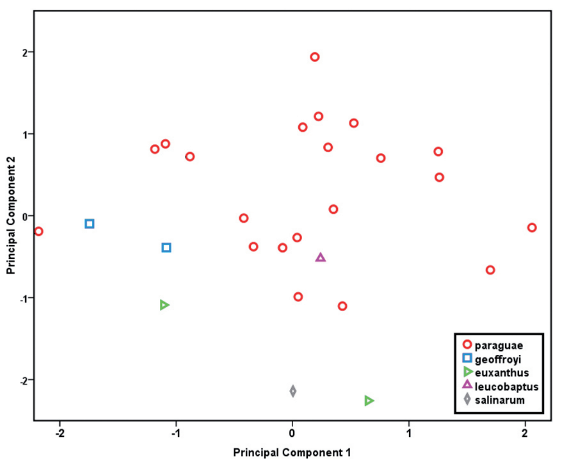

FIGURE 6: Distribution of the factorial scores in the first and second principal components of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* male specimens.

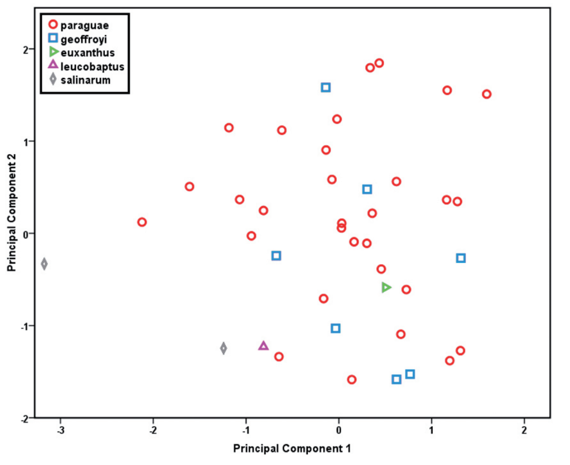

FIGURE 7: Distribution of the factorial scores in the first and second principal components of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* female specimens.

then be the lectotype, but Cabrera did not indicate which one. However, as can be seen in Fig. 1, present on the labels of all three specimens (which, by the way, are very old), is the term "type" contrasting with the information provided by Dorst. Later, Dr. Francis Petter (MNHN) reported in Ximénez (1971, 1975) that the holotype would be specimen number 91 which has "Republique Argentine" written on its label, while specimens numbers 90 and 92 had "Patagonie" on the respective labels. Furthermore, in the publication of Ximénez (1971), there is a picture of one of these specimens (page 68, fig. 1) with the word "type" written on its label. Ximénez informed that this specimen was set for exhibition, and it would be impossible to determine whether the original color was indeed clear or the lighter coloration was due to prolonged exposure to light. This specimen represented in the Ximénez article is the same showed here in Fig. 1c. In comparison to Fig. 1a, it can be concluded that this specimen – MNHN-ZM-MO-2001-298 (= "number 90") – was used as the basis for this plate, which was originally published in 1844 (plate 57; in d'Orbigny & Gervais, 1844b). Furthermore, this plate is the first formal representation of the species. In view of this, and contrary to what previous authors have suggested, I conclude that this specimen – MNHN-ZM-MO-2001-298 – is actually the lectotype of *L. geoffroyi*. Consequently, the other two specimens (MNHN-ZM-MO-2001-299 and MNHN-ZM-MO-2001-300) are the paralectotypes of the species.

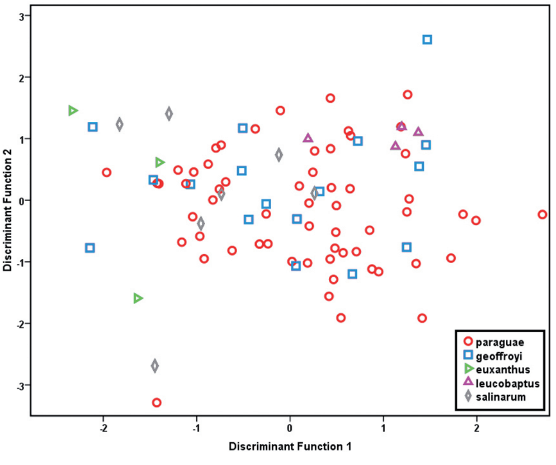

FIGURE 8: Distribution of the factorial scores in the first and second principal components of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* male, female and unknown sex specimens combined.

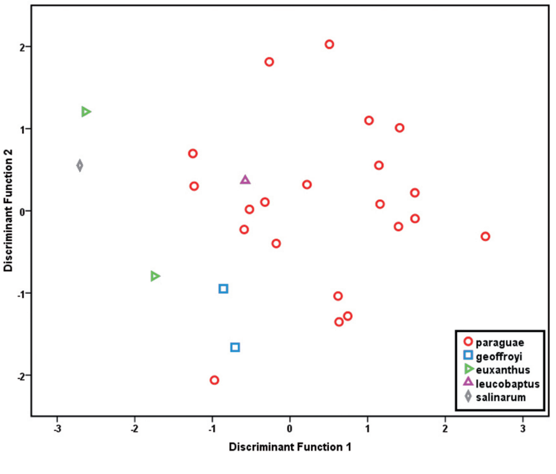

FIGURE 9: Distribution of the factorial scores in the first and second discriminant functions of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* males specimens.

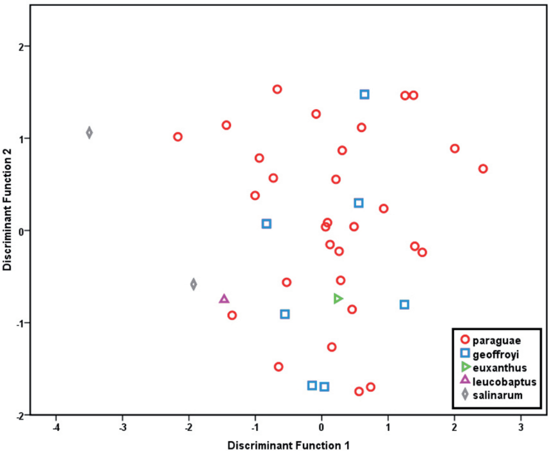

FIGURE 10: Distribution of the factorial scores in the first and second discriminant functions of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* females specimens.

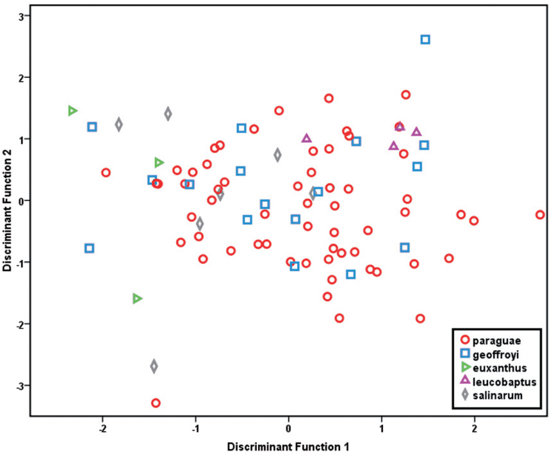

FIGURE 11: Distribution of the factorial scores in the first and second discriminant functions of the craniometrical variables (in decimal logarithm) of *L. geoffroyi* male, female and unknown sex specimens combined.

TABLE 11: Classification matrix for *L. geoffroyi* males obtained by discriminant function analysis concerning the probabilities of classifying each putative subspecies correctly into one of the five subspecific taxa.

			Classification Results[b,c]					
			Predicted Group Membership					
		Subspecies	***geoffroyi***	***paraguae***	***euxanthus***	***salinarum***	***leucobaptus***	**Total**
Original	Count	***geoffroyi***	2	0	0	0	0	2
		paraguae	2	13	0	0	6	21
		euxanthus	1	0	0	1	0	2
		salinarum	0	0	0	1	0	1
		leucobaptus	0	0	0	0	1	1
	%	***geoffroyi***	100.0	0.0	0.0	0.0	0.0	100.0
		paraguae	9.5	61.9	0.0	0.0	28.6	100.0
		euxanthus	50.0	0.0	0.0	50.0	0.0	100.0
		salinarum	0.0	0.0	0.0	100.0	0.0	100.0
		leucobaptus	0.0	0.0	0.0	0.0	100.0	100.0
Cross-validated[a]	Count	***geoffroyi***	2	0	0	0	0	2
		paraguae	2	12	0	0	7	21
		euxanthus	1	0	0	1	0	2
		salinarum	0	0	1	0	0	1
		leucobaptus	0	1	0	0	0	1
	%	***geoffroyi***	100.0	0.0	0.0	0.0	0.0	100.0
		paraguae	9.5	57.1	0.0	0.0	33.3	100.0
		euxanthus	50.0	0.0	0.0	50.0	0.0	100.0
		salinarum	0.0	0.0	100.0	0.0	0.0	100.0
		leucobaptus	0.0	100.0	0.0	0.0	0.0	100.0

a. Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
b. 63.0% of original grouped cases correctly classified.
c. 51.9% of cross-validated grouped cases correctly classified.

TABLE 12: Classification matrix for *L. geoffroyi* females obtained by discriminant function analysis concerning the probabilities of classifying each putative subspecies correctly into one of the five subspecific taxa.

			Classification Results[b,c]					
			Predicted Group Membership					
		Subspecies	***geoffroyi***	***paraguae***	***euxanthus***	***salinarum***	***leucobaptus***	**Total**
Original	Count	***geoffroyi***	0	3	4	0	0	7
		paraguae	3	18	5	2	2	30
		euxanthus	0	0	1	0	0	1
		salinarum	0	0	0	1	1	2
		leucobaptus	0	0	0	0	1	1
	%	***geoffroyi***	0.0	42.9	57.1	0.0	0.0	100.0
		paraguae	10.0	60.0	16.7	6.7	6.7	100.0
		euxanthus	0.0	0.0	100.0	0.0	0.0	100.0
		salinarum	0.0	0.0	0.0	50.0	50.0	100.0
		leucobaptus	0.0	0.0	0.0	0.0	100.0	100.0
Cross-validated[a]	Count	***geoffroyi***	0	3	4	0	0	7
		paraguae	4	15	6	2	3	30
		euxanthus	1	0	0	0	0	1
		salinarum	0	0	0	1	1	2
		leucobaptus	0	0	0	1	0	1
	%	***geoffroyi***	0.0	42.9	57.1	0.0	0.0	100.0
		paraguae	13.3	50.0	20.0	6.7	10.0	100.0
		euxanthus	100.0	0.0	0.0	0.0	0.0	100.0
		salinarum	0.0	0.0	0.0	50.0	50.0	100.0
		leucobaptus	0.0	0.0	0.0	100.0	0.0	100.0

a. Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
b. 51.2% of original grouped cases correctly classified.
c. 39.0% of cross-validated grouped cases correctly classified.

TABLE 13: Classification matrix for all *L. geoffroyi* specimens (males + females + unknown sex individuals) obtained by discriminant function analysis concerning the probabilities of classifying each putative subspecies correctly into one of the five subspecific taxa.

			Classification Results[b,c]					
			Predicted Group Membership					
		Subspecies	*geoffroyi*	*paraguae*	*euxanthus*	*salinarum*	*leucobaptus*	Total
Original	Count	***geoffroyi***	1	6	3	3	5	18
		paraguae	5	24	3	15	12	59
		euxanthus	0	0	3	0	0	3
		salinarum	1	1	2	3	0	7
		leucobaptus	0	0	0	0	3	3
	%	***geoffroyi***	5.6	33.3	16.7	16.7	27.8	100.0
		paraguae	8.5	40.7	5.1	25.4	20.3	100.0
		euxanthus	0.0	0.0	100.0	0.0	0.0	100.0
		salinarum	14.3	14.3	28.6	42.9	0.0	100.0
		leucobaptus	0.0	0.0	0.0	0.0	100.0	100.0
Cross-validated[a]	Count	***geoffroyi***	1	6	3	3	5	18
		paraguae	5	24	3	15	12	59
		euxanthus	0	0	0	3	0	3
		salinarum	1	1	3	2	0	7
		leucobaptus	1	0	0	0	2	3
	%	***geoffroyi***	5.6	33.3	16.7	16.7	27.8	100.0
		paraguae	8.5	40.7	5.1	25.4	20.3	100.0
		euxanthus	0.0	0.0	0.0	100.0	0.0	100.0
		salinarum	14.3	14.3	42.9	28.6	0.0	100.0
		leucobaptus	33.3	0.0	0.0	0.0	66.7	100.0

a. Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
b. 37.8% of original grouped cases correctly classified.
c. 32.2% of cross-validated grouped cases correctly classified.

Diagnosis: Small (2-5 kg); ground color of pelage varying from light yellowish brown to smoky gray; pattern of markings on the body predominantly composed of medium and/or small solid black spots; melanistic specimens may be present; long ringed tail; short and robust skull with well-developed zygomatic arches; profile of skull slightly convex in the frontal region; short and high sagittal crest; notch in the posterior margin of the palate may be present, sometimes with two small lateral projections.

Description: Small sized cat, length of head and body between 498 and 750 mm (601.58 ± 59.91 mm; n = 12) in males and between 390 and 515 mm (456.67 ± 62.92 mm; n = 3) in females, tail length between 300 and 410 mm (348.83 ± 27.36 mm; n = 12) in males and between 265 and 275 mm (271.67 ± 5.77 mm; n = 3) in females, hind foot length is between 115 and 150 mm (132.27 ± 10.56 mm; n = 11) in males and between 100 and 216 mm (140.33 ± 65.58 mm; n = 3) in females, and the body mass between 3590 and 5900 g (5205 ± 949.08 g; n = 6) in males and between 2000 and 3000 g (2500 ± 707.11 g; n = 2) in females. Rounded ears measuring between 45 and 62 mm (53.73 ± 4.67 mm; n = 11) in males and between 47 and 57 mm (51.33 ± 5.13 mm; n = 3) in females.

Overall coloration of the head varies from light yellowish brown to smoky gray, except, chin, cheeks, throat, and around the lips and eyes, which are white or very light gray. Two genal black or very dark brown stripes cross in parallel the cheeks in longitudinal direction. In the region of the posterior end of these stripes there is a stripe like an incomplete transversal necklace ("anterior transverse stripe or hyoid stripe"). The upper genal stripe connects with the black stripe around the eyes, the dark orbital stripe. In the mystacial region, there are four or five rows of spots that may or may not coalesce, and with the exception of the top two rows, the remaining ones extend to philtrum. The supraorbital spots or narrow stripes are arranged longitudinally on each side of the head and can connect to form frontal-parietal strips. Between these two stripes there are numerous, small, rounded or elliptical spots. Usually five longitudinal stripes run along the nape and the lateral region of the neck to the anterior part of the dorsum in the interscapular region. The hairs on head and neck are short and slightly harsh, and on nape they are pointing backward. Ears rounded with dorsal surface almost entirely black except at the base, which has the same color of the rest of the head, and a white spot is centrally disposed on the dark surface of the dorsal surface of the ear. The body shows the same overall coloration found in the head and neck, especially in the dorsum and the dorsal surface of the fore and hind limbs. In the dorsum, rounded and/or elliptical spots may be separated or interconnected forming more or less longitudinal rows. The spot pattern in the interscapular region shows high individual variation. On the side of the body, small and/or medium-sized solid rounded and elliptical black spots are present, generally not forming rosettes or oblique bands, but a few individuals may exhibit open and incomplete rosettes. The venter is white or very light gray and has small and medium-sized rounded very dark spots. The hairs on the body are short and slightly harsh, but slightly longer than the head, and in the inguinal region the hairs are longer than the rest of the body. Melanistic specimens are also present. The dorsal surface of limbs has the same color pattern of the dorsum of the body, while the ventral surface has the same pattern of the venter. On the dorsal surface of the fore and hind limbs are present round and/or elliptical spots of medium size in the proximal region, while only spots of smaller size are present in the distal region on the feet. On the ventral surface of the fore and hind limbs are present medium and small sized spots. The hairs on the feet are short and slightly harsh. The tail is relatively long, corresponding to between 52 and 63% of the length of the head and body, and displays black or very dark brown rings alternating with rings of the same color of the dorsum, and the tip is dark colored.

Robust skull with broad and short rostrum, corresponding to between 32.29 and 37.99% (RL/GLS: 35.09 ± 1.41%; n = 35) of the greatest length of skull in males and between 29.71 and 37.06% (RL/GLS: 34.49 ± 1.49%; n = 49) in females. The nasals are broad distally, and narrow shortly thereafter to converge at the posterior end, where they articulate with the frontal; there may or may not be a depression in this region. The anterior margin of the nasals is predominantly curved or moderately curved (Table 4). The anterior ends of the pre-maxillae are not projected and thus, in side view, they are aligned with the anterior end of the nasals. When the skull is in dorsal view, the nasals fully cover the incisive foramina. The orbits are large, rounded and forward-faced, being positioned entirely in the anterior half of the skull. The anteriormost margin of the orbit is aligned at the P3 parastyle, while the posteriormost point of the margin of the orbit coincides with the alignment of the end of the post-orbital process of the jugal. The upper and lower postorbital processes are not connected and, therefore, they do not form a complete and fused postorbital bar. The zygomatic plate, which is part of the maxilla, is well developed and forms the floor of the orbital region. The frontal is well developed and extends from the maxilla-frontal suture and nasal-frontal to the anterior portion of the braincase, articulating with the parietal. In lateral view, the skull has a slightly convex profile in the frontal region, providing a less evident curvature. The interorbital region is narrow and its width in proportion to the greatest length of skull shows values between 15.47 and 24.20% (IOB/GLS: 18.52 ± 1.69; n = 35) (Table 3) in males and between 15.78 and 20.33% (IOB/GLS: 18.26 ± 1.05; n = 50) (Table 3) in females. The braincase is large and oval, with the proportion of its width in relation to greatest length of skull varying between 39.44 and 47.51% (GBB/GLS: 43.01 ± 2.47; n = 34) (Table 3) in males and between 41.69 and 50.01% (GBB/GLS: 46.21 ± 1.83; n = 50) (Table 3) in females. The sagittal crest is present in most specimens, with most males showing type 2 (poorly developed and restricted to the region interparietal) (50.00%; n = 17) and type 3 (moderately developed) (35.29%, n = 12) (Table 4), while most females have type 2 (82.35%; n = 42) (Table 4). Only a small fraction of sampled specimens have the sagittal crest well developed; and they are all males (8.83%, n = 3) (Table 4) and one specimen of unknown sex. Overall, the sagittal crests are well developed and moderately high. Temporal lines are present and from the lyriform type. The lambdoidal crest may be present and poorly, moderately or well developed. The palate is relatively large and its width between P3 varies from 32.84 to 42.53 mm (GPB: 39.34 ± 2.07; n = 36) in males and 30.69 to 41.27 mm (GPB: 36.64 ± 1.92; n = 54) in females (Table 3). In most of cases, the length of palate is equal or less than the width of palate [GPL/GPB: 101.24 ± 5.12 (n = 35) in males; 99.07 ± 4.57 (n = 53) in females (Table 3)]. The notch of the postpalatine vein is broad and comparatively shallow in most specimens (males: 85.29%, n = 29; females: 75.00%, n = 39) (Table 4) and the posterior margin of the palate (or anterior margin of mesopterygoid fossa) has a U-shaped edge. It may or may not have a medial notch, which can be shallow or deep (Table 4). Furthermore, the posterior margin of the palate in *L. geoffroyi* distinguishes from other small and medium-sized Neotropical felids in two ways. Firstly, it is related to the shape of the margin when the notch is absent, in other words, this area of postpalatine may have a regular and uniform margin or may have a projection towards the mesopterygoid fossa, in the same line of the left and right palatine suture. Another point is when the notch is present. In addition to the aforementioned typical shape (deep or shallow), another shape can be found, which is the presence of two lateral projections to the central notch, one on each side, and it is represented in 23.58% of the overall sample (29 in 123 individuals), independent of the sex or geographic group. The presphenoid, centrally located in the mesopterygoid fossa, is narrow, very elongated and arranged longitudinally, showing lat-

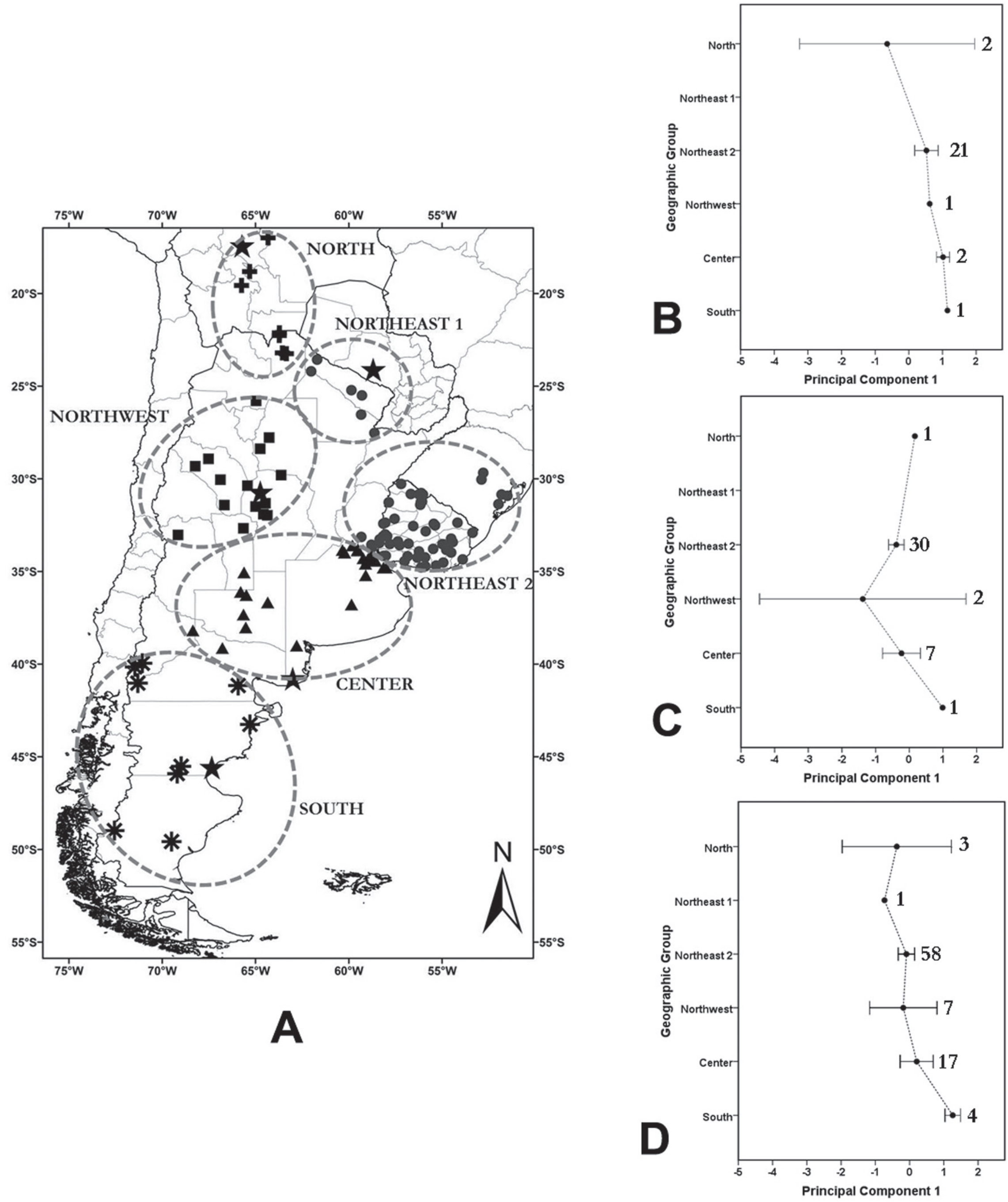

FIGURE 12: Geographical analysis of *L. geoffroyi:* **(A)** Population samples organized in six geographic groups (North, Northwest, Northeast 1, Northeast 2, Center and South) arranged on a southward direction from southern Bolivia to southern Argentina; **(B)** Diagrams of first principal component (see Figure 6) for male geographic groups; **(C)** Diagrams of first principal component (see Figure 7) for female geographic groups; **(D)** Diagrams of first principal component (see Figure 8) for the geographic groups of male, females and unknown sex specimens combined. Error bars show 95% interval of confidence the mean. The means are represented by black circles in the error bars. The number on the right side of each bar corresponds to the number of specimens for each geographical group.

eral expansions in the median area. The basioccipital, located between auditory bullae, is usually narrow. The mastoid processes are arranged in a posterolateral position in relation to the auditory bullae and they are anteriorly articulated to the paraoccipital processes. The mastoid processes shape in 96.97% of males (n = 32) and 83.76% of females (n = 41) (Table 4) is posteriorly poorly developed, separated from paraoccipital processes by a notch, enabling the visualization of the surface of the auditory bulla. The zygomatic arches are more expanded laterally, and the average width of the braincase relative to the zygomatic width (GBB/ZB) is around 65% in males (n = 34) and 69% in females (n = 51) (Table 3). The occipital condyle is elongated, robust and spirally curved and encloses the foramen magnum, which is well developed. The auditory bulla is relatively large and oval, with ectotympanic smaller than entotympanic in 93.94% of males (n = 31) and 86.0% of females (n = 43) (Table 4). The mandible is well developed, the horizontal ramus is high and curved, especially in the anterior region, and the masseteric fossa is deep and broad, extending almost the entire ascending ramus. The ascending ramus is high and extends from the angular process to the outermost end of the coronoid process. The coronoid process is well developed, can be broad or narrow, rounded and curved, resembling a hook in lateral view. The condyloid process is robust, bar shaped, aligned transversely to the ascending ramus, and on the same occlusional plane of the lower tooth row. The angular process is relatively large and rounded, which can be aligned to or positioned a little posteriorly to the condyloid process. The C-M1 length varies from 28.66 to 34.97 mm (CM1L: 31.96 ± 1.71 mm; n = 37) in males and from 25.86 to 33.78 mm (CM1L: 29.37 ± 1.38 mm; n = 53) in females (Table 3), while the p3-m1 length varies from 20.48 to 25.04 mm (p3m1L: 23.22 ± 1.19 mm; n = 35) in males and from 19.08 to 24.64 mm (p3m1L: 21.62 ± 1.11 mm; n = 31) in females (Table 3). The shape of P3 paracone may be narrow and long [males: 75.86% (n = 22); females: 63.83% (n = 30)] or short and wide [males: 24.14% (n = 7); females: 36.17% (n = 17)] (Table 4), and P3 parastyle is absent in all specimens, except for three unknown sexed specimens (Table 4). The P4 paracone is present in almost all studied specimens [males: 100% (n = 31); females: 96.15% (n = 50) (Table 4)]. Traces of a talonid on m1 are absent in most of the sample [males: 83.87% (n = 26); females: 91.67% (n = 44) (Table 4)].

Geographical distribution: Leopardus geoffroyi is found in a wide variety of temperate and subtropical habitat types from sea level to up to 3,300 m of altitude, associated to open vegetational formations, which includes the pampas grasslands, dry Chaco shrub and woodlands from southern Bolivia and northwestern Argentina, Paraguay, southern Brazil, Uruguay and south through Argentina and bordering areas of southern Chile to Patagonia and the Strait of Magellan (Figs. 4 and 5) (Ximénez, 1975; Redford & Eisenberg, 1992; Nowell & Jackson, 1996; Sunquist & Sunquist, 2002, 2009; Lucherini *et al.* 2006).

Geographic and local variation: Leopardus geoffroyi does not show sexual dimorphism on external morphology, but does for some craniodental characters. The size, shape and arrangement of spots, as well as the pattern of ground color, varies greatly between specimens from the same locality, resulting in a large individual variation in pelage. Some individuals show spots well separated and distinct from each other, while other specimens have solid spots very close together, making them almost indistinguishable and generating a speckled pattern. In some cases, the aggregation of spots generally occurs along the axis of the back, leaving some individuals with a pattern similar to a stripe. All these patterns are individual and are found widely in different geographic groups.

The ground color, which is the main criterion for defining the putative subspecies, shows high individual variation (Fig. 13). In a same population – for example in Uruguay – it is possible to find different specimens exhibiting color characters that define all subspecies (*e.g.,* ochraceous ground color and dark gray ground color). Ximénez (1971) reported that individuals from different locations (and by extension from different subspecies) showed similar ground color patterns. This author noted that specimens of Salta (MACN36.619 and MACN36.229) and southern Brazil are no different from those of Uruguay, a pattern that I also observed. Some southern individuals (*e.g.,* from Neuquén, Rio Negro, La Pampa) are slightly lighter than their northern counterparts, with a slight tendency to gray, but in La Pampa there is a specimen with the "typical" color (MACN51.168) and other more light grayish (MACN22025). In Pozo de Maza, Formosa, in the northern Argentina, a specimen (MACN47.404) shows a grayish color. Specimens from Jujuy are usually also lighter, very subtly, but one specimen (MACN34.556) from Villa Unión (La Rioja) has a dark ochraceous ground color. An individual, without known locality, identified as *"leucobapta"* (MACN31.248), has a more yellowish color than the other groups described above. Furthermore, in the six specimen series (all collected in July 1936) from Santiago de Estero, Lavalle, Argentina, some specimens (AMNH41551 and AMNH41555) exhibit colors tending to gray, resembling the specimen from Cañadon de las Vacas, Corpen Aike, Santa Cruz (AMNH16696); while other specimens (AMNH41550, 41552, 41553 and 41554) have a coloration similar to the predominant color in the

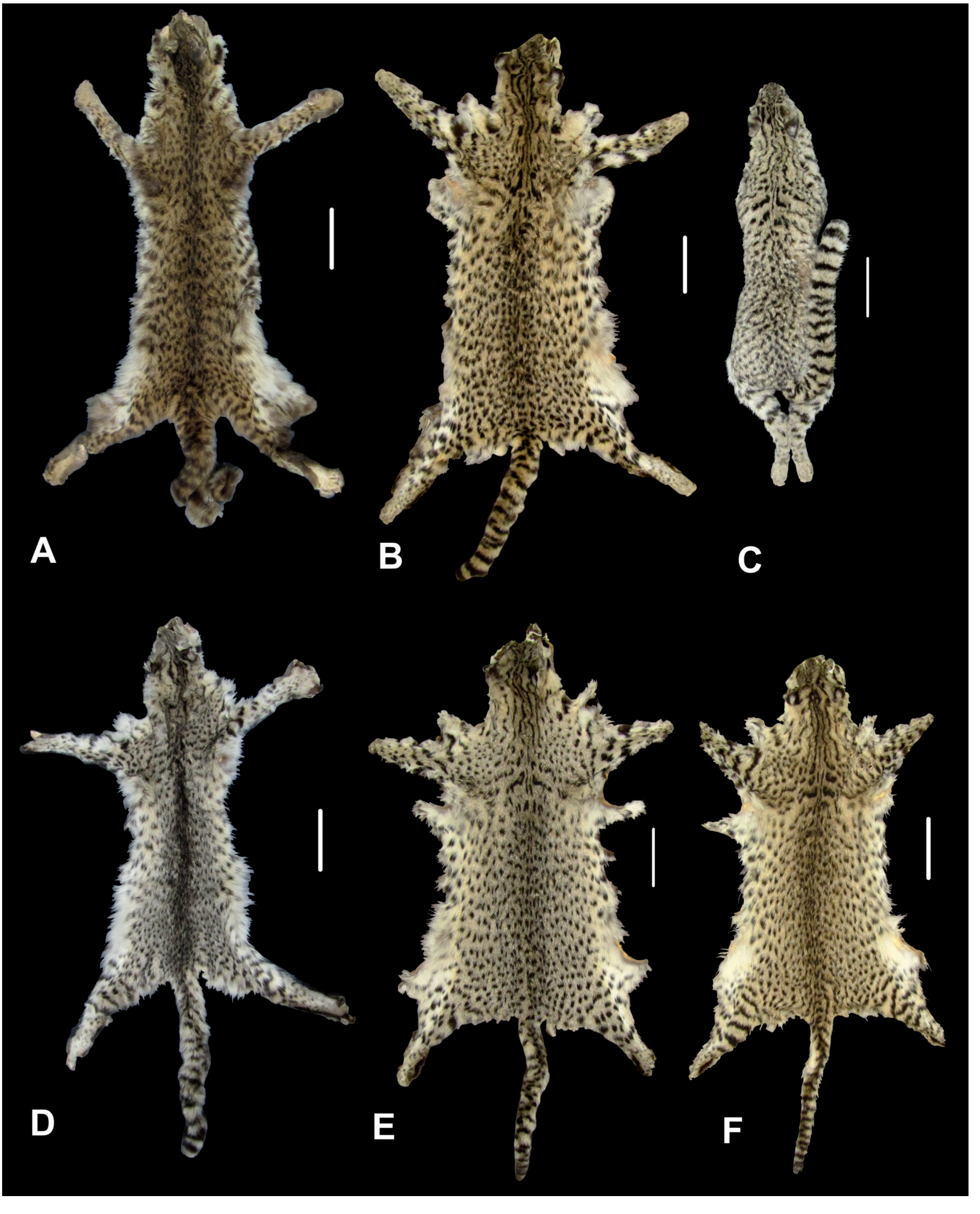

FIGURE 13: Pattern of coloration and markings in *L. geoffroyi:* **(A)** MACN34.556 (unknown sex) from Villa Unión, La Rioja, Argentina; **(B)** AMNH39010 (male) from Pulqui, Oropeza, Chuquisaca, Bolivia; **(C)** MACN14590 (female) from Estación Romero, El Cuy, Río Negro, Argentina; **(D)** MACN47.404 (unknown sex) from Pozo de Maza, Formoza, Argentina; **(E)** AMNH41555 (unknown sex) from Lavalle, Santiago del Estero, Argentina; **(F)** AMNH41550 (unknown sex) from Lavalle, Santiago del Estero, Argentina. Bar = 100 mm.

specimens of Uruguay (light yellowish brown to dark yellowish brown).

Regarding the craniodental characters, the sagittal crest is highly variable in individual and geographical terms, but the males usually have longer and higher sagittal crests (type III, moderately developed; no specimens shows the type IV, the well-developed crest) and broader, more robust zygomatic arches than are observed in females. Furthermore, regardless of sex, *L. geoffroyi* shows characters of the posterior margin of the palate that differ from other Neotropical felid species. Individuals who do not possess a notch in the postpalatine may have the regular margin, or there may be a projection toward the fossa mesopterygoid at the height of the suture that articulates left and right palatine, similar to what is observed in specimens of domestic cat, *Felis catus* Linnaeus, 1758. Some specimens who have the notch may also exhibit two projections lateral to it, one on each side. Aside from *L. geoffroyi,* I just noticed this character on one specimen of *L. wiedii* from Buena Vista, Bolivia (AMNH61790). There are no significant differences in cranial dimensions in the studied groups along the latitudinal distribution of the species.

Comparisions: Here I present the differences that distinguish *L. geoffroyi* from other small and medium sized felids found throughout its geographical distribution.

Leopardus geoffroyi is distinguished from *Leopardus pardalis* (Linnaeus, 1758) by the smaller body size, premaxilla not projected forward and holdings its anterior end aligned to the anterior end of the nasal, hairs on the nape facing backward, small and/or medium-sized solid rounded and elliptical black spots distributed almost all over the body; while *L. pardalis* shows medium body size, rosettes that can coalesce and form oblique bands arranged in scapular-inguinal direction, hairs on the nape facing forward, larger and more robust skull, premaxillary projected anteriorly in relation to the anterior end of the nasal, the region of the frontal slightly convex in profile, sagittal crest well developed and often high, lambdoidal crests well developed and robust and well developed zygomatic arches.

Leopardus geoffroyi is distinguished from *Leopardus wiedii* (Schinz, 1821) by the larger body size of the former, premaxilla not projected forward and holding its anterior end aligned to the anterior end of the nasal, hairs on the nape facing backward, small and/or medium-sized solid rounded and elliptical black spots distributed almost all over the body, whereas *L. wiedii* shows small size, presence of small rosettes on the sides of the body which usually coalesce and form small oblique bands arranged in scapular-inguinal direction, the tail proportionately longer, hairs on the nape facing forward, smaller and more gracile skull, the region of the frontal slightly convex, premaxilla projected forward in relation to the anterior end of the nasal, more rounded braincase, sagittal crest usually absent and narrow zygomatic arches, delicate.

Leopardus geoffroyi is distinguished from *Leopardus guttulus* by a the larger body size, larger and more robust skull, small to moderately developed sagittal crest, small and/or medium-sized solid rounded and elliptical black spots distributed almost all over the body, while *L. guttulus* has a smaller body size, presence of small distinctive rosettes on the body, smaller and more gracile skull, sagittal crest (when present) undeveloped and restricted to the interparietal region, and narrow and delicate zygomatic arches.

Leopardus geoffroyi is distinguished from *Leopardus guigna* by larger body size, light yellowish brown to smoky gray ground color of body, larger and more robust skull, small or moderately developed sagittal crest; while *L. guigna* has a smaller body size, grayish fawn, reddish brown or dark reddish brown ground color, a quite large and conspicuous lateral rostral stripe, presence of a third less extensive stripe running roughly parallel and between the upper and lower genal stripes, an even thicher tail, smaller and less robust skull, the presence of "internal temporal lines" that are located between each parietal suture and actual temporal lines (or "external temporal lines"), parietal slightly higher in the region between the internal temporal lines.

Leopardus geoffroyi is distinguished from the pampas cat group (*L. pajeros* and *L. braccatus*) by presenting more rounded ears with a white spot centrally disposed on the dark surface of its dorsal surface, small and/or medium-sized solid rounded and elliptical black spots distributed almost all over the body and tail with very dark rings, while the pampas cat group shows more triangular ears with hair tuft at the tip, spinal crest little darker than ground color, and legs with transverse stripes present in the proximal portion. The Northern forms of *Leopardus pajeros* (Desmarest, 1816) (which includes the putative Bolivian and northern Argentinean subspecies *budini* Pocock, 1941, *crespoi* Cabrera, 1957 and *steinbachi* Pocock, 1941) are distinguished from *L. geoffroyi* by a yellowish gray or grayish brown ground color with the flanks covered by rusty "ocelot-like" rosettes forming oblique bands. The Southern forms of *L. pajeros* (Desmarest, 1816) (which includes the putative subspecies *pajeros* Desmarest, 1816 and *crucina* Thomas, 1901) differ from *L. geoffroyi* by almost uniformly grayish brown ground color with faint and almost imperceptible oblique lines on the flanks, tail not ringed. *L. braccatus braccatus* (Cope, 1889) is distinguished from *L. geoffroyi* by its uniform brown agouti ground color, the presence of fainted traces of dark brown rosettes in the flanks, the black stripes in the proximal area of the legs and the feet all black. *L. braccatus munoai* differs from *L. geoffroyi* by uniform yellowish brown agouti ground color, traces of dark brown rosettes in the flanks, the black stripes in the proximal area of the legs, the feet black only in the ventral (= palmar and plantar) surfaces, tail with discontinuous rings or not ringed.

Leopardus geoffroyi is distinguished from *Leopardus jacobita* (Cornalia, 1865) by the spotted pattern of the pelage, the dorsal profile of skull being convex, and the ectotympanic chamber smaller than the entotympanic, while *L. jacobita* has spots that tend to be in vertical lines on the body, bushy and long ringed tail, the dorsal profile of skull is more flat and elongated, and the ectotympanic chamber is equal to or larger than the entotympanic.

Leopardus geoffroyi is distinguished from *Puma yagouaroundi* (É. Geoffroy, 1803) by the spotted pattern of the pelage, ringed tail, presence of dark lines across the cheeks, a fossa shallow along the posterior internasal and anterior interfrontal sagittal sutures, and broad auditory bullae, whereas *P. yagouaroundi* has a uniform coloration (gray, yellow, red, brown or black), not ringed tail, absence of dark lines across the cheeks, a deep fossa along the posterior internasal and anterior interfrontal sagittal sutures, and narrower auditory bullae.

Leopardus geoffroyi is distinguished from *Felis catus* by the spotted pattern of the pelage, the rounded ears without tufts in the tip, the posterior margin of palate with or without a medial notch, a small projection in the margin of the palate towards the mesopterygoid fossa may be present, while *F. catus* has a great individual variation in color pattern, but never consists of black spots on yellowish or orange background (Anderson, 1997), a triangular ear with small tufts in the tip, the zygomatic plate proportionally larger, the upper postorbital processes are large and almost reaching the lower postorbital processes, the posterior margin of the palate without a medial notch and a small projection in the margin of palate towards the mesopterygoid fossa is always present.

CONCLUSIONS

It is suggested that the body size of *L. geoffroyi* varies along the latitudinal gradient, with specimens from the northern parts of the range (in lower latitudes) showing smaller body size, while in the southern parts of the range (in higher latitudes) specimens are larger (Sunquist & Sunquist, 2002, 2009), following Bergmann's rule. However, a study that investigated the variation in body mass along the geographic distribution found no correlation between body mass and latitude, not supporting Bergmann's rule for this species. Similarly, in the investigation of cranial dimensions, represented here by the first principal component, I also found no relation to latitude.

Regarding the variation of ground color, there is a suggestion of a latitudinal variation of the color, with northern specimens having brighter and more yellowish colors whereas the southern forms show paler and more grayish colors (Nowak, 1999), a condition similar to that postulated by Gloger's rule. I have in fact detected that individuals from northern populations tend to have brighter, vivid and more yellowish colors than their southern counterparts, which are paler and grayish in color, but the changes between neighboring populations along the latitude occur in a subtle and gradual way. Furthermore, individuals from the same population, from any regions of the geographical range of these extremes, may exhibit variations in coloration that fall within the described ranges.

The evidence obtained from the analysis of qualitative and quantitative craniodental and external characters offered no support to the recognization of subspecies in *L. geoffroyi.* The results presented here corroborate the results obtained by molecular data, which suggests that there is no justification for the recognition of subspecies in *L. geoffroyi,* and it is probably a large panmictic population with no significant barriers to gene flow (Johnson *et al.,* 1999; Eizirik & Johnson, 2006).

RESUMO

O gato-do-mato-grande Leopardus geoffroyi *(d'Orbigny & Gervais, 1844) é um felídeo de pequeno porte encontrado no cone sul da América do Sul e, dependendo do autor, quatro ou cinco subespécies são habitualmente reconhecidas (*L. g. geoffroyi, L. g. paraguae, L. g. euxanthus, L. g. salinarum *e* L. g. leucobaptus*), principalmente baseadas em caracteres morfológicos externos,* *como o padrão de coloração da pelagem. Com a finalidade de esclarecer a taxonomia de* L. geoffroyi, *analisei aproximadamente 200 espécimes depositados em museus. Examinei a morfologia externa e craniodentária quantitativa e qualitativamente, procurando por padrões de caracteres congruentes que poderiam indicar a existência de unidades taxonômicas. Vinte medidas craniodentárias foram aferidas e posteriormente testadas através de procedimentos univariados e multivariados (MANOVA, PCA e DFA). Neste estudo detectei uma variação grande nos caracteres morfológicos, e com isso não foi possível determinar se alguns deles foram geograficamente consistentes e se poderiam ser utilizados para determinar alguma unidade taxonômica. Baseando-me nisso, não reconheço quaisquer divisões subespecíficas para* L. geoffroyi. *Ao longo de sua distribuição geográfica, uma mudança gradual e sutil de um padrão de coloração para outro foi detectada ao longo da latitude, porém os caracteres morfológicos que foram utilizados para definir as supostas subespécies foram detectados em uma mesma população. Além disso, o presente estudo é congruente com os resultados obtidos anteriormente através de dados moleculares, que sugeriram que* L. geoffroyi *tem um nível elevado de diversidade genética sem estruturação geográfica. Isto indica a existência de uma grande população panmítica sem barreiras significativas para o fluxo gênico e, como conseqüência, nenhuma subespécie poderia ser reconhecida.*

PALAVRAS-CHAVE: *Leopardus geoffroyi;* Taxonomia; Subespécies; Morfologia; Variação.

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APPENDIX 1

Specimens examined

Leopardus geoffroyi (194 specimens). **ARGENTINA: Buenos Aires:** alredores de Baradero: MACN24048 (skull); MACN24473 (skull); MACN23838 (skull); MACN24237 (skull); Azul: MUNHINA2482 (skull); Baradero, Lima: MACN23660 (skull); Diego Gaynor: MACN24746 (skull); Estación Experimental del INTA (Instituto Nacional de Tecnología Agropecuaria) del Delta del Paraná: MACN23711 (skull); Guillermo Enrique Hudson: MACN23715 (skull), MACN23716 (skull), MACN24488 (skull); Islas de Tigre: MACN15 (skull); Lobos, Arroyo Las Garzas (km 106): MACN24741 (skull); Luján: MACN23619 (skin); Manantiales (25 km al sur de Azul): MACN23693 (skull); Reserva Natural Otamendi, em proximidades del Río Luján: MACN23717 (skull); Ruta 8, km 204, 13 km al Norte de Viña: MACN24487 (skull); riverbanks of Rio Negro: MNHN-ZM-MO-2001-298, MNHN-ZM-MO-2001-299 and MNHN-ZM-MO-2001-300 (photographs of the skins of the syntypes of *F. geoffroyi*); Ruta Nacional 9 y Ruta Prov. 41, em proximidades de Baradero: MACN24928 (skull); San Pedro, Vuelta de Obligado: MACN21981 (skull); Sierra de la Ventana: MACN36.56 (skin), MACN36.57 (skin), MACN36.58 (skin); Zárate, Establecimiento El Oasis (Alto Paraná), Arroyo Águila Negra y Carabelas: MACN24715 (skull); Unknown locality: MACN193 (skin); **Catamarca:** Departamento Belén, Hualfin (14 km al S.): MACN13144 (skin); **Chaco:** Departamento Libertador, General San Martín, Campo Aurora: MACN23698 (skull), MACN23712 (skull); **Chubut:** Lago Colhue Huapi, Sarmiento: AMNH94331 (skull), AMNH94333 (skull); Trelew, Rawson: AMNH80298 (skull); **Córdoba:** Bialet Massé: MACN39.209 (skull); Calamuchita: MACN38.258 (skin), MACN38.260 (skin); Departamento Sobremonte, Los Hoyos: MACN13303 (skull); Los Cocos, Sierra de Córdoba: MACN22937 (skull); Parque Nacional Provincial y Reserva Natural "Chancaní": MACN23837 (skin); Valle Reartes: MACN24.16 (skull); Unkown locality: MACN33.120 (skin); **Corrientes:** Departamento Capital, Estero Valenzuela: MACN22923 (skull); **Entre Ríos:** Campo El Yarará, Arroyo Malambo, a 200 m Ruta 12: MACN19245 (skull); Gualeguay: MACN29.242 (skin and skull); Ruta 14, 7 km al S. de Ceibas: MACN24745 (skull); **Formosa:** Departamento Patiño, Colonia Ivanita, Ibarreta: MACN23710 (skull); Departamento Pirané, Palo Santo: MACN23689 (skull); Pozo de Maza: MACN47.404 (skin); Rio Teuco, La Florencia: MACN47.120 (skull); **La Pampa:** Departamento Lihue-Calel, Campo La Florida: MACN22024 (skin); Departamento Lihue-Calel, Parque Nacional Lihue-Calel: MACN23329 (skull), MACN23308 (skull), MACN22021 (skull), MACN22022 (skull), MACN22023 (skull), MACN22025 (skin), MACN22921 (skull), MACN22922 (skull), MACN22931 (skull), MACN22932 (skull), MACN24726 (skin), MACN22929 (skull); Departamento Utracán, Chacharramendi: MACN22926 (skull); La Elenita: MACN23704 (skull); Loventué: MACN39.381 (skull); Telén: MACN51.166 (skin); Toay: MACN51.168 (skin), MACN51.169 (skin); **La Rioja:** Famatina: MACN28.88 (skin); MACN34.335 (skin), MACN34.336 (skin); MACN34.337 (skin and skull); General Roca: MACN28.192 (skull); Patquía: MACN28.175 (skin), MACN28.176 (skull); Villa Unión: MACN34.334 (skin); MACN34.555 (skin), MACN34.556 (skin); **Mendoza:** Departamento Luján de Cuyo, sur de Sierra Cacheuta: MACN22925 (skull); **Neuquén:** Bajada del Palo: MACN23330 (skull); Junín de los Andes: MACN38.76 (skin); Lago Lacar, San Martín de los Andes: MACN15425 (skull); Nahuel Huapi: MACN36.946 (skin); **Río Negro:** Departamento El Cuy, Estación Ingeniero Julián Romero: MACN14590; Lago San Martin: MACN36.134 (skin); Sierras de Paileman: MACN22099 (skull); **Salta:** Aguaray, Iquiro: MACN36.229 (skin); Dragones: MACN36.233 (skin), MACN36.483 (skin); La Frontera, Termas de Rosano de la Frontera: MACN23714 (skull); Laguna Mendoza Hickman: MUNHINA2669 (skin and skull); Rio Carapari, Angostura: MACN36.619 (skin); **San Luis:** Potrerillos: MACN23175 (skull); La Toma: MACN40.215 (skin); Unknown locality: MACN50.458 (skin), MACN50.460 (skin), MACN50.463 (skin), MACN50.464 (skin); **Santa Cruz:** Cañadon de las Vacas, Corpen Aike: AMNH16696 (skin and skeleton); Pampa Maria Santísima: MACN29.892 (skull); **Santiago Del Estero:** Departamento Choya, Villa La Punta: MACN23294 (skull); Lavalle: AMNH41551 (skin and skull), AMNH41552 (skin), AMNH41553 (skin and skull), AMNH41555 (skin), AMNH41550 (skin), AMNH41554 (skin); **Tucumán:** Unknown locality: MACN29.249 (skin); **BOLÍVIA: Chuquisaca:** Pulqui, Oropeza: AMNH39010 (skin and skull); **Potosí:** Rio Cachimayo: AMNH39004 (skin and skull); **Santa Cruz:** Buena Vista, Ichilo, Rio Iraniá: MACN50.100 (skin); **Unknown locality:** MACN36.620 (skin); **BRAZIL: Rio Grande do Sul:** Arambaré: MPEG22184 (skin and skull); Cachoeira do Sul, BR 290: MPEG22228 (skull); Candelária: AMNH235996 (skin and skull); Rodovia BR 470, km 475, Vila Mirim, Rio Grande: MPEG22201 (skin); São Lourenço: MZUSP111 (skull), MZUSP110 (skull), MZUSP1432 (skull), MZUSP1443 (skull); **PARAGUAY: Unknown locality:** MACN28.37 (skin); **URUGUAY: Artigas:** Arroyo Catalán Grande y Ruta 30: MUNHINA5483 (skull and skeleton); Arroyo Cuaró, Paso Campamento: MUNHINA969 (skin and skull); Arroyo Del tigre, 3 km águas acima da barra com o Rio Cuareim: MUNHINA2021 (skin and skull), MUNHINA2022 (skin, skull and skeleton); Arroyo Três Cruces Grande: MUNHINA1353 (skin and skull), MUNHINA1352 (skin and skull), MUNHINA3412 (skull and skeleton); Punta del Arroyo Três Cruces Chico: MUNHINA2480 (skull); **Canelones:** Bañado Tropas Viejas, Atlántida: MUNHINA796 (skin and skull), MUNHINA1285 (skull), MUNHINA1286 (skull), **Cerro Largo:** 6 km SE Melo: AMNH205903 (skin, skeleton); **Colonia:** Arroyo Limetas, Estancia Sem Jose: MUNHINA2670 (skull); Arroyo Tigre, Martim Chico: MUNHINA1619 (skin); Estância San José, Conchillas: MUNHINA2483 (skin and skull); **Durazno:** km 329, Rio Negro: MUNHINA4069 (skull); Rio Negro, 15 km Noroeste de San Jorge: AMNH205904 (skin, skull and skeleton); **Flores:** Arroyo Porongos, 3 km Oeste Paso de Los Mudos: MUNHINA3168 (skin, skull and skeleton); **Florida:** Est. Arteaga, C. Copetón: MUNHINA806 (skin and skull); Isla Mala: MUNHINA1288 (skull); La Cruz: MUNHINA2461 (skull); **Lavalleja:** Estancia Bella Vista: MUNHINA1265 (skin, skull and skeleton); Pirarajá, Rio Cebollatí: MUNHINA1274 (skull and skeleton); Zapicán: MUNHINA1263 (skull), MUNHINA1264 (skull); **Maldonado:** Gruta de Salamanca: MUNHINA1259 (skin and skull), MUNHINA1327 (skull); Sierra de las Animas: MUNHINA1201 (skin, skull); **Paysandu:** MUNHINA1262 (skull); Rio Negro: Arroyo Negro, 15 km S. Paysandú: AMNH205905 (skin, skull and skeleton), AMNH205906 (skin and skeleton), AMNH205907 (skin, skull and skeleton); Barra del Arroyo Caracoles Grande 17 km SSO de Fray Bentos: MUNHINA1334 (skull), MUNHINA1335 (skull); Bopieva, Rio Uruguay, 10 km Noroeste de Fray Bentos: MUNHINA2537 (skin, skull and skeleton), MUNHINA2470 (skull and skeleton); **Rocha:** MUNHINA3227 (skull and, skeleton); **Salto:** Salto Grande: MUNHINA312 (skull), MUNHINA304 (skull); **San José:** Arazatí: MUNHINA1298 (skull); Paso del Rey: MUNHINA1325 (skull), MUNHINA1326 (skull); Puerto Arazatí: MUNHINA1299 (skull); MUNHINA1317 (skull); Santa Clara, Chamizo: MUNHINA1015 (skin and skull); **Soriano:** Arroio Cololó: MUNHINA2478 (skin and skull), MUNHINA2477 (skin and skull); Arroyo Perdido, Estancia Santa Elena: MUNHINA1108 (skin and skull); MUNHINA1200 (skull); Barra de San Salvador: MUNHINA303 (skin e skull), MUNHINA307 (skull); Est. La Central Bocas del Perdido: MUNHINA711 (skull); Estancia Santa Elena, Arroyo Perdido: MUNHINA1187 (skin, skull and skeleton); Proximidades de Palmitas: MUNHINA2460 (skull); Río Negro frente as ilhas Lobo y del Vizcaíno: MUNHINA1150 (skeleton), MUNHINA1186 (skin, skull and skeleton); Santa Elena: MUNHINA306 (skull); **Tacuarembó:** Laureles: MUNHINA311 (skin and skull); 40 km Noroeste Tacuarembó: AMNH205909 (skin, skull and skeleton); 40 km Noroeste Tacuarembó, Estancia "El Infernillo": AMNH205908 (skin, skull and skeleton); Barra del Arroyo Salsipuedes Grandes y Salsipuedes Chico: MUNHINA1289 (skull); Rincón de la Vassoura, Laureles: MUNHINA831 (skin and skull); Rio Negro 7 km águas acima da barra do Rio Taquarembó: MUNHINA2534 (skull), MUNHINA2481 (skull); Rio Negro 7 km águas acima do Rio Taquarembó: MUNHINA1157 (skin, skull and skeleton); Sierra del Infiernillo: MUNHINA1260 (skin and skull); MUNHINA1258 (skull); **Treinta y Tres:** 16 km SSW Boca del Río Tacuari: AMNH205910 (skin, skull and skeleton); AMNH205911 (skin, skull and skeleton); Olimar Chico: MUNHINA1261 (skin and skull); Rio Olimar Chico, 25 km W. SW. Treinta y Tres: AMNH205913 (skin, skull, skeleton), AMNH205914 (skin, skeleton); AMNH205912 (skeleton).

Leopardus pardalis (46 specimens). **ARGENTINA: Formosa:** Comandante Fontana: MACN29.840 (skull); **Santa Fé:** Villa Guillermina: MACN13464 (skull); **Misiones:** Departamento Guaraní, Cuartel Río Victoria: MACN23690 (skull); Departamento Monte Carlo, Arroyo El Doradito: MACN23174 (skull); Santa Ana: MACN33.95 (skull), MACN33.183 (skull); MACN51.132 Departamento Frontera: refúgio Piñalites: MACN13058 (skin and skull); Río Iguazú: MACN51.73 (skin and skull); Parque Nacional Iguazú: MACN21371 (skin and skull), MACN24910 (skin and skull), MACN24911 (skin and skull), MACN24890 (skin and skull), MACN24891 (skin and skull), MACN24892 (skin and skull), MACN24893 (skin and skull), MACN24894 (skin and skull); Ruta 101, Sección Timbo: MACN21370 (skin and skull); Arroyo Uruguay: MACN49.343 (skin), MACN50.540 (skin), MACN51.132 (skin and skull); **BOLÍVIA: Cochabamba:** mouth of the Chapare River: AMNH214742 (skull), 52 km S. mouth of the Chapare River: AMNH214743 (skull, skeleton), AMNH214744 (skull, skeleton); **Santa Cruz:** Buena Vista: AMNH61787 (skin, skull, skeleton), AMNH61789 (skin, skull, skeleton), MACN50.98 (skull), MACN50.99, MACN50.100 (skin and skull), MACN50.101

(skin and skull), MACN50.102 (skull), MACN13465 (skull), MACN29.241 (skull), MACN31.247 (skull); **BRAZIL: Paraná:** Parque Nacional do Iguaçu, Foz do Iguaçu: MHNCI3823 (skull), MHNCI3803 (skull), MHNCI3802 (skull), MHNCI3804 (skull), MHNCI3825 (skull), MHNCI3821 (skull, skeleton); **Rio Grande do Sul:** São Lourenço: MZUSP3336 (skull); **PARAGUAY:** Unkown locality: MACN19.37 (skin and skull), MACN28.34 (skull), MACN28.35 (skull), MACN31.238 (skull), MACN31.359 (skull).

Leopardus wiedii (29 specimens). **ARGENTINA: Jujuy:** Departamento Valle Grande, Santa Barbara: MACN21368 (skin); **Misiones:** Arroyo Uruguaí, km 10: MACN51.137 (skin and skull); Departamento Frontera, Tobuna: MACN52.26 (skin and skull), MACN54.21 (skin and skull); Departamento Montecarlo, Arroyo Doradito: MACN23694 (skull); Parque Nacional Iguazú: MACN24899 (skin), MACN24907 (skin); Ruta Nacional 12 y Ruta 101: MACN24898 (skin); **Salta:** Finca Lipeo, limite norte Parque Nacional Baritú: MACN19.148 (skin and skull); **BOLÍVIA: Santa Cruz:** Buena Vista: AMNH61788 (skin, skull, skeleton), AMNH61790 (skull), MACN50.94 (skin and skull), MACN50.95 (skin and skull), MACN50.96 (skin and skull), MACN50.97 (skin and skull); **PARAGUAY: Alto Paraná:** Capitán Meza (skull): MACN47.371 (skull); **Unknown locality:** MUNHINA1340 (skin); **URUGUAY: Cerro Largo:** Estancia Santa Lucia, Río Negro em la barra del arroyo Tupambae: MUNHINA2576 (skin); **Durazno:** Río Negro, 7 km águas arriba de la barra del Río Taquarembó: MUNHINA1401 (skin); **Rocha:** 10 km aguas abajo Arroyo Aiguá: MUNHINA5486 (skull and skeleton); alrededores de ciudad de Rocha: MUNHINA4293 (skin); Ruta 13 km 266: MUNHINA(EMG)1947; **Tacuarembó:** Estancia Casalas, Rincón de Zamora: MUNHINA888 (skin and skull); Río Negro 7 km de la barra com el Tacuaembo: MUNHINA1162 (skin, skull and skeleton), MUNHINA1163 (skin, skull and skeleton), MUNHINA1401 (skull); Rincón de los Matos, Pueblo del barro, Rio Tacuarembo: MUNHINA2781 (skin); **Treinta y Tres:** Costa del Río Tacuarí, em confluencia com la cuñada del Palmar, 3a Sección: MUNHINA4821 (skin); Río Tacuarí y Cda del Palmar, 3a sec.: MUNHINA AMSI207 (skull).

Leopardus guttulus (20 specimens). **ARGENTINA: Chaco:** Unknown locality: MACN 38.21 (skin); **Misiones:** Aguarai-Guazú Inferior: MACN48.295 (skin); MACN48.296 (skin); Arroyo Uruguaí, km 10: MACN52.56 (skin and skull); MACN52.57 (skin and skull); MACN51.121 (skin and skull); MACN51.141 (skin and skull); MACN51.142 (skin and skull); Departamento General Manuel Belgrano: MACN24912 (skin); Departamento Cainguás, Dos de Mayo: MACN23696 (skull); Departamento Guaraní, Cuartel Río Victoria: MACN23709 (skull); Departamento Montecarlo, Arroyo Doradito: MACN23695 (skull); Parque Nacional Iguazú, Area Cataratas: MACN24909 (skin); Rio Aguaraiguazú Superior: MACN48.294 (skull); **Salta:** Rio Carapavi, Angostuta: MACN36.726 (skin); **BRAZIL: Rio Grande do Sul:** Caxias do Sul: MN-UFRJ44359 (skin); Pinambi: MZUSP 3188 (skull); Rio Pardo, BR 290, km 141: MPEG 22183 (skin and skull), São Lourenço: AMNH 36948 (skin); **PARAGUAY:** Unknown locality: MACN31.191 (skin).

Leopardus guigna (7 specimens). **CHILE: Araucania:** Maquegua, Temuco: AMNH33283 (skin and skull), AMNH33285 (skin and skull), AMNH33284 (skin and skull), AMNH33286 (skin and skull), AMNH33288 (skin and skull), AMNH33280 (skin and skull); **Malleco:** Angol: AMNH93323 (skin and skull).

***Leopardus pajeros* (northern form)** (5 specimens). **ARGENTINA: Jujuy:** Santa Victoria: MACN41.163 (skin); **La Rioja:** Velazco: MACN34.322 (skin), MACN34.326 (skin); Villa Unión: MACN34.565 (skin); **Salta:** Los Andes, Chorrillos: MACN30.103 (skin and skull).

***Leopardus pajeros* (southern form)** (16 specimens). **ARGENTINA: Chubut:** Departamento Biedma, Istmo Carlos Ameghino, Península Valdés: MACN24236 (skull); **La Pampa:** Departamento Caleu-Caleu: MACN49.169 (skin), Estac. Aguas Blancas, aledaño a Parque Nacional Lihué Calel: MACN22934 (skull); General San Martin, Estancia El Retorno: MACN15582 (skin and skull); Lihuel-Caleu, Ruta 152, km 152: MACN24727 (skin); Pampa Central: AMNH36934 (skin); Puelches: MACN17821 (skin); Telén: MACN51.164 (skin); Toay: MACN51.167 (skin); **Neuquén:** Collón-Cura: MACN16489 (skin); Departamento Catán Lil, Las Coloradas, Campo Grande: MACN14086 (skull); Sierra Portezuela: MACN23176 (skull); **Río Negro:** Ramos Mejia: MACN50.456 (skin), MACN50.457 (skin); **San Luis:** Unknown locality: MACN25.33 (skin); **Santa Cruz:** Rio Gallegos, Patagônia: AMNH16695 (skin, skull and skeleton).

Leopardus braccatus braccatus (10 specimens). **BRAZIL: Goiás:** Parque Nacional das Emas: MN63629 (skin and skull); Palma: MN3148 (skin); Rio São Manuel, Adelândia: MN3149 (skin); **Mato Grosso:** Chapada dos Guimarães: AMNH354 (skin and skull; holotype); **Mato Grosso do Sul:** Aquidauna (Fazenda Pequi): MZUSP7786 (skin, skull and skeleton); Maracaju: AMNH133977 (skin), MN-UFRJ4868 (skull); Três Lagoas: MZUSP7670 (skin); **PARAGUAY: Central:** Asunción: AMNH243110 (skin, skull and skeleton); **Boqueron:** Juan de Zolagan, Gran Chaco: AMNH148573 (skin).

Leopardus braccatus munoai (18 specimens). **URUGUAY: Cerro Largo:** Estancia Juan Escoto, Tarariras: MUNHINA875 (skin); **Colonia:** 3 km North of Punta Pereyra: MUNHINA2433 (skin, skull and skeleton); Arroyo Limetas, Conchillas: MUNHINA4705 (skull); Arroyo Limetas, Estancia San Jorge: MUNHINA1315 (skin and skull); Arroyo Migulete em Ruta 21, Paso del Pelado: MUNHINA2926 (skin, skull, esqueleto); Arroyo Tigre: MUNHINA3374 (skull); Cañada Sauce, Estancia San Jorge, Conchillas: MUNHINA2479 (skull and skeleton); Estancia San Jorge, Arroyo Lunetas, Cochillas: MUNHINA2780 (skin, skull and skeleton); Estancia dos Cerros de San Juan Paraje Punta Francesa: MUNHINA1400 (skin and skull); Estancia San Cristobal, Arroyo Yimetas, Conchillas: MUNHINA2432 (skin, skull, skeleton); Estancia San Jorge, Martin Chico: MUNHINA1385 (skin and skull); **Florida:** Arteaga, Ruta 7, km 137: MUNHINA4706 (skin, skull and skeleton); **Lavalleja:** Estancia Bella Vista, Zapicán: MUNHINA971 (skin and skull); **Río Negro:** Bupicuá 10 km a leste de Fray Bentos: MUNHINA3413 (skin, skull and skeleton); **San José:** Bañados de Plaja Pascual: MUNHINA3224 (skull and skeleton); Parque San Gregório, Estancia Herminia: AMNH189394 (skin and skull); Estancia Santa Clara, Chamizo: MUNHINA879 (skin and skull); San Gregorio: MUNHINA1375 (skin, skull and skeleton); **Soriano:** Estancia Santa Elena, Arroyo Perdido: MUNHINA884 (skin and skull).

Leopardus jacobita (21 specimens). **ARGENTINA: Catamarca:** MACN15.586 (skin), MACN29.200 (skin), MACN37.31 (skin), MACN37.32 (skin), MACN37.33 (skin); MACN37.34 (skin), MACN37.36 (skin), MACN37.37 (skin), MACN37.38 (skin), MACN37.106 (skin), MACN37.107 (skin); MACN37.108 (skin); MACN37.109 (skin), MACN37.111 (skin), MACN37.112 (skin), MACN37.114 (skin), MACN37.116 (skin), MACN37.142 (skin), MACN37.143 (skin); **Catamarca, caminho San Francisco:** MACN42.113 (skin); **PERU: Arequipa:** 57 km ENE Arequipa: MVZ116317 (photographs of skull and the skin).

Puma yagouaroundi (29 specimens). **ARGENTINA: Chaco:** Charata: MACN50.455 (skin); El Zapallar: MACN30.12 (skin); **Córdoba:** Unknown locality: MACN34.627 (skin); **Corrientes:** Departamento San Luis, San Luis del Palmar: MACN14053 (skull); **Formosa:** El Colorado: MACN23172 (skull); Fortín Nuevo Pilcomayo: MACN43.56 (skin), MACN43.57 (skin); **La Rioja:** entre Zalamuyuma y Punta de Los Llanos: MACN29.777 (skin); **Mendoza:** Departamento Santa Rosa, Nacuñán: MACN23692 (skull); **Río Negro:** Departamento Avellaneda, Colonia Josefa: MACN13801 (skin); **Salta:** Angostura, Rio Carapavi: MACN36.618 (skin); Dragones: MACN36.484 (skin and skull); Orán: MACN17253 (skin), MACN17254 (skin and skull); **Santiago del Estero:** Colonia Dora: MACN42.10 (skin); Quimilí: MACN39.724 (skin); Saenz Peña: MACN 34.633 (skin); Unkown locality: MACN42.9 (skin); **Limit between Province of Buenos Aires and Province of Rio Negro:** a 150 km C. de Patagones: MACN13375 (skin); **BRAZIL: Rio Grande do Sul:** São Lourenço: MZUSP37 (skull, skin), MZUSP 1003 (skull), MZUSP1399 (skull), MZUSP1647 (skull), MZUSP2031 (skull); **BOLÍVIA: Santa Cruz:** Buena Vista: MACN50.103 (skull), MACN50.104 (skull); **PARAGUAY: Paraná:** Capitán Meza: MACN47.372 (skull); **Villeta:** Colonia Nova Italia: MACN40.190 (skin and skull); **Unknown locality:** MACN30.240 (skin).

Felis catus (3 specimens). **BRAZIL: São Paulo:** Cocuera: MZUSP22441 (skull) (labeled as *F.* cf. *wiedii*); **Unknown locality:** MZUSP19903 (skull); **CHILE:** Unknown locality: MZUSP43 (labeled as *F. guigna*).

APPENDIX 2

Gazetteer

Bolivia: **1.** Rio Iraniá, Ichilo, Buena Vista, Santa Cruz [17°00'00"S, 64°19'48"W]; **2.** Tiraque, Cochabamba (type locality of *Felis euxantha*) [17°25'48"S, 65°43'12"W]; **3.** Abra de Pulqui, Oropez, Chuquisaca [18°49'12"S, 65°19'12"W]; **4.** Rio Cachimayo, Potosí [19°34'12"S, 65°45'00"W].

Argentina: **5.** Rio Carapari, Angostura, Salta [22°07'48"S, 63°43'12"W]; **6.** Aguaray, Iquiro, Salta [22°16'12"S, 63°43'48"W]; **7.** Laguna Mendoza Hickman, Salta [23°12'36"S, 63°33'36"W]; **8.** 3 léguas SE de Dragones, Salta [23°15'00"S, 63°21'00"W]; **9.** al rededores de Dragones, Salta [23°15'00"S, 63°21'00"W]; **10.** Pozo de Maza, Formosa [23°34'12"S, 61°42'00"W]; **12.** Rio Teuco, La Florencia, Formosa [24°12'00"S, 62°01'12"W]; **13.** Departamento Patiño, Colonia Ivanita, Ibarreta, Formosa [25°13'12"S, 59°51'36"W]; **14.** Departamento Pirané, Palo Santo, Formosa [25°30'00"S, 59°18'00"W]; **15.** La Frontera, Termas de Rosano de la Frontera, Salta [25°48'00"S, 64°58'12"W]; **16.** Departamento Libertador, General San Martín, Campo Aurora, Chaco [26°32'24"S, 59°20'24"W]; **17.** Hualfin (14 km al S.), Departamento Belén, Catamarca [27°13'48"S, 66°50'00"E]; **18.** Departamento Capital, Estero Valenzuela, Corrientes [27°31'48"S, 58°37'48"W]; **19.** Lavalle, Santiago del Estero [27°46'48"S, 64°16'12"W]; **20.** Departamento Choya, Villa La Punta, Santiago del Estero [28°22'48"S, 64°45'00"W]; **21.** Famatina, La Rioja [28°55'12"S, 67°31'12"W]; **22.** Tres Cerros, Famatina, La Rioja [28°55'12"S, 67°31'12"W]; **23.** Villa Unión, La Rioja [29°19'12"S, 68°13'48"W]; **25.** Departamento Sobremonte, Los Hoyos, Córdoba [29°48'00"S, 63°37'48"W]; **27.** "La Represa", Patquia, La Rioja [30°03'00"S, 66°52'48"W], **28.** Patquía, La Rioja [30°03'00"S, 66°52'48"W]; **30.** Parque Nacional Provincial y Reserva Natural "Chancaní", Córdoba [30°22'12"S, 65°25'48"W]; **31.** Cruz del Eje, Córdoba [30°43'12"S, 64°44'24"W] (Type locality of *Felis salinarum*); **46.** General Roca, La Rioja [31°00'00"S, 67°00'00"W]; **47.** Los Cocos, Sierra de Córdoba, Córdoba [31°30'00"S, 65°00'00"W]; **48.** Valle Reartes, Córdoba [31°54'36"S, 64°34'48"W]; **49.** Calamuchita, Córdoba [31°58'12"S, 64°22'12"W]; **58.** Potrerillos, San Luis [32°40'12"S, 65°39'00"W]; **63.** Departamento Luján de Cuyo, sur de Sierra Cacheuta, Mendoza [33°01'48"S, 69°09'00"W]; **66.** Gualeguay, Entre Ríos [33°08'24"S, 59°19'48"W]; **81.** Ruta 14, 7 km al S. de Ceibas, Entre Ríos [33°33'36"S, 58°47'24"W]; **83.** San Pedro, Vuelta de Obligado, Buenos Aires [33°35'24"S, 59°48'36"W]; **84.** Campo El Yarará, Arroyo Malambo, a 200 m Ruta 12, Entre Ríos [33°43'12"S, 58°46'12"W]; **86.** Baradero, Lima, Buenos Aires [33°48'00"S, 59°31'12"W]; **87.** Partido de Baradero, alrededores de Baradero, Buenos Aires [33°48'00"S, 59°31'12"W]; **89.** Departamento Azul, Manantiales, 25 km al sur de Azul, Buenos Aires [33°50'24"S, 60°21'00"W]; **90.** Ruta Nacional 9 y Ruta Prov. 41, em proximidades de Baradero, Buenos Aires [33°51'36"S, 59°32'24"W]; **92.** Ruta 8, km 204, 13 km al Norte de Viña, Buenos Aires [33°58'48"S, 60°13'48"W]; **97.** Partido de campana, Delta de Paraná, Est. Experimental INTA, Buenos Aires [34°10'48"S, 58°49'48"W]; **99.** Campana, Canal 6, Delta – Estación Experimental del INTA del Delta del Paraná, Buenos Aires [34°13'12"S, 58°54'00"W]; **100.** Reserva Natural Otamendi, em proximidades del Río Luján, Buenos Aires [34°13'48"S, 58°53'24"W]; **103.** Alredores de Diego Gaynor, Buenos Aires [34°16'48"S, 59°13'48"W]; **104.** Partido de Campana, Los Cardales, Ruta 4, km 4.5, 4.5 km al oeste de al Panamericana, Buenos Aires [34°20'24"S, 58°59'24"W]; **106.** Islas de Tigre, Buenos Aires Argentina [34°25'12"S, 58°34'12"W], **109.** Luján, Buenos Aires [34°34'48"S, 59°06'36"W]; **113.** Guillermo Enrique, Hudson, Buenos Aires [34°47'24"S, 58°09'00"W]; **114.** Partido de Ensenada, Reserva Provincial Punta Lara, sobre el Camino Negro, Buenos Aires [34°47'24"S, 58°00'00"W]; **115.** La Toma, San Luis [35°03'00"S, 65°37'12"W]; **116.** Lobos, Arroyo Las Garzas, km 106, Buenos Aires [35°12'0.00"S, 59°6'0.00"W]; **117.** La Elenita, La Pampa [36°06'00"S, 65°48'00"W]; **118.** Loventué, La Pampa [36°10'48"S, 65°18'00"W]; **119.** Telén, La Pampa [36°16'12"S, 65°30'00"W]; **120.** Toay, La Pampa [36°40'12"S, 64°21'00"W]; **121.** Azul, Buenos Aires [36°46'48"S, 59°51'36"W]; **122.** Departamento Utracán, Chacharramendi, La Pampa [37°19'12"S, 65°39'00"W]; **123.** Departamento Lihue-Calel, Campo Aguas Blancas, aledaño al P.N. Lihue-Calel, La Pampa [38°01'12"S, 65°31'48"W]; **124-126.** Departamento Lihue-Calel, P.N. Lihue-Cahel, La Pampa [38°01'12"S, 65°31'48"W]; **127-129.** Sierra de la Ventana, Buenos Aires, [38°09'00"S, 61°48'00"W]; **130.** Bajada del Palo Neuquén Argentina [38°10'48"S, 68°21'36"W]; **131.** Puerto do Zárate, Establecimiento El Oasis (Alto Paraná), Arroyo Águila Negra y Carabelas, Buenos Aires [39°00'00"S, 62°48'00"W]; **132.** Departamento El Cuy, Estación Ingeniero Julián Romero, Río Negro [39°07'48"S, 66°46'48"W]; **133.** Junín de los Andes, Neuquén [39°57'00"S, 71°04'12"W]; **134.** Lago Lacar, San Martín de los Andes Neuquén [40°09'00"S, 71°28'12"W], **135.** Orillas del Río Negro, Buenos Aires [40°46'48"S, 63°00'00"W] (Type locality of *Felis geoffroyi*); **136.** Nahuel Huapi, Neuquén [41°01'12"S, 71°18'36"W]; **137.** Sierras de Paileman, Río Negro [41°09'00"S, 65°55'48"W]; **138.** Trelew, Rawson, Chubut [43°15'00"S, 65°18'00"W]; **139.** Lago Colhue Huapi, Sarmiento, Chubut [45°30'36"S, 68°59'24"W]; **140.** Pico Salamanca, Chubut [45°34'12"S, 67°20'24"W] (Type locality of *Oncifelis geoffroyi leucobapta*]; **141.** Pampa Maria Santísima, Santa Cruz [45°54'00"S, 69°12'00"W]; **142.** Lago San Martin, Rio Negro [48°58'48"S, 72°33'36"W]; **143.** Cañadon de las Vacas, Corpen Aike, Santa Cruz [49°34'12"S, 69°30'00"W].

Paraguay: **11.** Precise locality unknown (type locality of *Oncifelis geoffroyi paraguae;* Pocock (1940) did not give a precise locality where the specimen was collected).

Brazil: **24.** Candelária, Rio Grande do Sul [29°40'48"S, 52°48'00"W]; **26.** Cachoeira do Sul (entrada), BR 290, Rio Grande do Sul [30°02'24"S, 52°53'24"W]; **36.** Rodovia BR 470, km 475, Vila Mirim, Rio Grande, Rio Grande do Sul [30°51'00"S, 51°48'36"W]; **38.** Arambaré, Rio Grande do Sul [30°55'12"S, 51°30'00"W]; **43.** São Lourenço, Rio Grande do Sul [31°22'12"S, 51°58'48"W].

Uruguay: **29.** Arroyo Tres Cruces Grande, Artigas [30°16'48"S, 57°12'00"W]; **32.** Arroyo del tigre, 3 km aguas arriba de la barra com el Río Cuareim, Artigas [30°46'12"S, 56°07'12"W]; **33.** Arroyo Cuaró, Paso Campamento, Artigas [30°49'12"S, 56°40'48"W]; **34.** Arroyo Catalán Grande y Ruta 30, Artigas [30°50'24"S, 56°14'24"W]; **35.** Artigas [30°50'24"S, 56°14'24"W]; **37.** Punta del Arroyo Tres Cruces Chico, Artigas [30°51'00"S, 56°01'48"W]; **39.** Laureles, Tacuarembo [31°13'48"S, 56°04'48"W]; **40.** Rincón de la Vassoura, Laureles, Tacuarembó [31°15'36"S, 56°08'24"W]; **41.** Salto Grande, Salto [31°16'12"S, 57°51'36"W]; **42.** Bialet Massé, Córdoba [31°19'12"S, 64°28'12"W]; **44.** 40 km NW Tacuarembó, Tacuarembó [31°24'00"S, 56°10'12"W]; **45.** Sierra del Infiernillo Tacuarembó [31°24'00"S, 56°10'12"W]; **50.** Paysandu [32°09'36"S, 57°33'00"W]; **51.** 6 km SE Melo, Cerro Largo [32°22'12"S, 54°10'48"W]; **52.** Arroyo Negro, 15 km S. Paysandú, Rio Negro, [32°22'12"S, 58°03'00"W]; **53.** Paysandu [32°25'12"S, 58°09'00"W]; **54.** Río Negro 7 km aguas arriba del Río Taquarembó, Tacuarembó [32°25'48"S, 55°27'00"W]; **55.** Río Negro 7 km aguas arriba de la barra del Río Taquarembó, Durazno [32°25'48"S, 55°27'00"W]; **56.** km 329, Río Negro, Durazno [32°30'36"S, 55°22'48"W]; **57.** Barra del Arroyo Salsipuedes Grandes y Salsipuedes Chico, Tacuarembó [32°33'00"S, 56°33'00"W]; **59.** Rio Negro, ca. 15 km NNW San Jorge, Durazno [32°49'48"S, 55°52'48"W]; **60.** 16 km SSW Boca del Río Tacuari, Treinta y Tres [32°54'36"S, 53°22'12"W]; **61-62.** Bopieva, Río Uruguay, 10 km NW de Fray Bentos, Río Negro [33°00'00"S, 58°03'00"W] **64.** Arroyo Cololó, Soriano [33°06'00"S, 57°57'00"W]; **65.** Fray Bentos, Río Negro [33°06'36"S, 58°10'12"W]; **67.** Olimar Chico, Treinta y Tres [33°13'48"S, 54°31'12"W]; **68.** Rio Olimar Chico, 25 km W. SW., Treinta y Tres [33°13'48"S, 54°31'12"W]; **69.** Barra del Arroyo Caracoles Grande, 17 km SSO de Fray Bentos, Río Negro [33°16'12"S, 58°21'00"W]; **70-72.** Estancia Santa Elena, Arroyo Perdido, Soriano [33°22'48"S, 57°22'12"W]; **73.** Treinta y Tres [33°25'12"S, 54°25'48"W]; **74-75.** Río Negro frente a las islas Lobo y del Vizcaíno, Soriano [33°28'12"S, 58°22'12"W]; **76-77.** Barra de San Salvador, Soriano [33°28'12"S, 58°23'24"W]; **78.** Flores; Arroyo Poroeigis, 3 km W Paso de los Mudos [33°30'00"S, 56°48'00"W]; **79.** Proximidades de Palmitas, Soriano [33°31'12"S, 57°48'00"W]; **80.** Estancia Bella Vista, Lavalleja/Zapilau [33°31'48"S, 54°58'48"W]; **82.** Estancia La Central, Bocas del Perdido, Soriano [33°34'48"S, 57°16'48"W]; **85.** Estancia Arteaga, C. Copetón, Florida [33°46'48"S, 55°28'48"W]; **88.** Pirarajá, Río Cebollatí, Lavalleja [33°49'48"S, 54°46'48"W]; **91.** La Cruz, Florida [33°55'12"S, 56°14'24"W]; **93.** Gruta de Salamanca, Maldonado [33°58'48"S, 54°31'12"W]; **94.** Estancia San José, Conchillas, Colonia [34°09'00"S, 58°01'12"W]; **95.** Arroyo Tigre, Martim Chico, Colonia [34°09'36"S, 58°08'24"W]; **96.** Arroyo Limetas, Estancia San Jose, Colonia [34°09'36"S, 58°01'48"W]; **98.** Paso del Rey, San José [34°10'48"S, 56°51'00"W]; **101.** Santa Clara, Chamizo, San José [34°14'24"S, 55°55'12"W]; **102.** Isla Mala, Florida [34°15'00"S, 56°19'48"W]; **105.** Rocha, Uruguai [34°21'00"S, 53°54'00"W]; **107.** Arazatí San José Uruguai 34°27'00"S, 57°01'12"W; **108.** Zapicán, Lavalleja [34°31'12"S, 54°56'24"W]; **110.** Sierra de las Animas, Maldonado [34°40'48"S, 55°19'12"W]; **111.** Bañado Tropas Viejas, Atlántida, Canelones [34°43'12"S, 55°54'00"W]; **112.** Montevideo [34°46'48"S, 56°07'48"W].