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TAXONOMIC REVISION OF THE TIGRINA *LEOPARDUS TIGRINUS* (SCHREBER, 1775) SPECIES GROUP (CARNIVORA, FELIDAE)

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ABSTRACT

The tigrina *Leopardus tigrinus* (Schreber, 1775) is a small-sized Neotropical spotted cat found from northern Argentina and southern Brazil to Costa Rica. Four subspecies are traditionally recognized: *L. t. tigrinus* (Schreber, 1775) from northern Brazil, the Guianas and eastern Venezuela; *L. t. pardinoides* (Gray, 1867) from western Venezuela, Colombia, Ecuador and Peru; *L. t. guttulus* (Hensel, 1872) from southern Brazil, Paraguay and northern Argentina; and *L. t. oncellus* (Thomas, 1903) from Costa Rica. We studied external and craniodental morphology in quantitative and qualitative terms from 250 specimens in order to clarify the taxonomic status of tigrina. Based on the characters analyzed in this study, we recognize three diagnosable morphogroups, each with a distinct geographic distribution: northern/northwestern (samples from northern Brazil, the Guianas, Venezuela, Colombia, Ecuador, Peru, northwestern Argentina and Costa Rica), eastern (samples from northeastern and central Brazil), and southern (samples from southern Brazil, Paraguay and northeastern Argentina). Taking into account the morphologic evidence presented here, supported by biogeographic data and molecular studies available, we recognize three full species for tigrinas: *L. tigrinus* (including the putative subspecies *L. t. pardinoides* and *L. t. oncellus* as junior synonyms) for northern/northwestern/west group; *L. emiliae* (Thomas, 1914) for eastern group; and *L. guttulus* for southern group.

KEY-WORDS: *Leopardus tigrinus*; *L. guttulus*; *L. emiliae*; Subspecies; Morphological variation.

INTRODUCTION

The tigrina, oncilla, tiger cat or little spotted cat *Leopardus tigrinus* (Schreber, 1775) is a small-sized felid (1.8-3.8 kg) (Sunquist & Sunquist, 2002; Macdonald

et al., 2010) member of the “ocelot lineage”, a group that includes the small and medium-sized Neotropical spotted cats (Johnson & O’Brien, 1997; Johnson *et al.*, 1999; Mattern & MacLennan, 2000; Johnson *et al.*, 2006). It is found from Costa Rica to southern Brazil

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and northeastern Argentina (Cabrera, 1958; Nowak, 1999; Sunquist & Sunquist, 2002, 2009; Macdonald *et al.*, 2010; Nascimento, 2010), but in Central America it has been recorded only from Costa Rica and northern Panama, but not from the remainder of the Darien Peninsula connecting Central America to South America (Cabrera 1958, 1961; Nowell & Jackson, 1996; Sunquist & Sunquist, 2002, 2009). In the Amazon Basin its geographical distribution appears largely marginal (Oliveira, 2004), but the possible lack of records in this region may be either a sampling artifact, due to the low population density, or perhaps these animals may really not occur in this region (Nascimento, 2010).

The taxonomic history of the tigrina began with *Felis tigrina* by Schreber in 1775, who published an illustration based on the plate of Buffon (1765) named “Le Margay”, which in turn was based on an individual from Cayenne, French Guiana. Later, Schreber (1777) published the text with a description of the species. Ninety years later, Gray (1867a) described a new species, *Felis pardinooides*, with “India” as its type locality, but he subsequently changed his opinion and fixed “Bogotá” (in Colombia) as the new type locality of the species (Gray, 1874). Additionally, Hensel (1872) described *Felis guttula* from southern Brazil (state of Rio Grande do Sul), which was recognized as a subspecies of *F. tigrina* by subsequent authors (Cabrera, 1958, 1961; Wozencraft, 2005).

In the beginning of the 20th century, new species and subspecies of tigrinas were described, especially from Central America and northern South America: *Felis pardinooides oncilla* Thomas, 1903 (type locality: “Volcan de Irazu, Costa Rica”); *Felis pardinooides andina* Thomas, 1903 (type locality: “Jima, Province of Azuay, Ecuador”); *Felis carrikeri* Allen, 1904 (type locality: “Poza Azul, Costa Rica”); *Felis pardinooides emerita* Thomas, 1914 (type locality: “Montes de la Cutala, Merida, Venezuela”); *Margay tigrina elenae* Allen, 1915 (type locality: “Santa Elena, Colombia”); and *Margay caucensis* Allen, 1915 (type locality: “Las Pavas, Colombia”). Furthermore, Thomas (1903) recognized two species from southern Brazil, *Felis pardinooides* and *F. guttula*, but, according to Pocock (1917), these species were, in fact, respectively a female and a male of the same species. Thus, the name *Felis pardinooides* Thomas, 1903 is a junior homonym of *Felis pardinooides* Gray, 1867a, and also a junior synonym of *Felis guttula* Hensel, 1872. Years later, Thomas (1914) described *Felis emiliae* based on specimens from Brazil (“Ipu, Ceará”), which was classified in the “*F. guttula* group” (Thomas, 1914:348-349).

For a long time the names of the forms related to margays (*Leopardus wiedii*) and tigrinas (*L. tigrinus*) were confused with each other, owing to their similarity in size and coloration, and it created doubts regarding the exact identity of the animals that bear these names. Elliot (1877, 1883) placed as synonyms of *Felis tigrina* a series of names associated to margay (e.g., *Felis macroura* Wied, 1826; *Felis elegans* Lesson, 1830), guigna (e.g., *Felis guigna* Molina, 1782; *Felis (Noctifelis) guigna* Severtzov, 1858) and ocelots (e.g., *Felis mitis* F. Cuvier, 1820; *Felis chati* Gray in Griffith, 1827), and also placed *F. pardinooides* Gray, 1867a as synonym of Geoffroy’s cat *L. geoffroyi* (d’Orbigny & Gervais, 1844). This confusion was further increased by Allen (1919), which recognized two genera, *Margay* and *Oncilla*, to include the forms related to margays and tigrinas. In *Margay*, he included two species, *M. tigrina* Schreber, 1775 (= *L. tigrinus*), with three subspecies [*M. t. tigrina*, *M. t. wiedii* Schinz, 1821 (= *L. wiedii*) and *M. t. vicens* (= *L. wiedii*)], and *M. glaucula* (Thomas, 1903), which comprised two subspecies (*M. g. glaucula* and *M. g. nicaraguae*; both *L. wiedii*). In *Oncilla*, Allen recognized three species: *O. pardinooides*, which included five subspecies (*O. p. pardinooides*, *O. p. oncilla*, *O. p. andina*, *O. p. emerita* and *O. p. elenae*); *O. guttula*, with two subspecies (*O. g. guttula*, and *O. g. emiliae*); and *O. caucensis*. Years later, Weigel (1961) recognized all forms associated with *wiedii* together with *tigrina* Schreber, 1775, *i.e.*, she put all traditionally recognized *wiedii* subspecies into *tigrina* (*L. t. tigrinus*, *L. t. wiedii*, *L. t. bolivae*, *L. t. amazonicus*, *L. t. nicaraguae*, *L. t. salvinius*, *L. t. yucatanicus*, *L. t. glauculus*, *L. t. oaxacensis* and *L. t. cooperi*), while she allocated in *O. pardinooides* the other taxa traditionally recognized as subspecies of *F. tigrina* (*O. p. pardinooides*, *O. p. oncilla*, *O. p. guttula* and *O. p. emiliae*). However, Cabrera (1958, 1961) recognized only one species, *Felis (Leopardus) tigrina*, with four subspecies, three from South America – *F. (L.) t. tigrina* [includes *emiliae*] (from northeastern Brazil to eastern Venezuela), *F. (L.) t. pardinooides* [includes *andina*, *emerita*, *elenae* and *caucensis*] (western Venezuela, Colombia, Ecuador and Peru) and *F. (L.) t. guttula* (Eastern and southern Brazil, Paraguay and northern Argentina) – and another from Central America – *F. (L.) t. oncilla*. This taxonomic arrangement in four subspecies was widely followed by subsequent authors in the second half of the 20th century and the first decade of the 21st century (Hall & Kelson, 1959, Hall, 1981; Wozencraft, 2005). However, depending on the author, the species was placed either in *Leopardus* (Ewer, 1973; Leyhausen,

1979; Nowak, 1999; Wozencraft, 2005; Sunquist & Sunquist, 2009) or in *Oncifelis* (Hemmer, 1978; Wozencraft, 1993), either as full genera or as subgenera of *Felis*.

Molecular data, based on mtDNA, suggested the existence of two highly divergent phylogeographical groups, one from southern Brazil and the other from Central America, which have a long period of isolation (around 3.7 million of years ago) (Johnson *et al.* 1999), and this divergence is comparable to the differences observed between Geoffroy's cat *Leopardus geoffroyi* (d'Orbigny & Gervais, 1844) and guigna *Leopardus guigna* (Molina, 1782) or between ocelot *Leopardus pardalis* (Linnaeus, 1758) and margay *L. wiedii* (Schinz, 1821) (Johnson *et al.* 1999). Furthermore, Leyhausen & Falkena (1966) previously found that certain subspecies of *L. tigrinus* did not mate with each other in captivity, which led them to suggest that this taxon could consist of two or more distinct species. Trigo *et al.* (2013) reaffirmed the taxonomic status of *L. guttulus* as a full species, which was previously revalidated by Nascimento (2010) based on morphology. This molecular study also showed no evidence of gene flow between the southern population (*L. guttulus*) and the northeastern Brazilian population (named in the article as *L. tigrinus*), which have contiguous geographical distributions. Although these two closely related species do not interbreed, there are reports of hybridization between *L. guttulus* and *L. geoffroyi* in the state of Rio Grande do Sul, southern Brazil (Eizirik *et al.*, 2006; Trigo *et al.*, 2008, 2013, 2014), and with *Leopardus braccatus* (named in the article as *Leopardus colocolo*) in Central Brazil (Trigo *et al.*, 2008, 2013, 2014). In a recent molecular study, Li *et al.* (2016) reported that the tigrinas from Northeastern Brazil had pampas cat mtDNA within a tigrina nDNA background, as well as nuclear signatures indicating an ancient hybridization with *L. geoffroyi*. On Central American tigrinas, the results of these authors gave more support for high genetic divergence between these tigrinas and those from Brazil, showing 0.5%-0.6% of mitochondrial divergence and 11.0%-15.3% of nuclear divergence. However, Li *et al.*'s study did not include specimens from northern South America.

It is clear that the identification and delimitation of species and subspecies are main issues concerning the taxonomy of the tigrinas, and have not been subject to critical analysis. In order to clarify the taxonomy of *L. tigrinus*, our goals are: (1) to characterize and define the taxa on morphologic and morphometric terms, and to describe their variation; (2) to define their geographical distribution; and

(3) to provide a synonymy and attribute valid names for the recognized taxa.

MATERIAL AND METHODS

Samples and collections

We obtained quantitative and qualitative data from skins and skulls of *L. tigrinus* group specimens (n = 250) housed 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, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Biologia Professor Mello Leitão, Santa Teresa, Brazil (MBML), Museu de História Natural Capão da Imbuia, Curitiba, Brazil (MHNCI); Coleção de Mamíferos do Departamento de Sistemática e Ecologia da Universidade Federal da Paraíba, João Pessoa, Brazil (UFPB); Coleção de Mamíferos do Departamento de Zoologia da Universidade Federal de Pernambuco, Recife, Brazil (UFPE); Coleção de Mamíferos do Departamento de Zoologia da Universidade Federal de Mato Grosso, Cuiabá, Brazil (UFMT); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN); Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz, Bolivia (MNK); Museo de Historia Natural Javier Prado, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Museo do Instituto de Ciências Biológicas de la Escuela Politécnica Nacional, Quito, Ecuador (MEPN); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH); Museo de la Estación Biológica Rancho Grande, Maracay, Venezuela (EBRG); American Museum of Natural History, New York, USA (AMNH); Field Museum of Natural History, Chicago, USA (FMNH); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); Naturhistorisches Museum Wien, Vienna, Austria (NMW); Zoologisches Museum Berlin (= Museum für Naturkunde), Berlin, Germany (ZMB); and Naturhistoriska Riksmuseet, Stockholm, Sweden (NRM). We also examined photographs of the specimens deposited in Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Natural History Museum, London, United Kingdom (NHM); and Naturalis Biodiversity Center, Leiden, Netherlands (RMNH). The list of the specimens studied is provided in the Appendix I.

Geographic data

Geographical distribution of each taxon was accessed through the collection locations obtained on the labels of the specimens. Coordinates are the most accurate as possible and were obtained directly from the labels when available, from published gazetteers (Paynter Jr., 1982, 1989, 1995, 1997; Stephens & Traylor Jr., 1983, 1985; Paynter Jr. & Traylor Jr., 1991; Vanzolini & Traylor Jr., 1992) or online databases (Global Gazetteer 2.3, www.fallingrain.com/world/index.html; GeoNames, www.geonames.org). In some cases, the exact locality was not available or not found in the methodologies employed, so we used the coordinates of the nearest country. The gazetteers, ordered alphabetically by country, state or province, and collection locality, are provided in the Appendix II.

Analysis of characters

All specimens were examined in qualitative and quantitative terms based on external and cranial features regardless of the previously attributed name of the taxon.

The external qualitative characters are the color and spots pattern of the pelage of the head, body, fore limbs, hind limbs and tail. The quantitative external characters are the measurements taken from the specimen's labels 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

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

The craniodental qualitative characters are based on García-Perea (1994), Yamaguchi *et al.* (2004) and Nascimento (2010, 2014). The quantitative craniodental characters comprised 19 craniodental dimensions from adults of both sexes (Fig. 1): (1) GLS: greatest length of the skull; (2) CBL: condylobasal length; (3) RL: rostral length; (4) IOB: interorbital length; (5) POB: postorbital breadth; (6) ZB: zygomatic breadth; (7) GBB: greatest breadth of braincase; (8) IFB: breadth between the infraorbital foramina; (9) GPB: greatest palatal breadth; (10) GPL: greatest palatal length; (11) CM1L: C-M1 length; (12) P4L: greatest length of P4; (13) P4B: greatest breadth of P4; (14) TH: temporal fossa height; (15) ALT: anteroposterior length of temporal fossa; (16) ALM: anteroposterior length of masseter scar on skull; (17) p3m1L: p3-m1 length; (18) MH: mandible height; and (19) ML: mandible length. All craniodental measurements were taken with digital calipers to nearest 0.01 mm.

We defined the age classes based on dental morphology (sequence of emergence; replacement of deciduous teeth by permanent ones; tooth wear) and fusion of the cranial sutures (especially the speno-occipital suture) (Ximenez, 1974; García-Perea, 2002) and consequently seven classes were recognized: (1) age class I or juvenile I (deciduous teeth starting to emerge and speno-occipital suture does not fused); (2) age class II or juvenile II (deciduous teeth totally emerged and speno-

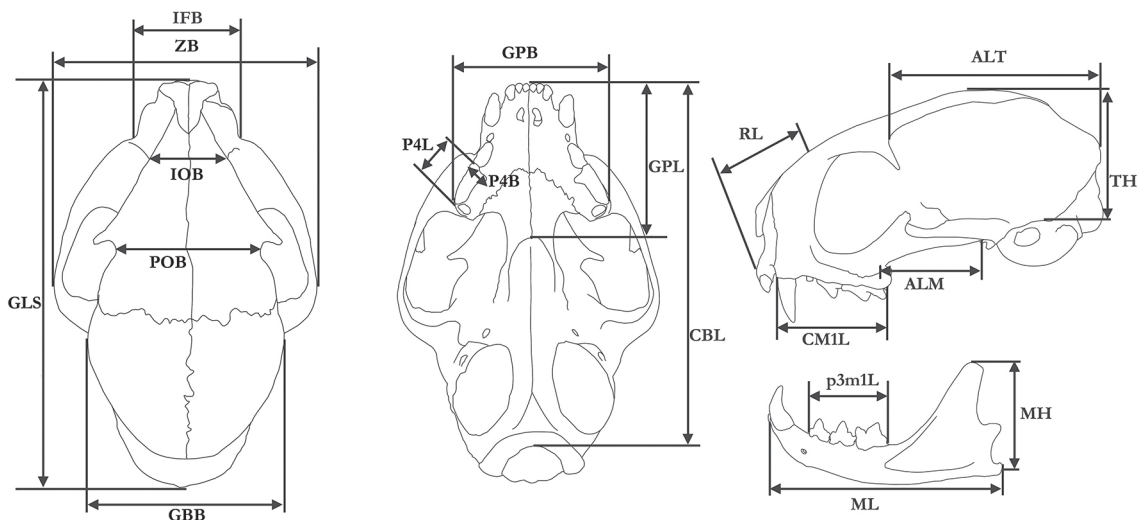


FIGURE 1: Dorsal, ventral and lateral view of skull and lateral view of mandible of an tigrina (*L. tigrinus*), showing 19 craniometrical variables used in the study. The abbreviations assigned to craniometrical variables correspond to those mentioned in the “Materials and methods” section of the text. Image: Guilherme S.T. Garbino.

occipital suture does not fused); (3) age class III or juvenile III (deciduous teeth being replaced by permanent ones and speno-occipital suture does not fused); (4) age class IV or young adult (permanent teeth totally emerged and speno-occipital suture does not fused); (5) age class V or adult I (permanent teeth with no or very little wear and speno-occipital suture fused); (6) age class VI or adult II (permanent teeth with moderate wear and speno-occipital suture fused); and (7) age class VII or adult III (permanent teeth with excessive wear and speno-occipital suture fused). We used only young adults and adults in our analyses.

Statistical analyses

The Kolmogorov-Smirnov test was applied for all craniodental variables. When the craniodental variables were normally distributed, we performed Hotelling's T^2 to evaluate the existence of sexual dimorphism and to check whether the differences were statistically significant ($p < 0.05$). For the multivariate analyses all craniodental variables were \log_{10} transformed. Principal Component Analysis (PCA) was extracted from the correlation matrix and it applied as an exploratory tool for investigating the patterns of variation among the groups, as well as to evaluate the degree of separation among them. Only principal components with eigenvalues greater than 1 were extracted. We performed the Discriminant Function Analysis (DFA) to investigate whether the groups of *L. tigrinus* studied could be distinguished based on craniodental morphology and also to construct a predictive pattern of different group memberships. All statistical analyses were performed with SPSS 17.0 software and missing values were estimated using Amelia package (Honaker *et al.*, 2011) of R software (R Core Team, 2013).

RESULTS

Geographic distribution of samples and definition of morphogroups

The geographic distribution of samples is found in Fig. 2. Based on the combinations of external characters (ground color of the body, and size, shape and arrangement of the rosettes on the sides of the body), we recognized three diagnosable morphogroups, each with a distinct geographic distribution (Figs. 3 and 4):

Morphogroup I: specimens from northern, northwestern and western South America (Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname, northern Brazil, northwestern Argentina, and Costa Rica), which are characterized by dark brown and orangish brown to yellowish brown and grayish brown ground color, white or light gray venter, and medium-sized rosettes on the sides of the body forming medium-sized oblique bands arranged in scapular-inguinal direction.

Morphogroup II: specimens from eastern South America (northeastern and central Brazil), which have overall color ranging from light yellowish brown to pale yellow or pale grayish buff, presence of small sized rosettes that rarely form small-sized oblique bands, the rosettes have thin and discontinuous black rims, and white, very light gray or slightly yellowish venter, with medium and small-sized dark spots.

Morphogroup III: specimens from southern and southeastern South America (southern Brazil, Paraguay and northeastern Argentina). Overall ground color dark yellowish brown, lighter on the sides of the body, white or light gray venter, and small rosettes on the sides of the body.

Data analyses

Statistical analyses were based on the morphogroups previously recognized. The descriptive statistics of the skull and external morphology (mean, standard deviation, minimum and maximum values, and number of specimens) are available in Tables 1 and 2. The Hotelling's T^2 test yielded a p value close to our threshold to reject the null hypothesis (T^2 : 1.742; $p = 0.056$), nevertheless we decided to combined in subsequent analyses males, females, and unknown sex specimens.

For PCA and DFA we select only specimens that have both skull and skin in order to test whether skin morphogroups also separate in the cranial morphospace. A total of 93 specimens were selected for PCA and DFA: 31 for morphogroup I, seven for morphogroup II and 55 for morphogroup III. The four first principal components resulting from the PCA (Table 3) are respectively responsible for 53.84, 10.87, 6.72 and 6.70 of variance (78.14% of total variance). The first principal component (PC1) is usually interpreted as a component associated to the overall size of skull (Jolicœur & Mosimann, 1960; Gotelli & Ellison, 2004), and in our results it

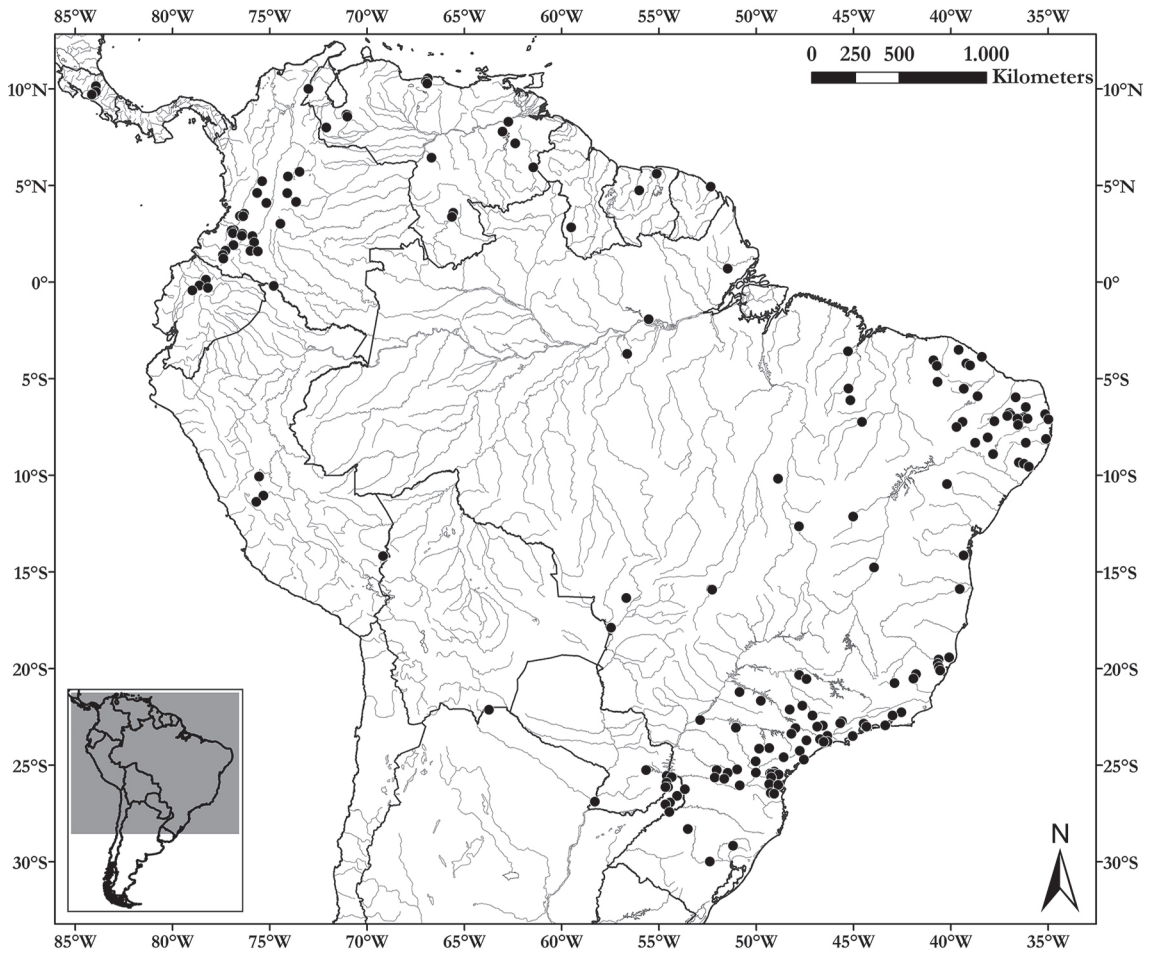


FIGURE 2: Distribution of the specimens of tigrinas (*L. tigrinus* group) studied. Black dots correspond to the specimens from scientific collections.

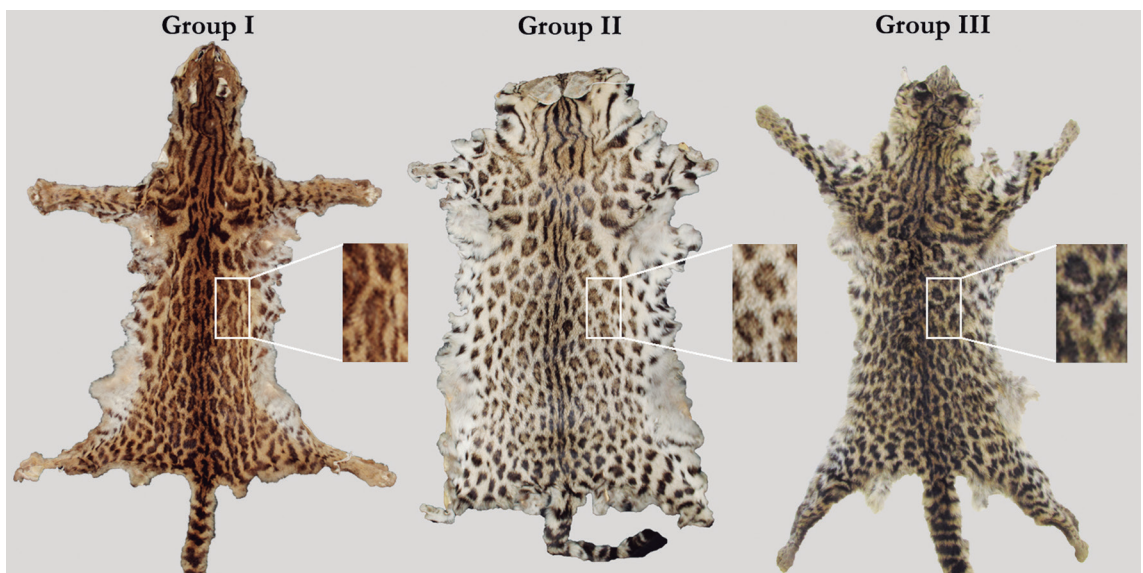


FIGURE 3: External characters of the three diagnosable and geographically distinct morphogroups of tigrinas recognized in this study. Left: IAVH1781 (Coper, Boyacá, Colombia); middle: UFPB6267 (Sítio Corea, Várzea, Paraíba, Brazil); right: MZUSP24234 (Dourado, São Paulo, Brazil). Note the difference in the ground color and the shape and arrangement of rosettes among morphogroups. For color figure, see online version.

showed positive signals for all coefficients, indicating a positive correlation to each other. The greatest coefficient (loadings) is associated to the variable GLS, the dominant craniodental measurement of PC1, followed in decreasing order by ZB, ML, GPL, CM1L, IFB, MH, ALT, GPB, RL, p3m1L, IOB, HT, GBB, CBL, P4L, P4B, and POB. In the second principal component (PC2), which is usually related to shape (Gotelli & Ellison, 2004), the greatest coefficient is P4B, followed in decreasing order by P4L, p3m1L, GPB, IOB, ML, GLS, GBB, RL, ALT, ZB, CBL, HT, POB, MH, GPL, IFB, and CM1L.

Regarding to the third component (PC3), the greatest coefficient in decreasing order are HT, GBB, ALT, CM1L, POB, p3m1L, CBL, P4L, ML, RL, MH, GPL, IOB, ZB, P4B, GLS, IFB, and GPB, while in the fourth component are POB, CBL, IOB, RL, GBB, P4B, GLS, IFB, GPL, HT, ML, GPB, CM1L, MH, ALT, ZB, P4L, and p3m1L. In PC1 and PC2 plot (Fig. 5) all specimens of three morphogroups are widely mixed, but specimens of morphogroup II tend to show higher values on the PC2 than the other morphogroups. Other plots (first and third principal components, first and fourth components, second and

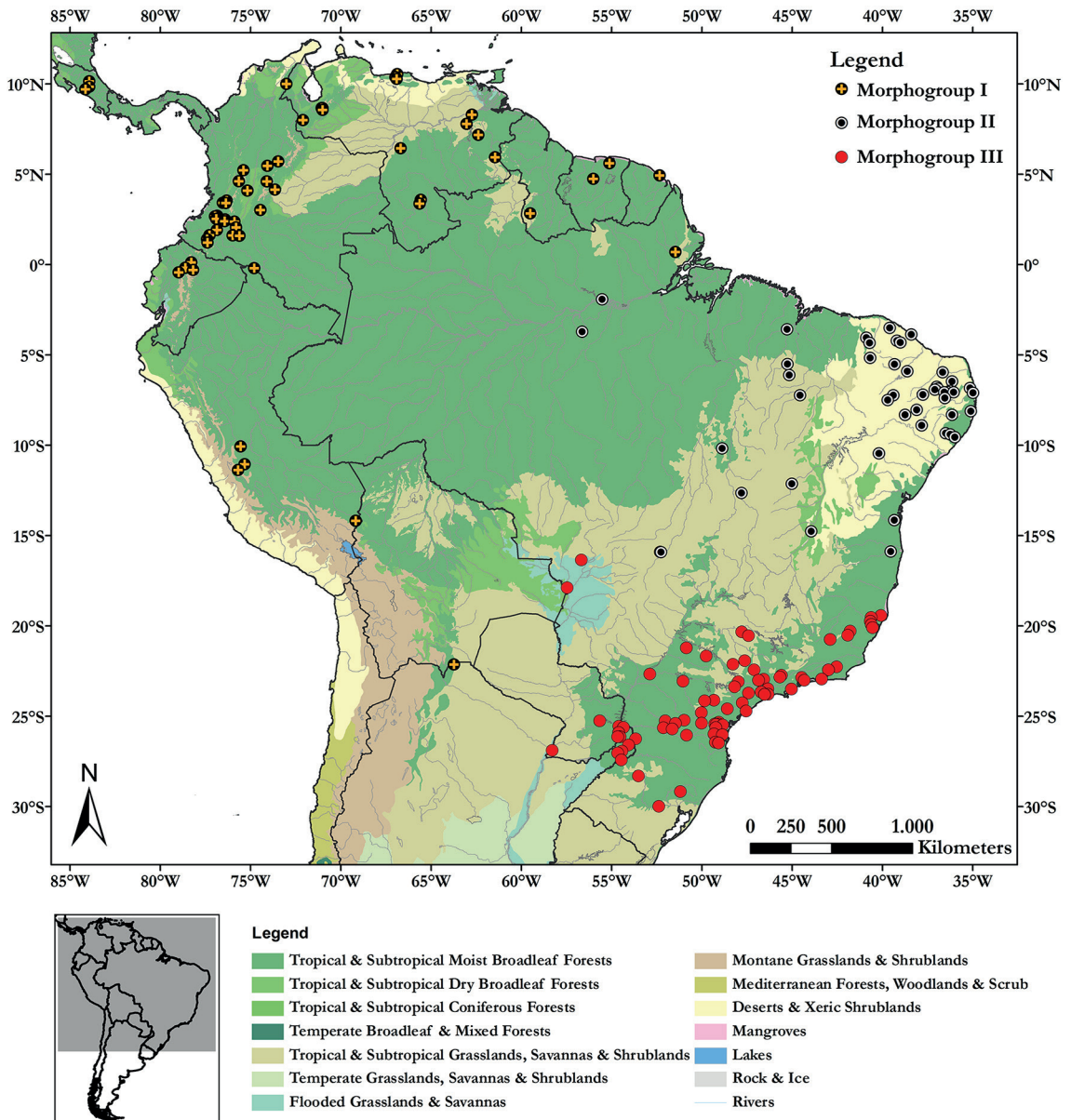


FIGURE 4: Distribution of morphogroups of tigrinas (*L. tigrinus* group) over the biomes of South America and part of Central America (data obtained from WWF – World Wide Fund for Nature). For color figure, see online version.

TABLE 1: Descriptive statistics of the craniodental variables (in millimeters) for the morphogroups of tigrinas. $\frac{M \pm SD(N)}{MIN - MAX}$.

Variables	Morphogroup I	Morphogroup II	Morphogroup III
GLS	86.59 ± 3.72 (31) 80.82-95.56	84.07 ± 4.11 (7) 78.09-89.28	86.02 ± 3.71 (55) 78.15-94.68
CBL	77.67 ± 5.15 (31) 69.13-87.31	76.9 ± 3.43 (7) 70.87-80.53	80.75 ± 3.64 (55) 70.81-87.77
RL	29.64 ± 1.95 (31) 25.87-32.9	28.42 ± 2.35 (7) 26.02-32.64	28.47 ± 1.77 (55) 24.58-32.61
IOB	15.72 ± 0.86 (31) 14.35-17.27	14.72 ± 1.08 (7) 12.83-16	15.09 ± 0.9 (55) 12.96-16.9
POB	28.46 ± 1.57 (31) 25.32-31.17	28.61 ± 1.4 (7) 26.3-30.54	27.39 ± 1.53 (55) 23.81-31.74
ZB	55.14 ± 3.41 (31) 48.9-61.56	54.68 ± 2.96 (7) 50.61-58.73	54.11 ± 2.92 (55) 48.86-63.03
GBB	38.93 ± 1.06 (31) 36.85-40.64	40.6 ± 2.01 (7) 37.15-43.23	40.18 ± 1.67 (55) 36.46-43.88
IFB	21.31 ± 0.94 (31) 19.27-22.89	21.07 ± 1.34 (7) 19.8-23.35	20.85 ± 1.14 (55) 18.85-23.48
GPB	30.54 ± 1.42 (31) 27.08-33.55	31.9 ± 1.77 (7) 29.71-35.46	31.09 ± 1.41 (55) 28.52-34.79
GPL	31.54 ± 1.72 (31) 28.13-35.68	31.28 ± 2.11 (7) 27.95-34.37	31.14 ± 1.82 (55) 27.19-34.66
CM1L	25.2 ± 1.05 (31) 23.15-27.83	24.52 ± 1.39 (7) 22.98-26.73	25.01 ± 1.14 (55) 22.72-27.85
P4L	9.92 ± 0.63 (31) 8.04-10.93	10.2 ± 0.69 (7) 8.99-10.94	9.91 ± 0.59 (55) 8.5-11.31
P4B	4.7 ± 0.48 (31) 3.97-5.52	5.13 ± 0.46 (7) 4.4-5.53	4.58 ± 0.39 (55) 3.85-5.53
HT	34.62 ± 1.51 (31) 32.43-38.62	36.44 ± 2.00 (7) 34.03-39.04	35.49 ± 1.73 (55) 31.82-39.66
ALT	52.03 ± 2.64 (31) 46.25-56.41	51.93 ± 3.74 (7) 47.11-57.49	51.39 ± 3.03 (55) 44.76-59.65
ALM	25.04 ± 2.82 (31) 21.16-32.67	23.24 ± 2.69 (7) 19.68-27.91	24.54 ± 1.98 (55) 20.29-30.9
p3m1L	18.65 ± 0.82 (31) 17.06-20.61	18.98 ± 1.15 (7) 17.52-20.63	18.8 ± 0.83 (55) 17.1-20.75
MH	23.13 ± 1.72 (31) 20.82-27.39	23.91 ± 1.69 (7) 21.85-26.46	22.44 ± 1.64 (55) 19.1-25.95
ML	55.36 ± 2.97 (31) 49.71-62.45	52.99 ± 2.88 (7) 49.54-57.38	52.82 ± 2.76 (55) 47.32-59.51

Legends: M = mean; SD = standard deviation; MIN = minimum; MAX = maximum; and N = number of specimens.

third components, second and fourth components, and third and fourth components) are not graphically represented, but they showed mixed pattern among the three morphogroups.

The DFA created two canonical variables from the original craniodental variables used in the analysis (Table 4, Fig. 6). The first function, which is responsible for 88.25% of the total variance, was explained by variables ML, HT, CBL, POB, GPB and CM1L, which have the highest coefficients in descending order, and the three morphogroups are separated along its axis. The second function, which is responsible for 11.75% of the total variance, the

TABLE 2: Descriptive statistics of the external measurements (in millimeters) and body mass (in grams) for the morphogroups of tigrinas. $\frac{M \pm SD(N)}{MIN - MAX}$.

Variables	Morphogroup I	Morphogroup II	Morphogroup III
TL	782.92 ± 62.85 (12) 697-901	753.00 ± 46.34 (9) 680-800	740.54 ± 50.57 (24) 628-840
HB	496.67 ± 33.15 (12) 452-556	464.33 ± 35.99 (9) 415-510	472.65 ± 39.82 (24) 365-539
T	286.25 ± 35.14 (12) 240-345	288.67 ± 17.42 (9) 260-320	263.57 ± 23.64 (24) 228-350
HF	112.00 ± 19.11 (12) 96-165	110.25 ± 4.33 (9) 105-116	108.26 ± 7.72 (22) 90-120
E	40.40 ± 4.86 (12) 30-45	45.25 ± 4.89 (9) 37-52	42.40 ± 6.61 (24) 24-52
BM (g)	2450 (1)	1924 ± 899.52 (8) 1270-3500	2378.64 ± 912.19 (24) 1030-4600

Legends: TL = Total length; HB = head and body length; T = tail length; HF = hind foot length; E = ear length; B = body mass; M = mean; SD = standard deviation; MIN = minimum; MAX = maximum; and N = number of specimens.

TABLE 3: Factor loadings, eigenvalues and percentage of variance of Principal Component Analysis (PCA) for morphogroups of tigrinas using 19 craniodental variables.

Variables	Component			
	1	2	3	4
GLS	0.887	-0.301	-0.039	-0.192
CBL	0.574	-0.166	-0.242	-0.586
RL	0.736	-0.270	-0.128	0.280
IOB	0.678	-0.376	-0.110	0.420
POB	0.301	0.107	0.261	0.616
ZB	0.880	-0.225	0.073	0.020
GBB	0.580	0.273	0.543	-0.268
IFB	0.855	-0.018	-0.029	0.172
GPB	0.748	0.380	-0.009	-0.064
GPL	0.871	-0.063	-0.122	-0.150
CM1L	0.862	0.012	-0.272	-0.050
P4L	0.568	0.639	-0.237	0.013
P4B	0.508	0.681	-0.073	0.200
HT	0.644	0.119	0.635	-0.108
ALT	0.787	-0.251	0.301	-0.027
p3m1L	0.689	0.527	-0.254	-0.012
MH	0.852	-0.079	0.125	-0.045
ML	0.875	-0.324	-0.170	0.083
Eigenvalues	9.693	1.956	1.210	1.207
Variance (%)	53.847	10.868	6.723	6.705

variables that most explained the variation were MH, GLS, CM1L, GPB, IOB and ALT, and along the axis the sample was separated into two major morphogroups, one composed by morphogroup II and the other consisting by the morphogroups I and III, which overlapped each other (Fig. 6). The predict group membership (Table 5) shows that 97.8% of original grouped cases were correctly classified,

TABLE 4: Function loadings, eigenvalues, percentage of variance, canonical correlation and Wilks' Lambda of Discriminant Function Analysis (DFA) for morphogroups of tigrinas using 18 craniodental variables.

Variables	Function	
	1	2
GLS	0.197	-1.011
CBL	-0.980	0.249
RL	0.068	0.150
IOB	-0.392	-0.474
POB	0.767	0.347
ZB	0.033	-0.130
GBB	-0.452	0.097
IFB	0.634	-0.013
GPB	-0.724	0.530
GPL	-0.116	0.076
CM1L	-0.654	-0.837
P4L	0.567	-0.194
P4B	0.471	0.428
HT	-1.117	-0.157
ALT	0.206	0.432
p3m1L	-0.633	-0.031
MH	0.393	1.080
ML	1.798	-0.048
Eigenvalues	4.414	0.588
Variance (%)	88.25	11.75
Canonical Correlation	0.903	0.608
Wilks' Lambda	0.000	0.003

with 96.77% (N = 30) of morphogroup I, 85.71% (N = 6) of morphogroup II and 100% (N = 55) of morphogroup III correctly classified. Regarding to cross-validated membership, 84.9% of grouped cases

were correctly classified, with 87.10% (N = 27) of morphogroup I, 57.14% (N = 4) of morphogroup II and 87.27% (N = 48) of morphogroup III correctly classified (Table 5).

TAXONOMIC ASSESSMENT

Under this scenario, we postulate two hypotheses to explain the morphometric variation present in *L. tigrinus* in South America, either all three morphogroups are valid subspecies from one widely distributed species; or each morphogroup are valid monotypic species.

Different species and subspecies concepts have been proposed over the years, creating an endless discussion among biologists, especially the systematics. We will not discuss here the different concepts of these two taxonomic ranks and their applicability, which is a vast subject and can be found in more detail elsewhere (e.g., Simpson, 1961; Mayr, 1963, 1970; Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Cracraft, 1983; Wilkins, 2009). Regardless the theoretical concepts involved in practice, the morphological differences are always fundamental to empirically recognize and define species and subspecies (Mayr, 1942). Therefore, our study is based on searching for consistent morphological and geographical patterns. The recognition of species-group taxa involves the study of the characteristics of the specimens in terms of their individual, sexual, population and geographic variation (de Vivo, 1991).

TABLE 5: Classification matrix for morphogroups of tigrinas obtained by Discriminant Function Analysis concerning the probabilities of classifying each morphogroup correctly into one of morphogroup.

	Groups	Classification Results ^{b,c}			Total	
		Predicted Group Membership				
		I	II	III		
Original	Count	I	30	1	0	31
		II	0	6	1	7
		III	0	0	55	55
	%	I	96.77	3.23	0	100
		II	0	85.71	14.29	100
		III	0	0	100	100
Cross-validated^a	Count	I	27	4	0	31
		II	1	4	2	7
		III	3	4	48	55
	%	I	87.10	12.90	0	100
		II	14.29	57.14	28.57	100
		III	5.45	7.27	87.27	100

^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 97.8% of original grouped cases correctly classified.

^c 84.9% of cross-validated grouped cases correctly classified.

Thus, we interpret as evidence of the existence of different taxonomic entities when the variation was not ontogenetic, sexual or individual. As a result we consider as valid taxa, populations who share unique characters in common, including the variation, and which differ from the other also in the geographic attributes.

Subspecies, on the other hand, represent geographical subdivisions of the species and are described mainly based on differences in measurements or difference in the tones of general coloration (Mayr 1942; Bonvicino *et al.* 1989; Burbrink *et al.* 2000; Helgen *et al.*, 2013). The recognition of subspecies was historically based on one or few specimens (*e.g.*, Pocock, 1939, 1940, 1941a, 1941b, 1941c; Goldman, 1946; Kitchener & Yamaguchi, 2010), however, studies have demonstrate that to the properly recognition and description of it, a set of characters throughout the range of the species should be carefully evaluated (Mayr, 1942; Burbrink *et al.*, 2000; Helgen *et al.*, 2013), which has never been done for tigrinas until the present study.

All 80 skins from southern Brazil, Paraguay and northeastern Argentina specimens (= morphogroup III) analyzed have a unique pattern

of rosettes characterized by small dark rosettes with a thick and continuum black borders on the body sides that rarely coalescing into small oblique bands. While the 59 skins from northeast and central Brazil (= morphogroup II) have paler ground color, and smaller and lighter rosettes with a thinner and discontinuous borders. In contrast, the 59 skins from northern, northwestern and western South America (= morphogroup I) have larger rosettes with a thicker dark border coalescing into small to medium oblique bands on the sides of the body (Fig. 3). These three distinct patterns have no overlapping with each other, even in close sites as exemplified by the records at south Bahia for morphogroup II (locality 45 of the Fig. 11) and north of Espírito Santo for morphogroup III (locality 2 of the Fig. 16) distant 400 km. In the multivariate space, the cranial measurements of our three skin-groups are also supported with a clear separation (Fig. 6).

Trigo *et al.* (2013) found that population of Northeastern Brazil of *L. tigrinus* (= our morphogroup II) has a genetic distinctiveness in relation to the southeastern population (= our morphogroup III) similar to those found between well-established *Leopardus* species (*e.g.*, *L. geoffroyi* and

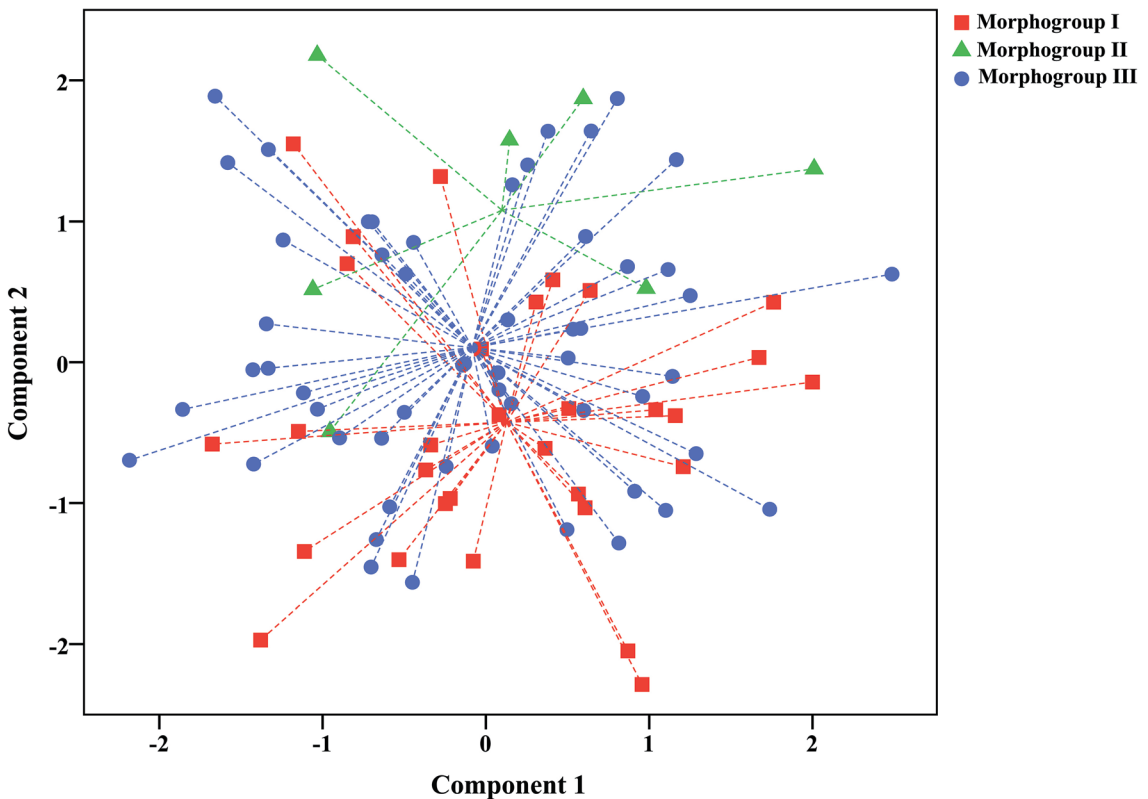


FIGURE 5: Distribution of the factorial scores in the first and second principal components of the craniometrical variables of geographic morphogroups of tigrinas. For color figure, see online version.

L. colocolo). This, in combination with the absence of allele at that X-linked and Y-linked markers shared between those populations, indicates no gene flow, which supports the recognition of two valid species (Trigo *et al.*, 2013). On the other side, Johnson *et al.* (1999), based in mitochondrial genes, found two highly divergent clades of tigrina group, one from Central America (= our morphogroup I) and other from southern Brazil (= our morphogroup III), which is comparable to the differences observed between *L. geoffroyi* and *L. guigna*, and between *Leopardus pardalis* and *L. wiedii* (Johnson *et al.* 1999).

Therefore, taking into account the morphological (external and cranial) argument, in combination with a distinct geographic pattern and the available genetic evidence (Johnson *et al.*, 1999; Trigo *et al.*, 2013), we hypothesized that each of our morphogroups are three distinct species and propose a new taxonomic arrangement.

Morphogroup I: Oldest available name is *Leopardus tigrinus* (Schreber, 1775).

Morphogroup II: *Leopardus emiliae* (Thomas, 1914) – traditionally recognized as junior synonym of *L. t. tigrinus*, includes part of this putative subspecies (the population from north, northeast and central Brazil).

Morphogroup III: *Leopardus guttulus* (Hensel, 1872) – this taxon was traditionally recognized as a subspecies of *L. tigrinus*, but our results suggest that it is a full species, in accordance with Nascimento (2010) and Trigo *et al.* (2013).

SPECIES ACCOUNT

The species of *L. tigrinus* group share many craniodental characters, and to avoid repetition in the each species account, we list below the general description of the features observed in the skull and skin of these species. After, we provide the list of synonyms, type locality, type material, diagnosis, body measurements, geographic distribution, variation and taxonomic notes of each species of tigrina

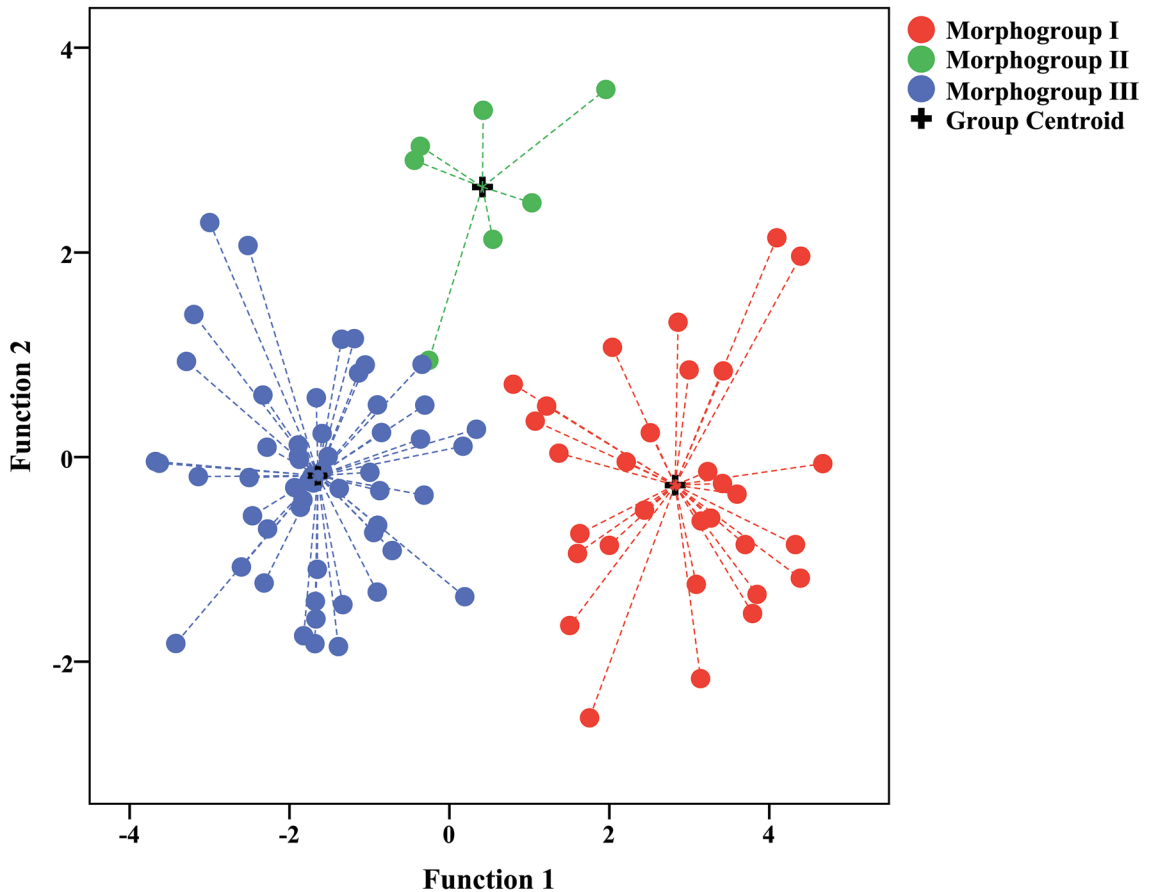


FIGURE 6: Distribution of the factorial scores in the first and second discriminant functions of the craniometrical variables of geographic morphogroups of tigrinas. For color figure, see online version.

here recognized. The list of specimens examined and list of localities (*gazetteer*) are provided in the Appendixes I and II, respectively.

General Description

External morphology: Small-sized cats, length of head and body between 365 and 556 mm, tail length between 228 and 350 mm, hind foot length between 90 and 165 mm, ears between 24 and 52 mm and the body mass between 1,030 and 4,600 g (Table 2). The overall ground color of the head varies from dark brown to light yellowish brown or grayish brown in *L. tigrinus*, from light yellowish brown to pale yellow and grayish yellow in *L. emiliae*, and from dark yellowish brown to ochraceous buff in *L. guttulus*. The lips, chin, cheek and throat are white, light gray or light cream. In the cheeks there are two black or very dark brown genal stripes crossing in parallel in longitudinal direction. A transversal stripe is present in the region of the posterior end of the genal stripes. The supraorbital spots or narrow stripes are present on each side of the head and they are arranged in a longitudinal direction. Sometimes these supraorbital spots or stripes can connect to form frontal-parietal stripes. Numerous, small, rounded or elliptical spots are present in the top of the head, between these frontal-parietal stripes. Four or 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 nape are facing backward. The ears are round shape with dorsal surface black, except the base, which has the same color of the rest of the head. A white spot is centrally disposed in the dark region of the dorsal surface of the ear. The overall coloration of the body – especially in the dorsum, the dorsal surface of the limbs, the space inside the rosettes and bands – is the same that present in the head and neck, but on the sides of the body the coloration becomes lighter towards the venter. Rounded and/or elliptical spots may be separated or interconnected forming more or less longitudinal rows in the dorsum, while the interscapular region shows high individual variation in the spot pattern. Solid spots and rosettes are present on the sides of the body, and the rosettes coalesce to form small and/or medium-sized oblique bands arranged in scapular-inguinal direction in *L. tigrinus*, rarely coalesce in *L. guttulus*, or not coalesce in *L. emiliae*. As solid spots, the rosettes and bands have black or very dark brown rims, and inside them the coloration is darker than that found in the spaces

between adjacent rosettes and bands, either showing a similar tone found in the dorsum or almost similar to the color of the rims. The venter is white, very light gray or slightly yellowish with small and medium-sized rounded spots. The hairs on 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. The dorsal surface of the limbs has the same color pattern present in the dorsum, showing medium-sized rosettes and spots in the proximal region and only smaller spots in the distal region, whereas the ventral surface of the limbs has similar coloration of the venter and shows small and medium-sized spots. The hairs of limbs are short and slightly harsh. The tail is long, relatively thick, representing almost 60% of the length of head and body. Black or very dark brown rings alternate with rings of the same color of the dorsum. The tip of the tail is dark. The most basal portion of the tail may have spots and/or rosettes in some specimens.

Craniodentary morphology: Broad and short rostrum, corresponding to between 30% and 40% of the greatest length of skull. The nasals are broad distally, and narrow shortly thereafter to converge at the posterior end, where they articulate with the frontal, may or may not be a depression in this region. If the depression is present, it may be shallow or deep. The anterior margin of the nasals is curved. 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. 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 postorbital 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 interorbital region is narrow with width in proportion to greatest length of skull between 15% and 20%. 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. The upper postorbital process is long and narrow, with a triangular shape. In lateral view, the skull has a slightly convex profile in the frontal region, providing a less evident curvature. The braincase is large and oval, with the proportion of its width in relation to greatest length

of skull varying between 40% and 50%. The sagittal crest is absent or is a very low and short line restricted to the interparietal region. Temporal lines are present and lyriform. The lambdoidal crest may be present and slightly developed. The length and the width of palate have approximately the same dimensions. The notch of postpalatine vein is broad and comparatively shallow in most of specimens and the posterior margin of the palate (= anterior margin of mesopterygoid fossa) has a U-shaped edge and it may or not have a medial notch, which can be shallow or deep. The presphenoid is centrally located in the mesopterygoid fossa and is narrow, very elongated and arranged longitudinally, showing lateral 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 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 little expanded laterally, and the average width of the braincase relative to zygomatic width is 70% to 80%. The occipital region has rounded margin, giving this region of the skull a shape similar to a semicircle. 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. The mandible is well developed and the horizontal ramus is low. 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. Narrow and long upper canines. The C-M1 length varies from 22.72 to 27.85 mm, while the p3-m1 length varies from 17.10 to 20.75 mm. The length of P4 corresponding to around 40% of the length of the series of the maxilla. The shape of P3 paracone may be narrow and long or short and wide and P3 parastyle is absent in all specimens. The P4 paracone is present in all studied specimens. Traces of a talonid on m1 is present in the most of sample.

Leopardus tigrinus (Schreber, 1775)

Northern tigrina

- Felis tigrina* Schreber, 1775: plate CVI [based on the plate XXXVII, "Le Margay", Buffon (1765)]; 1777:396 (text). Type locality "südlichen Amerika" (= "South America"), subsequently restricted to "Cayenne" by J.A. Allen (1919:356).
- Felis margay* Müller, 1776:29. Based on "Le Margay" Buffon (1765).
- Felis (Oncooides) tigrina*: Severtzov, 1858:386 (name combination).
- Felis pardinoides* Gray, 1867a:400. Type locality "India", subsequently redefined to "Bogotá" by Gray (1874:475).
- Felis geoffroyi*: Elliot, 1872:203 (part) (*non* d'Orbigny & Gervais, 1844).
- Felis tigrina*: Thomas, 1880:396 (*non Felis tigrina* Schreber, 1775).
- Felis pardinoides andina* Thomas, 1903:238. Type locality "Jima, Province of Azuay, Ecuador".
- Felis pardinoides emerita* Thomas, 1912:44. Type locality "Montes de la Cutala, Merida, Venezuela".
- Margay tigrina emerita*: Allen, 1915:631 (name combination).
- Margay tigrina elenae*: Allen, 1915:631 (name combination).
- Margay caucensis* Allen, 1915:631. Type locality "Las Pavas, Colombia".
- Margay tigrina wiedi*: Allen, 1916:233 (part) (*non Felis wiedii* Schinz, 1821).
- Margay tigrina andina*: Allen, 1916:581 (name combination).
- Margay tigrina tigrina*: Allen, 1919:350 (name combination).
- Oncilla pardinoides emerita*: Allen, 1919:359 (name combination).
- Oncilla pardinoides elenae*: Allen, 1919:360 (name combination).
- Oncilla caucensis*: Allen, 1919:360 (name combination).
- Leopardus tigrinus*: Pocock, 1941a:237 (name combination, first use of current name combination).
- Felis (Leopardus) tigrina pardinoides*: Cabrera, 1958:286 (name combination).
- Felis (Leopardus) tigrina tigrina*: Cabrera, 1958:287 (part) (name combination).
- Oncifelis tigrina*: Wozencraft, 1993:290 (part).
- Leopardus tigrinus tigrinus*: Wozencraft, 2005:539 (part) (name combination).
- Leopardus tigrinus pardinoides*: Wozencraft, 2005:539 (name combination).

Type locality: “südlichen Amerika” [= “South America”], restricted by J.A. Allen (1919:356) to “Cayenne” [French Guiana]: “Based on Buffon’s description and figure of a specimen from Cayenne” [“Le Margay (pl. XXXVII) qui a servi de sujet pour cette description, ayant été tué à Cayenne (...)” (Buffon, 1765:252)] (Husson, 1978; Wozencraft, 2005).

Type material: Schreber (1775, 1777) based his *Felis tigrina* on “Le Margay” of Buffon (1765) (plate XXXVII) (Fig. 7A). The plate of Schreber’s *F. tigrina* (Fig. 7B) was published in 1775 [as plate CVI (= 106)] and the text with its description in 1777. Husson (1978) stated that the animal figured in the Schreber’s plate is the holotype of the species, but Thomas (1903:235) had previously designated the Buffon’s as the type. Thus, following the opinion of Thomas (1903) and in accordance with the ICZN Code (articles 74.4 and 74.6) (1999), we recognize the Buffon’s plate as the lectotype of *L. tigrinus*.

Diagnosis: Small sized; fur relatively harsh; ground color dark brown and orangish brown to yellowish brown and grayish brown, becoming lighter on the sides of the body; venter white or light gray; medium-

sized rosettes on the sides of the body form small and/or medium-sized oblique bands arranged in scapular-inguinal direction.

Body measurements: See Morphogroup I in Table 2.

Geographical distribution: The map of the Fig. 8 shows the points where the museum specimens were collected, which include the northern Brazil (State of Amapá; left bank of the Amazon River), Guyanas, Venezuela, Colombia, Ecuador, Peru, northwestern Argentina and Costa Rica. *Leopardus tigrinus* probably occurs in Bolivia, but there is no museum record (see Anderson, 1997:334). A specimen (MNK4595; not MNK3730) from Puerto Limón, Santa Cruz, Bolivia, was identified as a *L. tigrinus* by Huáscar Azurdúy (2005), but it is in fact a specimen of *L. wiedii* (it exhibits directed backwards hair on the nape and overall softer fur). There is a gap in the geographic distribution between Central American and northern South American population (Figs. 2, 4 and 8), but it is unknown whether the absence in this gap is natural or a sampling artifact. The distribution of *L. tigrinus* is mainly associated to lowland, premontane and montane forests (Eisenberg, 1989; Garrido & González-



A



B

FIGURE 7: Reproduction of the original plates: (A): “Le Margay” of Buffon (1765) (obtained from Gallica – Bibliothèque Nationale de France), the lectotype of the species; and (B): *Felis tigrina* of Schreber (1775). For color figure, see online version.

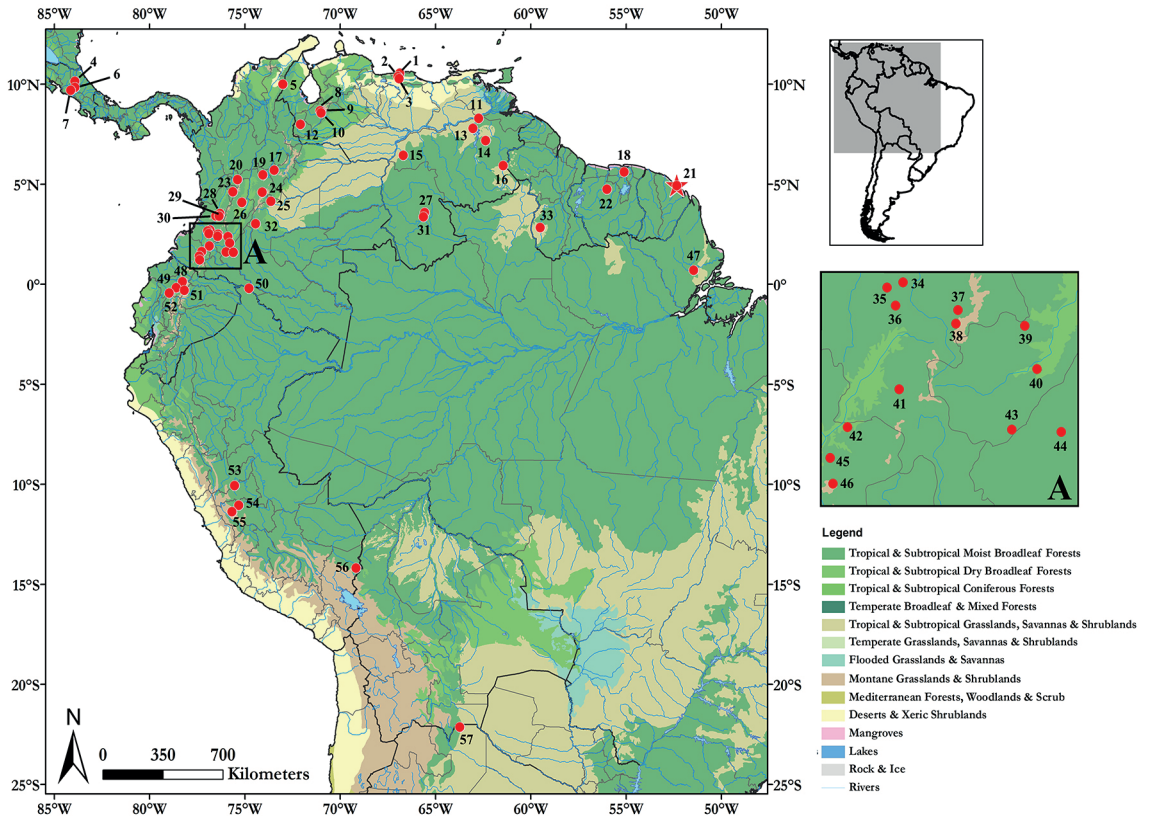


FIGURE 8: Geographic distribution of the specimens of *L. tigrinus* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix II) and the star refers to the type locality. For color figure, see online version.

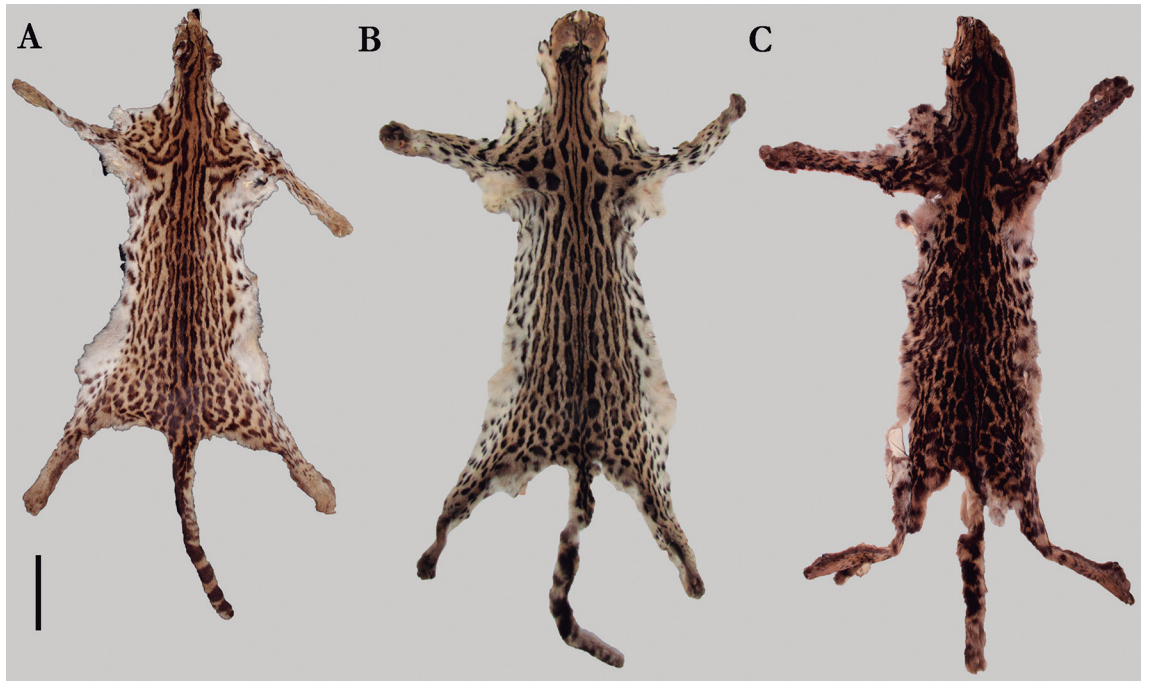


FIGURE 9: Pattern of coloration and markings in *L. tigrinus*: (A): EBRG9609 (Raul Leoni, Bolivar, Venezuela); (B): USNM374861 (Los Patos, El Manteco, Bolivar, Venezuela); AMNH69116 (Rio Chili, Manizales, Loreto, Colombia); (C): NMW-B455 (Carrillo, S des Llano de Santa Clara, San Jose, Costa Rica). Bar = 100 mm. For color figure, see online version.

Maya, 2011), from sea level up to 3,000-3,200 m (Mondolfi, 1986; Sunquist & Sunquist, 2002, 2009), but some individuals have been recorded as high as 4,500-4,800 m (Melquist, 1984; Cuervo *et al.*, 1986; Nowell & Jackson, 1996; Macdonald *et al.*, 2010). Apparently it has a marginal distribution in the open areas of the Llanos (Fig. 4: Morphogroup I, Fig. 8).

Variation: *L. tigrinus* does not show sexual dimorphism for external characters. The overall ground color of the head and body varies from dark brown to light yellowish brown orange, with the sides of the body usually lighter (buff colored) towards the venter (Fig. 9). The rosettes and the small and medium-sized oblique bands on the sides of body have black or very dark brown rims with most specimens the color inside the rosettes and bands is similar to that show in the dorsum, which may be brownish orange or dark

brown. These patterns of ground color and markings in *L. tigrinus* are very similar those found in *L. wiedii* (Fig. 10). It likely may lead to a misidentification of these species in the field, especially in a quick observation. However, these two species can be distinguished from each other by a series of characters, in special the direction of the hairs on nape, which are facing back in *L. tigrinus* and forward in *L. wiedii*. Furthermore, some individuals of *L. tigrinus* (for example: AMNH14187, from Pavas, Valle del Cauca, Colombia; AMNH149319, from El Tambo, Cauca, Colombia; and USNM362126, from Guyana) have a darker color inside the rosettes and bands, almost similar to the rims that surround them, a pattern very similar to that observed in some specimens of *L. wiedii* (Nascimento, *pers. obs.*). Furthermore, melanistic specimens are present in *L. tigrinus* (for example, USNM371278, from Caracas, Venezuela).



FIGURE 10: Comparison of the patterns of ground color and markings in **(A):** northern tigrina (*L. tigrinus*) (USNM374861, Los Patos, El Manteco, Bolivar, Venezuela) and **(B):** margay (*L. wiedii*) (NMNH388255, Rio Cunucunuma, Belen, Amazonas, Venezuela). Bar = 100 mm. For color figure, see online version.

Taxonomic notes: Despite some authors (Erxleben, 1777; Gmelin, 1788; F. Cuvier, 1826; Temminck, 1827; Fischer, 1829; Jardine, 1834; Gray, 1867a, 1867b, 1869) in 18th and 19th century followed Schreber's *F. tigrina*, other authors associated this name with the forms related to *wiedii* Schinz, 1821 (and in a lesser extent to *pardalis* Linnaeus, 1758 and *guigna* Molina, 1782) due to their morphologic similarities among the specimens studied by them, creating doubts regarding the exact identity of the animals that bear these names (see Elliot, 1877, 1883; Allen, 1919). Besides *tigrina* Schreber, 1775, the names *pardinoides* Gray, 1867a, *guttula* Hensel, 1872, *pardinoides* Thomas, 1903 and *oncilla* Allen, 1904 are commonly considered as subspecies of *L. tigrinus* (Pocock, 1941a; Cabrera, 1958; Wozencraft, 2005). According to our results, the putative subspecies *L. t. pardinoides* (Gray, 1867a) does not differ significantly from *L. t. tigrinus*, and so we recognize the former as the junior synonym of the latter, rather than its subspecies or a distinct taxon. In addition, specimens from the northeastern Brazil are traditionally considered to belong to *tigrinus* Schreber, 1775 (e.g., Cabrera, 1958), but our results indicate that they belong to a distinct taxon, *L. emiliae* (Thomas, 1914).

Regarding to the taxonomy of Central American population, Thomas (1903:237) described a specimen from Volcan de Irazu, Costa Rica, as *Felis pardinoides oncilla*, which showed size and general characters as in *F. pardinoides* Gray, 1867a, but with ground color of pelage "much richer and deeper", and the lateral rosettes little elongated. According to Gardner (1971), the specimens from Central America resemble the type of *Margay caucensis* J.A. Allen, 1915 (from Las Pavas, Rio Cauca, Colombia) [which was synonymized in *Felis (Leopardus) tigrina pardinoides* by Cabrera (1958)] in the intensity of markings and richness of color. Nevertheless, due the apparent absence of the tigrina between southern Panama and northern South America (Figs. 2, 4 and 8), Gardner recognized the Central American population as distinct from the northern South American population (= *O. t. pardinoides*). According to the molecular data, the Central American population of tigrinas is highly genetically divergent from the southern South American tigrina, a divergence higher than that between *L. pardalis* and *L. wiedii* and *O. geoffroyi* and *O. guigna* (Johnson *et al.*, 1999). However, samples from other populations, mainly from northwestern South America (for example, from Colombia and Venezuela), were not included in the molecular study.

Leopardus emiliae (Thomas, 1914)

Eastern or Sneath's tigrina

Felis emiliae Thomas, 1914:348. Type locality "Ipu, Ceará, N.E. Brazil".

Oncilla guttula emiliae: Allen, 1919:360 (new combination).

Oncifelis pardinoides emiliae: Weigel, 1961:34.

Felis (Leopardus) tigrina tigrina: Cabrera, 1958:287 (part).

Leopardus tigrinus tigrinus: Wozencraft, 2005:539 (part).

Type locality: "Ipu, Ceará, N.E. Brazil. Alt. 300 m". Based on the information provided by Paynter Jr. & Traylor Jr. (1991), Ipu is located on eastern edge of Serra da Ibiapaba, northwestern Ceará (04°19'S, 41°42'W).

Type material: "Adult male. B.M. no. 13.12.18.3. Original number 11. Collected 24th May, 1910, by Fräulein Dr. E[milie]. Sneath. Presented by the authorities of the Goeldi Museum, Para. Two specimens" (Thomas, 1914) (Fig. 11).

Diagnosis: Small sized; fur relatively harsh; ground color light yellowish brown to pale yellow and grayish yellow; venter white, very light gray or slightly yellowish with medium and small-sized dark spots; small dark rosettes on the body sides, not coalescing into small-sized oblique bands; rims of rosettes narrow and usually discontinuous.

Body measurements: See Morphogroup II in Table 2.

Geographical distribution: *L. emiliae* is the only Felidae species endemic of Brazil, distributed in the north (right bank of the Amazonas River), northeastern and central portion of this country (states of Pará, Tocantins, Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Bahia and Goiás), which includes Caatinga, Cerrado, Amazonia and Atlantic Forest biomes (Fig. 12).

Variation: The material here referring to *L. emiliae* that we had for study was constituted by 15 skulls and 59 skins. Regarding to the skins, which have a comparatively larger sample, we noted that individuals in northern, northeastern and central Brazil have much more yellowish coloration and pale (Fig. 13) compared to specimens of neighboring *L. guttulus*. For example, the specimens BMNH13.12.18.3 (ho-



FIGURE 11: Dorsal (up) and ventral (bottom) views of the skin of the holotype of *L. emiliae*, specimen from Ipu, Ceará, Brazil (BMNH13.12.18.3; male). Bar = 100 mm. Photo: Thiago Semedo. For color figure, see online version.

lotype) (Fig. 11) and MPEG588 (topotype) from Ipu, Ceará, Brazil, exhibit a distinct pattern of pale yellowish brown coloration on the back and white (holotype) or slightly yellowish (topotype) color in the venter, when compared them with specimens of *L. guttulus* and *L. tigrinus*.

The overall coloration of pelage vary from pale orangish yellow (UFPB6592 and UFPB6266), dark yellow on the dorsum, and pale yellow on the sides of the body (UFPB983), to uniformly dark yellow (UFPB6265). Some specimens show distinctive continuous black lines that run throughout the posterior half of the dorsum to the base of the tail (UFPB6265), while in others these lines are not continuous or barely perceptible (UFPB6266). *Leopardus emiliae* exhibits circular rosettes that do not coalesce to form lateral bands. The rosettes are surrounded by small black spots (UFPB3243 and UFPB6592) or thin black lines that encircle in higher (UFPB6265) or lesser (UFPB6270 and UFPB983) extent the rosettes, but rarely surround them completely. Melanistic individuals were not recorded for this species.

Taxonomic notes: Thomas (1914) described a new species of tigrina from Ceará, Brazil, which was named *Felis emiliae*, and according to the author, it would be-

long to *F. guttula* group. Two specimens were collected, one of them, the holotype (BMNH13.12.18.3), was deposited in the Natural History Museum, London, and the other (MPEG588) in the collection of Museu Paraense Emilio Goeldi, Belém, Brazil. Later, Allen (1919) classified this cat as *Oncifelis guttula emiliae*, a decision followed by Weigel (1961). Cabrera (1958), however, questioned the validity of this taxon, because Thomas (1914) had not compared the specimens with material from French Guiana, the type locality of *Felis tigrina* Schreber, 1775. Thus, Cabrera considered the form from northeast Brazil as a junior synonym of *Felis (Leopardus) tigrinus tigrinus*, decision also followed by subsequent authors, including Wozencraft (2005). However, according to the results shown here, we recognize *F. emiliae* Thomas, 1914 as valid name, and therefore, *L. emiliae* as a full species.

Leopardus guttulus (Hensel, 1872)

Southern tigrina

Felis guttula Hensel, 1872:73. Type locality “Urwald von Rio Grande do Sul” (Rio Grande do Sul, Brazil).

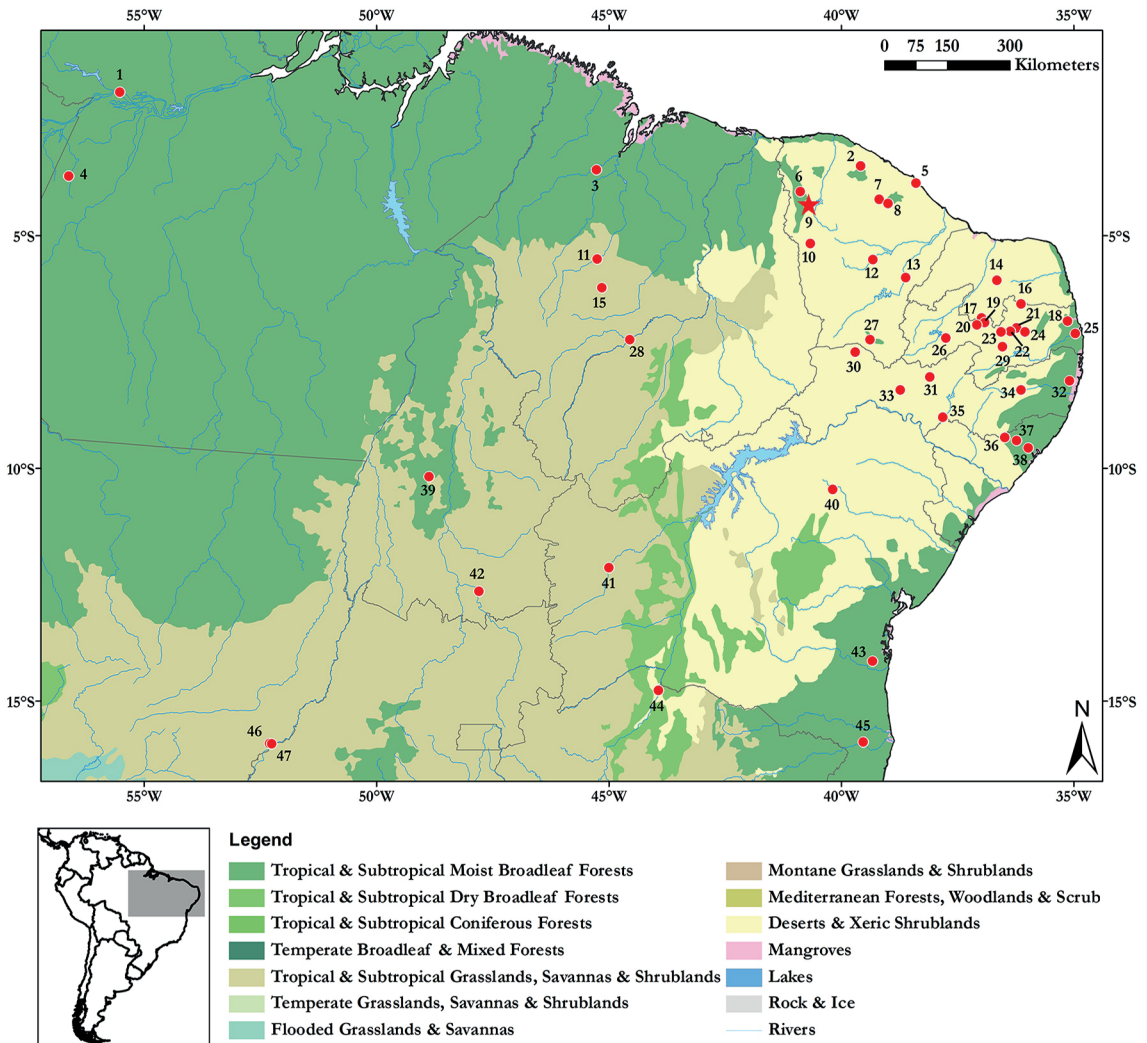


FIGURE 12: Geographic distribution of the specimens of *L. emiliae* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix II) and the star refers to the type locality. For color figure, see online version.

Felis guigna: Hensel, 1872:74 (part) (*non Felis guigna* Molina, 1782).

Felis guttata: Lydekker, 1896:145; typographical error of *Felis guttula* (*non Felis guttata* Hermann, 1804).

Felis (Oncoides) tigrina guttula: Trouessart, 1897:359 (name combination).

Felis (Oncoides) mitis: Lahille, 1899:178 (*non Felis mitis* F. Cuvier, 1820).

Felis pardinoides: Thomas, 1903:236 (*non Felis pardinoides* Gray, 1867a).

Oncilla pardinoides pardinoides: Allen, 1919:358 (*non Felis pardinoides* Gray, 1867a).

Oncilla guttula guttula: Allen, 1919:360 (name combination).

Felis (Leopardus) tigrina guttula: Cabrera, 1958:286 (name combination).

Type locality: “Urwald von Rio Grande do Sul” (Hensel, 1872:74) [= Rio Grande do Sul, Brazil (Cabrera, 1958, 1961; Nascimento, 2010)]. Unfortunately Hensel did not give a more precise locality where the specimens were collected. However, according to information about the places visited by Hensel in the state of Rio Grande do Sul between 1863 and 1865 (Hensel, 1867; Buckup, 1999), the specimens were probably collected somewhere in the northeastern part of this Brazilian state.

Type material: Two skulls deposited in the Museum für Naturkunde, Berlin, Germany, under the numbers ZMB-MAM21229 and ZMB-MAM21231 (Figs. 14 and 15). Hensel pointed these two specimens in his description, but their collection numbers were not indicated in the text and, more importantly,

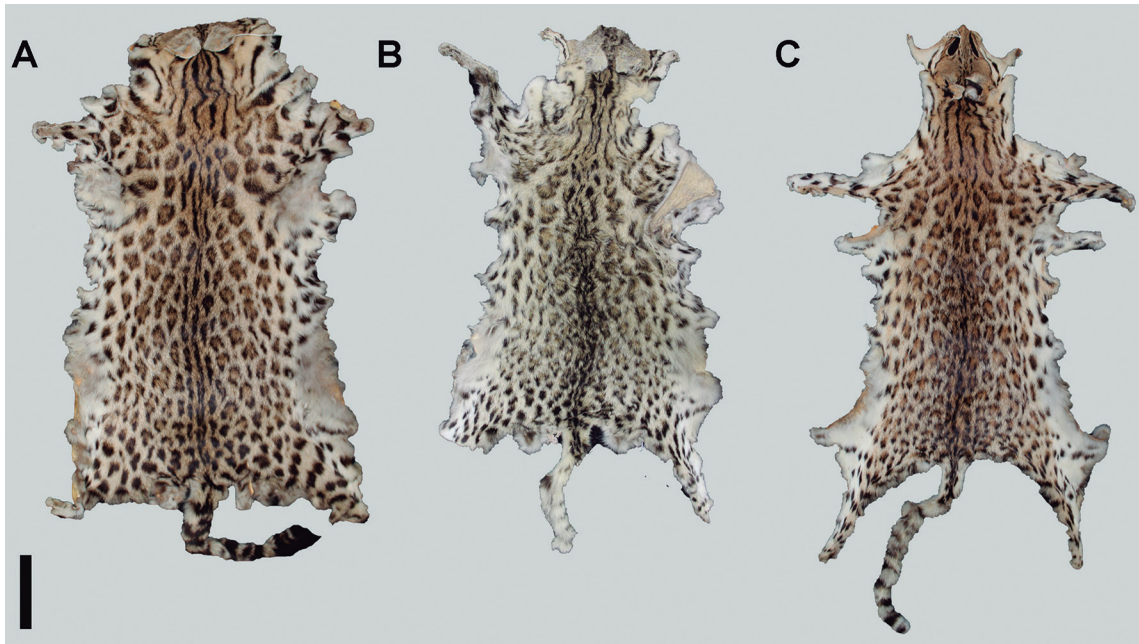


FIGURE 13: Pattern of coloration and markings in *L. emiliae*: (A): UFPB6267 (Sítio Corea, Várzea, Paraíba, Brazil); (B): UFPB7061 (Comunidade Soledade, Paraíba, Brazil); (C): UFPB3243 (Jaguaribe, Ceará, Brazil). Bar = 100 mm. For color figure, see online version.

he did not indicate which specimen is the holotype. Thus, the two specimens are considered syntypes of *L. guttulus*. The specimen ZMB-MAM21229 is a male and the other, ZMB-MAM21231, was identified as a female by Hensel presumably due to the smaller overall size, to relatively smaller canines, and more delicate structures of the skull (Hensel, 1872). In addition, he described the pelage of the species, but he does not indicate whether this description is based on one of two specimens, a combination of the two specimens or another unknown individual. Nevertheless, only the two skulls mentioned above are recorded as types of the species in the ZBM.

Diagnosis: Small sized; fur relatively harsh; ground color dark yellowish brown to ochraceous buff, lighter on the sides of the body; venter white or very light gray; small dark rosettes on the body sides with thick and continuous black rims, rarely coalescing into small-sized oblique bands.

Body measurements: See Morphogroup III in Table 2.

Geographic distribution: *L. guttulus* is found in Brazil (southeast, south and center-west regions), northeastern Argentina and Paraguay (Fig. 16). It has a contact zone with *L. geoffroyi* in the Central Depression region in the state of Rio Grande do Sul, where hybrid specimens were found and they showed pelage pattern

with intermediate characteristics between these two species (Eizirik *et al.*, 2006; Trigo *et al.*, 2008, 2013). Possibly the Chaco in northern Argentina could be the contact zone between *L. tigrinus* and *L. guttulus*.

Variation: *L. guttulus* does not show sexual dimorphism for external characters, and the overall ground color varies from dark yellowish brown to ochraceous buff, with the sides of the body usually lighter towards the venter, which is white or light gray colored (Fig. 17). Regarding to the rosettes on the sides of the body, they usually do not coalesce to form small or medium-sized oblique bands. Melanistic individuals are known for *L. guttulus*.

Taxonomic notes: As mentioned above, Hensel (1872) described *Felis guttula* to southern Brazil (Rio Grande do Sul state), which subsequently it was recognized as a subspecies of *L. tigrinus*. Furthermore, in the same work, Hensel described a skull also collected in the state of Rio Grande do Sul and identified it as *Felis guigna* Molina, 1782. Thomas (1903) received specimens from “Roca Nova” [= Roça Nova, municipality of Piraquara], Paraná, Brazil, collected by A. Robert and then requested to Paul Matschie, former mammal curator of Berlin Zoological Museum (nowadays Museum für Naturkunde), to compare three skulls with the material of Hensel. One of skulls was identified as *Felis macroura* (= *Leopardus wiedii*),

another (a male) as indistinct of *F. guttula* Hensel, 1872, and the other as *F. guigna* Hensel, 1872 (not *F. guina* Molina, 1782). However, Thomas did not agree with him and based on the type locality of *Felis guigna* Molina, 1782, which is Valdivia, Chile, on the western side of the Andes, and from the comparison between the skull of the specimen from Paraná and the skull of the type of *F. pardinooides*, he concluded that *F. guigna* Hensel, 1872 is a junior synonym of *F. pardinooides* Gray, 1867a (Thomas, 1903; Pocock, 1917). Strangely, Thomas (1903) designated a new locality for *F. pardinooides*, “Espiritu Santo” (= Espírito Santo), and as Allen (1919:358) quoted: “No reference is made [by Thomas] to Gray’s previous designation [in Gray, 1874] of Bogotá as the type locality of his *Felis pardinooides*” (see *L. tigrinus*’ Taxonomic Notes for more details). Also Pocock (1917) did not made reference to Gray’s article when he revised the

specimens analysed by Thomas (1903) [either both Thomas and Pocock were unaware about this article (something unlikely) or they rejected Gray’s latter decision].

In short, Thomas (1903) recognized two species from Roça Nova, a larger one, *F. guttula*, and a smaller, *F. pardinooides*, but Pocock (1917) disagreed and re-examined the specimens, concluding that *F. pardinooides* and *F. guttula* recognized by Thomas (1903) are actually a female (melanistic individual) and a male (spotted specimen), respectively, of the same species. Furthermore, Pocock (1917) pointed out that a second male from the same locality had little difference in the characters of the skull and the pelage in comparison to other male. Thus, the name *F. pardinooides* Thomas, 1903, besides it was preoccupied by *F. pardinooides* Gray, 1867a, is a junior synonym of *F. guttula* (Hensel, 1872).



FIGURE 14: The skull of one of the syntypes of *L. guttulus* (Hensel, 1872), the specimen ZMB-MAM21231 (female?). Bar = 20 mm. Photo: Carola Radke (Museum für Naturkunde, Berlin, Germany). For color figure, see online version.

COMPARISONS

In Table 6 we summarize the main differences that distinguish the tigrinas species (*L. tigrinus*, *L. emiliae* and *L. guttulus*) from other small and medium sized felids found throughout their *geographical distribution*: ocelot (*L. pardalis*), margay (*L. wiedii*), Geoffroy's cat (*L. geoffroyi*), Pantanal cat (*L. braccatus*), pampas cat (*L. pajeros*), jaguarundi (*Herpailurus yagouaroundi*), and domestic cat (*Felis catus*).

CONCLUSIONS

We proposed a new taxonomic arrangement for the tigrina group, based on the complementary morphological approach supported by the molecular evidence available, with three species, *L. tigrinus*,

L. emiliae and *L. guttulus*. Up to now, the previously taxonomic studies used mostly specimens from the northwest and northern South America, but our study is the first to cover a larger sample of specimens in quantitative and geographical terms from the entire distribution of the group, especially from southern and eastern areas of the range, which hitherto have been neglected (Elliot, 1877, 1883; Thomas, 1903; Allen, 1919; Cabrera, 1961).

As pointed out by Helgen *et al.* (2013), the order Carnivora had been for long time considered taxonomically stable, with very few changes in the Neotropical assemblage in last 100 years (Patterson, 2001). Similar scenario could be extends to other medium and large-sized Neotropical mammals (de Vivo, 1996; Rossi, 2000; Patterson, 2001, Feijó & Langguth, 2013; Nascimento, 2014; Feijó & Cordeiro-Estrela, 2016). This putative stability, however, is



FIGURE 15: The skull of one of the syntypes of *L. guttulus* (Hensel, 1872), the specimen ZMB-MAM21229 (male). Bar = 20 mm. Photo: Carola Radke (Museum für Naturkunde, Berlin, Germany). For color figure, see online version.

TABLE 6: Comparisons of some external and craniodental characters between tigrinas species (*L. tigrinus*, *L. emiliae* and *L. guttulus*) and other small and medium-sized Neotropical cats that occur along the geographic distribution of the tigrinas (*L. pardalis*, *L. wiedii*, *L. geoffroyi*, *L. braccatus*, *L. pajeros*, *Herpailurus yagouaroundi*, and *Felis catus*).

Taxa	Body size	Nape hairs orientation	Tail length/head and body length ratio (on average)	Overall ground color of the body	Pattern of spots on the sides of body	Dorsal profile of skull	Curvature at the frontal and parietal area	Anteriomost point of premaxillary in relation to anteriomost point of nasal	Sagittal crest
<i>Leopardus tigrinus</i>	small (2.5 kg)	backward	-60%	dark brown to yellowish brown; orange light; venter white or light gray	usually coalescing into medium oblique bands	slightly arched	slightly convex	aligned	absent or a very low and short line restricted to the interparietal region
<i>Leopardus emiliae</i>	small (1.2-3.5 kg)	backward	-60%	light yellowish brown to pale yellow; venter white, very light gray or slightly yellowish	rarely coalescing into oblique bands	slightly arched	slightly convex	aligned	absent or a very low and short line restricted to the interparietal region
<i>Leopardus guttulus</i>	small (1.0-2.5 kg)	backward	-60%	dark yellowish brown; venter white or very light gray	rarely coalescing into oblique bands	slightly arched	slightly convex	aligned	absent or a very low and short line restricted to the interparietal region
<i>Leopardus pardalis</i>	medium (7.0-16.0 kg)	forward	-50%	bright and pale orangish buff color to grayish buff and gray; venter white or very light gray	usually coalescing into large bands	highly arched	well convex	not aligned	poorly developed and restrict to interparietal region, moderately developed and occupying posterior half of parietal suture, or well developed occupying total length of parietal suture
<i>Leopardus wiedii</i>	small (2.0-4.0 kg)	forward	-70%	bright and pale orangish buff color to grayish buff and gray; venter white or very light gray	usually coalescing into medium oblique bands	highly arched	well convex	not aligned	absent or a very low and short line restricted to the interparietal region
<i>Leopardus geoffroyi</i>	small (2.0-6.0 kg)	backward	-55%	yellowish brown to smoky gray; venter white or very light gray	never coalescing into bands	slightly arched	slightly convex	aligned	poorly developed and restrict to interparietal region or moderately developed and occupying posterior half of braincase
<i>Leopardus braccatus</i>	small (2.5-4.0 kg)	backward	-55%	brown aguti	fading oblique lines	slightly arched	slightly convex	aligned	poorly developed and restrict to interparietal region or moderately developed and occupying posterior half of braincase
<i>Leopardus braccatus</i>	small (2.5-4.0 kg)	backward	-55%	yellowish brown aguti	fading oblique lines	slightly arched	slightly convex	aligned	poorly developed and restrict to interparietal region or moderately developed and occupying posterior half of braincase
<i>Leopardus pajeros</i> (Northern form) ¹	small (2.5-4.0 kg)	backward	-50%	yellowish gray or grayish brown	usually coalescing into medium oblique bands	slightly arched	slightly convex	aligned	poorly developed and restrict to interparietal region or moderately developed and occupying posterior half of braincase
<i>Leopardus pajeros</i> (Southern form) ²	small (2.5-4.0 kg)	backward	-50%	grayish brown	fading oblique lines	slightly arched	slightly convex	aligned	poorly developed and restrict to interparietal region or moderately developed and occupying posterior half of braincase
<i>Herpailurus yagouaroundi</i>	small (3.2-7.0 kg)	backward	-60%	gray; reddish, yellow, dark brown or black	spots absent	slightly arched	slightly convex	aligned	moderately developed and restrict to interparietal region
<i>Felis catus</i>	small (2.5-4.0 kg)	backward	-50-65%	variable	variable but never coalescing into bands	slightly arched	slightly convex	aligned	moderately developed and occupying posterior half of parietal suture

¹ includes the putative subspecies: *L. p. garleppi* (Matschie, 1912), *L. p. thomasi* (Lönnerberg, 1913), *L. p. budini* (Pocock, 1941), *L. p. steinbachi* (Pocock, 1941) and *L. p. ersepoi* (Cabrera, 1957).
² includes the putative subspecies *L. p. pajeros* (Desmarest, 1816) and *L. p. crucinus* (Thomas, 1901).

potentially more reflective of the scarcity of taxonomic studies rather than actual diversity. Recent taxonomic revisions of medium and large-sized mammals have shown that the potential diversity in different groups (*e.g.*, Carnivora, Cingulata, Rodentia Hystricognathi,

Lagomorpha) have been underestimated (Nascimento, 2010, 2014; Feijó & Langguth 2013; Helgen *et al.*, 2013; Feijó & Cordeiro-Estrela, 2016). Regardless the taxa, the proper evaluation of the species and subspecies ranks should be based on a geographic

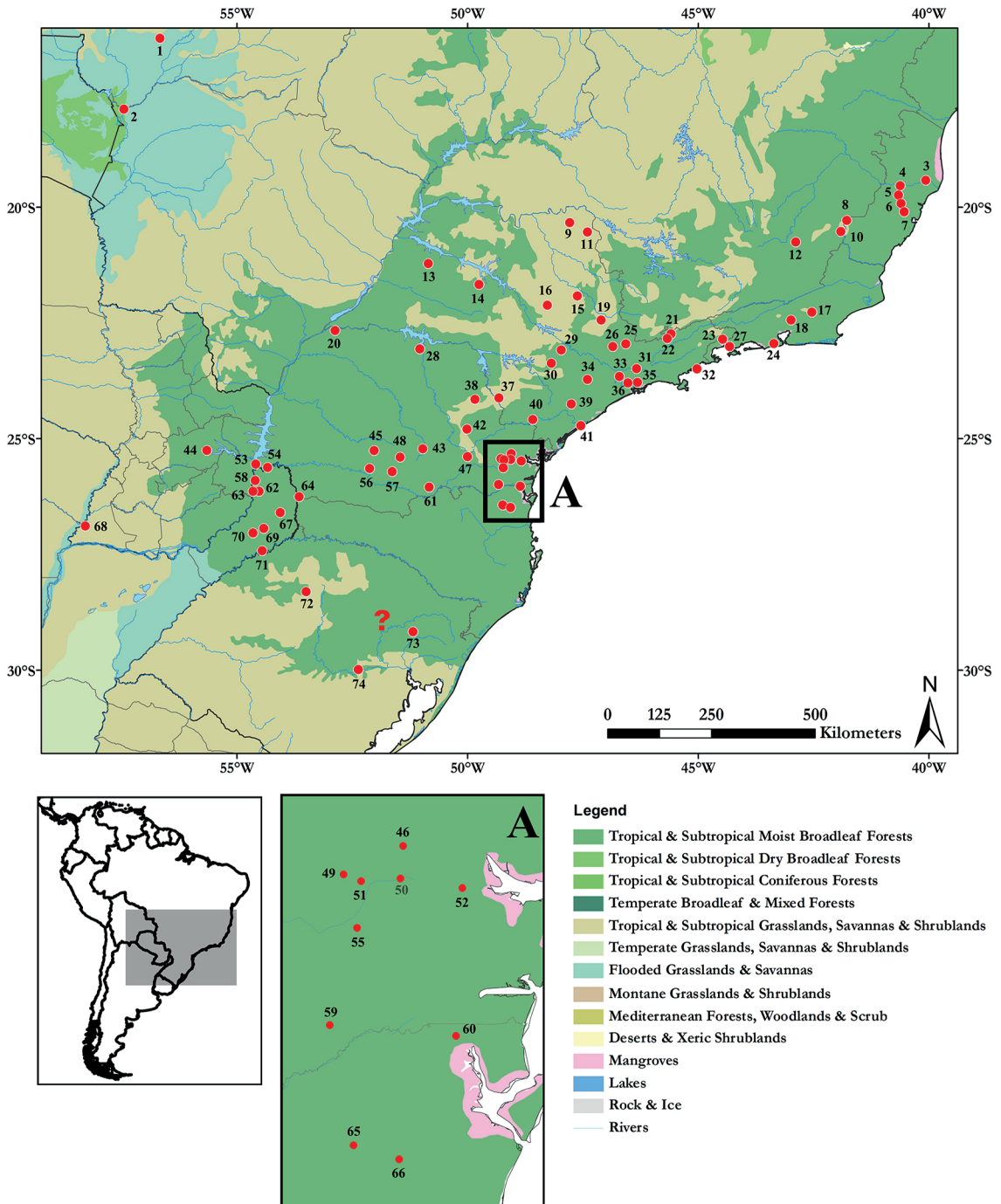


FIGURE 16: Geographic distribution of the specimens of *L. guttulus* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix II) and the question mark refers to the type locality, which does not have a precise location [Hensel (1872) only cited “Rio Grande do Sul” as the type locality]. For color figure, see online version.



FIGURE 17: Pattern of coloration and markings in *L. guttulus*: (A): MZUSP24234 (Dourado, São Paulo, Brazil); (B): MNRJ6693 (São Francisco, Jacarépaguá, Rio de Janeiro, Rio de Janeiro, Brazil); (C): MNRJ3889 (Santa Teresa, Espírito Santo, Brazil). Bar = 100 mm. For color figure, see online version.

broad scale, taking into account the individual, sexual, population and geographic variation, and preferable using complementary approaches. In this sense, the scientific museums have a key role for house a sample of the biological diversity (de Vivo *et al.*, 2014; Moratelli, 2014).

From a conservation perspective, the split into three species of the tigrina group may change our view about the extinction susceptibility risk. *Leopardus tigrinus*, as previously recognized, and *L. guttulus* are both classified as Vulnerable by the IUCN mainly due to its presence in areas with high rate of forest loss (Oliveira *et al.*, 2016a,b). Considering the new taxonomic arrangement, the resulting geographic distribution of each taxon is now considerably smaller than previously accepted for the entire tigrina group. Therefore, this dramatically increases the risk of extinction for each these taxa. Thus, the current situation and status of *L. tigrinus*, *L. emiliae* and *L. guttulus* should be urgently assessed.

RESUMO

O gato-do-mato-pequeno *Leopardus tigrinus* (Schreber, 1775) é um felídeo neotropical de pequeno porte encontrado desde o norte da Argentina e sul do Brasil até a

Costa Rica. Quatro subespécies são tradicionalmente reconhecidas: *L. t. tigrinus* (Schreber, 1775) do Brasil setentrional, Guianas e Venezuela oriental; *L. t. pardinoides* (Gray, 1867) da Venezuela ocidental, Colômbia, Equador e Peru; *L. t. guttulus* (Hensel, 1872) do Brasil meridional, Paraguai e Argentina setentrional; e *L. t. oncillus* (Thomas, 1903) da Costa Rica. Analisamos quantitativa e qualitativamente a morfologia externa e crânio-dentária de 250 espécimes com o objetivo de esclarecer o estado taxonômico do gato-do-mato-pequeno. Baseado nos caracteres analisados, nós reconhecemos três morfogrupos, cada com uma distinta distribuição geográfica: norte/noroeste/leste (amostras do Brasil setentrional, Guianas, Venezuela, Colômbia, Equador, Peru, noroeste da Argentina e Costa Rica), leste (amostras do nordeste e centro do Brasil) e sul (amostras do Brasil meridional, Paraguai e nordeste da Argentina). Considerando as evidências morfológicas apresentadas neste estudo, ligado ao suporte biogeográfico e dos estudos moleculares disponíveis, reconhecemos três espécies plenas de gato-do-mato-pequeno: *L. tigrinus* (inclui as supostas subespécies *L. t. pardinoides* and *L. t. oncillus* como sinônimos juniores) para o grupo norte/noroeste/leste; *L. emiliae* (Thomas, 1914) para o grupo do leste; and *L. guttulus* para o grupo do sul.

PALAVRAS-CHAVE: *Leopardus tigrinus*; *L. guttulus*; *L. emiliae*; Subespécies; Variação morfológica.

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APPENDIX I

List of Specimens Examined

***Leopardus tigrinus* (Schreber, 1775) – 75 specimens.** **ARGENTINA:** *Chaco:* Unknown locality: MACN38.20 (skin); *Salta:* Rio Carapavi, Angostuta: MACN36.726 (skin); **BRAZIL:** *Amapá:* Estrada Campo Verde, Porto Peaton: MNRJ24894 (skull). **COLOMBIA:** *Amazonas:* Rio Putumayo; Puerto Leguizamo: AMNH149316 (skin), AMNH149317 (skin), AMNH149318 (skin); *Antioquia:* Santa Elena: AMNH37788 (skin and skull) (holotype of *Margay tigrina elenae* Allen, 1915); *Boyacá:* Coper: IAVH1781 (skin); Villa de Leyva, Mamarramos: IAVH8608 (skin); *Caldas:* cuenca alta del rio Tapias, Neira: IAVH7343 (skin); *Caquetá:* Florencia: IAVH783 (skin); *Cauca:* Almaguer: AMNH 33897 (skin); Charguayaco: AMNH181498 (skin and skull), FMNH89231 (skin and skull); El Tambo: AMNH149319 (skin); Las Pabas (= valle de Las Papas), near Santo Antonio, 6000ft (1830 m): AMNH14187 (skin and skull) (holotype of *Margay caucensis* Allen, 1915); La Quintana: FMNH85823 (skin and skull); Leticia, Moscopán: AMNH149321 (skin); Malvatá: AMNH181497 (skin); Sabanetas: FMNH84554 (skin and skull); Totoro: FMNH89230 (skin and skull); Uribe: ZMB105209 (skull), ZMB105210 (skull) and ZMB105211 (skull); *Cundinamarca:* Bogotá: FMNH70570 (skin, skull and skeleton), FMNH70571 (skin, skull and skeleton), FMNH70572 (skin, skull and skeleton); *Huila:* Acevedo, San Adolfo: FMNH70569 (skin, skull and skeleton); Altamira, Andalucía: AMNH33896 (skin and skull); La Plata, Vereda La Segoviana: IAVH710 (skin); *Meta:* Villavicencio: AMNH139224 (skin and skeleton); *Nariño:* P.N.N. Volcan Galeras: IAVH5857 (skin); Quindío: Reserva Florestal Bremen, Circasia: IAVH7331 (skin); *Tolima:* Rio Chili, Sul de Manizales: AMNH69165 (skin and skull), AMNH69166 (skin and skull). **COSTA RICA:** *Cartago:* Cartago: ZMB17196 (skin); *San Jose:* Carrillo, S Llano (Llanuras) de Santa Clara: NMW-B4559 (skin); Parrita: Pozo Azul: AMNH19211 (skin and skull; holotype of *Felis carrikeri* Allen, 1904); **ECUADOR:** *Cotopaxi:* San Francisco de Las Pampas: QCAZ205 (skin); *Napo:* Rio Chalpichico entre Papallacta y Cuyuja: MEPN10931 (skin); Pichincha: Alanguineho, Mojanda (south): NRM585404 (skull), NRM585413 (skull); Mt. Pichincha: NRM595402 (skull). **GUYANA:** *Rupununi:* Dadanawa Ranch, 60 miles E: USNM541506 (skull) (misidentified as *Herpailurus jagouaroundi* on the specimen tag); *Unknown locality:* USNM395089 (skull and skeleton); USNM395090 (skull and skeleton); USNM362126 (skin, skull and skeleton). **PERU:** *Junín:* Chanchamayo: Chanchamayo: USNM255135 (skull), FMNH65780 (skin and skull); La Florida (region Alto Yurinaki): MUSM5046 (skin); *Pasco:* Oxapampa: Pozuzo: FMNH34674 (skin); *Puno:* Sandia: San Juan: FMNH78404 (skin and skull), FMNH78463 (skin), FMNH79923 (skin, skull and skeleton); *Unknown locality:* monte del Peru: MUSM2154 (skin). **SURINAME:** *Para District:* Onoribo, on Para River, 5 km West of Paramam, about 25 km South of Paramaribo: RMNH18221 (skin); *Saramaca District:* RMNH17764 (skin); *Unknown locality:* NRM582004 (skull). **VENEZUELA:** *Amazonas:* Rio Negro frente Isla Chicharral: EBRG2214 (skin and skull); Aproximado 3 km S San Carlos de Rio Negro: EBRG21031 (skull); *Bolívar:* Cedeño, Serranía de Los Pijiguaos 140 km SO de Caicara: EBRG15796 (skin, skull and skeleton); El Manteco, 28 km SE, Los Patos: USNM374861 (skin and skull); Porto Ordaz: AMNH176298 (skin and skull); Raul Leoni, 2 km NO Represa Guri 1 km e Alcabala Obra: EBRG9609 (skin and skull); Sierra de Lema, km 753: EBRG27346 (skin, skull and skeleton); *Distrito Federal:* Caracas, 9.4 km N. Hotel Humboldt: EBRG3159 (skin and skull); USNM371278 (skin and skull); *Merida:* AMNH21638 (skin); Montes de la Sierra: AMNH34349 (skin and skull); Páramo de San Antonio (near Merida): MCZ20979 (skin and skull); Sierra Nevada: NRM595411 (skull); *Miranda:* Autopista Coche-Tejerías, Distribuidor Los Totumos: MHNLS4372 (skin); Altos de Pipe, a 200 m del Instituto Venezolano de Investigaciones Científicas, Via San Antonio de Los Altos (100 m Reactor RV-1 Del Ivic): EBRG3004 (skull); *Táchira:* Páramo El Zumbador: ZMB33350 (skull); *Zulia:* Yamayaujaina, Rio Negro, Serranía de Perijá: MHNLS176 (skin).

***Leopardus emiliae* (Thomas, 1914) – 62 specimens.** **BRAZIL:** *Alagoas:* Fazenda São Manuel, Viçosa: MPEG24895 (skull); Quebrângulo: MZUSP8292 (skull, skin and skeleton); between the municipalities of Pilar and Atalaia: UFPB3567 (skin); *Bahia:* BR 101, km 397, ponte Rio Ouriço: UFPB797 (skin); BR 101, km 645, 36 km Sul do Rio Pardo: UFPB795 (skin); Barreiras: UFPB981 (skin), UFPB982 (skin); UFPB983 (skin); Senhor do Bonfim: MZUSP2646 (skin and skull), MZUSP24903 (skin); *Ceará:* Comunidade Balança, Caridade: UFPB6592 (skin); Cratêus: UFPE2411 (skin); Fazenda Carrapato (João Cativo), Itapipoca: UFPE1999 (skin); Iguatu: UFPE2412 (skin); Ipu: BMNH13.12.18.3 (skin; holotype of *Felis emiliae* Thomas,

1914); MPEG588 (skin; topotype of *Felis emiliae* Thomas, 1914); Jaguaribe: UFPB3243 (skin); São Benedito, Macapá: MNRJ24896 (skull); Serra do Baturité, Mulungu: UFPE1942 (skin), UFPE1997 (skin), UFPE1998 (skin), UFPE2002 (skin) and UFPE2003 (skin); Chapada do Araripe, Crato: MNRJ1543 (skull and skin in alcohol); Tijuco, Aquiraz: UFPB2413 (skin); **Goiás:** Aragarças: MZUSP19900 (skin and skeleton); Palma: MNRJ3158 (skin); **Maranhão:** Aldeia do Ponto: MZUSP7975 (skin); Barra do Corda: FMNH23966 (skull and skin); Sítio Novo, Boa Lembrança, Grajaú: MPEG22685 (skin); **Mato Grosso:** Rio das Garças: MNRJ25722 (skin); **Minas Gerais:** Manga: MNRJ29078 (skin), MNRJ30025 (skin) and MNRJ29077 (skin); **Pará:** Óbidos: MPEG5618 (skull); Rio Jamari, Terra Santa: MZUSP13605 (skull, skin and skeleton); **Paraíba:** Comunidade Soledade: UFPB7061 (skin); Cuité: UFPB796 (skin); Distrito de Socorro, Olho d'Água: UFPB6443 (skin); Estrada de Lucena a Santa Rita: UFPB6471 (skin); Juazeirinho: UFPB798 (skin); Olivedos: UFPB6939 (skin); Pocinhos: UFPB6653 (skin); REBIO Guaribas, Área II, Estrada de Jacaraú, 300 m da sede, Mamangape: UFPB6469 (skin); São João do Cariri: UFPB6806 (skin); São Mamede: UFPB6266 (skin); Tabuleiro de Patrocínio, Usina São João, Santa Rita: UFPB2083 (skin and skull); Várzea (Sítio Coreia): UFPB6267 (skin) and UFPB6270 (skin); **Unknown Locality:** UFPB6242 (CETAS, IBAMA) (skull and skin), UFPB6791 (CETAS, IBAMA) (skull and skin); **Pernambuco:** Carnaubeira: MZUSP13609 (skull and skin), MZUSP13610 (skull and skin); BR 232, Distrito de Varzinha, Serra Talhada: UFPB6447 (skin); Fazenda Genipapo, Exu: UFPB6938 (skin); Ladeira do Timbó, BR 232, km 29, Moreno: UFPE1976 (skin); São Caetano: UFPE840 (skin and skull); vicinity of the REBIO Serra Negra, Inajá: UFPE693 (skin and skull); **Piauí:** Uruçuí: UNB2109 (skin); **Rio Grande do Norte:** Fazenda Juazeiro, Santana do Matos: UFPB6755 (skin); **Tocantins:** BR 153, Paraíso do Tocantins: UNB2750 (skin); **Unknown locality:** UFPB1023 (skin).

Leopardus guttulus (Hensel, 1872) – 113 specimens. ARGENTINA: **Chaco:** Unknown locality: MACN38.21 (skin), MACN38.22 (skin), MACN38.23 (skin); MACN38.24 (skin); **Misiones:** Aguaraí-Guazú Inferior: MACN48.295 (skin); MACN48.296 (skin); Arroyo Uruguái, 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 Cainguaús, Dos de Mayo: MACN23696 (skull); Departamento Guaraní, Cuartel Río Victoria: MACN23709 (skull); Departamento Montecarlo, Arroyo Doradito: MACN23695 (skull); Parque Nacional Iguazú: MHNCI3828 (skull); Parque Nacional Iguazú, Area Cataratas: MACN24909 (skin); Rio Aguaraiguazú Superior: MACN48.294 (skull); Ruta Nacional N° 14, 5 km al N de San Pedro: MACN24896 (skin); **BRAZIL:** **Espírito Santo:** Colatina: MBML216 (skin and skull); Reserva Florestal de Linhares ES CVRD final da estrada do Parajá: MBML1837 (skull and skeleton); Rio do Norte, Santa Leopoldina: MBML2069 (skin and skull); Santa Teresa: MBML2418 (skin and skull), MBML381 (skin and skull), MBML1771 (skull), MBML395 (skin and skull), MBML314 (skin and skull), MBML2028 (skin), MBML279 (skin), MNRJ3889 (skin); MNRJ5885 (skull); Serra do Mamão, São Roque do Canaã: MBML2452 (skin and skull); **Unknown locality:** MNRJ49356 (skin); **Mato Grosso:** Pantanal: MPEG23854 (skin and skull); **Minas Gerais:** Viçosa: MNRJ4247 (skin and skull), MNRJ1363 (skin); BR 262-MG (near the border of the states of Minas Gerais and Espírito Santo): MBML1957 (skin and skull); Rio Caparaó, Serra do Caparaó: AMNH80396 (skin and skull); **Paraná:** Agudos do Sul: MHNCI3858 (skull); Bela Vista, Morretes: MHNCI13402 (skin and skull); Campina Grande do Sul: MHNCI3859 (skull); Candói: MHNCI3862 (skin and skull); Capão Rico, Fazenda Pirai-Guarapuava: MHNCI52 (skin and skull); Colombo: MHNCI3867 (skin and skull), MHNCI3861 (skull); Estação Ecológica do Caiuá, Diamante do Norte: MHNCI5714 (skin and skull); Estrada do Encantamento, Rio Iraí, Piraquara: MHNCI2672 (skin and skull); Fazenda Lagoa, Castro: MHNCI124 (skin and skull); Fazenda Banestado, Cajuru, Jaquariaíva: MHNCI5573 (skull); Parque Nacional da Foz do Iguacu, Foz do Iguacu: MHNCI4378 (skin and skull); Horto São Nicolau, Arauco Florestal, Arapoti: MHNCI5993 (skin and skull); Paulo de Frontim, BR 153: MHNCI3982 (skull); Palmeira: MHNCI5835 (skin and skull); Pinhão: MHNCI5712 (skin and skull); Relógio, Prudentópolis: MHNCI2740 (skull); Represa do Passaúna, Curitiba: MHNCI3868 (skull); Sertanópolis: MHNCI3739 (skin and skull); **Unknown locality:** AMNH36225 (skin); **Rio de Janeiro:** Angra dos Reis: MNRJ3133 (skin); Nova Friburgo: MZUSP2810 (skin and skull); São Francisco, Jacarepaguá: MNRJ6693 (skin and skull); Teresópolis: MNRJ3137 (skin); Teresópolis, Fazenda Boa Fé: MNRJ7261 (skull). **Rio Grande do Sul:** Caxias do Sul: MNRJ44359 (skin); Pinambi: MZUSP3188 (skull); Rio Pardo, BR 290, km 141: MPEG22183 (skin and skull), São Lourenço: AMNH36948 (skin); Unknown locality [Hensel (1872) did not give a precise locality where the specimens were collected]: ZMB-MAM21229 (skull) and ZMB-MAM21231 (skull) (syntypes of *Felis*

guttula Hensel, 1872). **Santa Catarina:** Corupá: MZUSP1765 (skin and skull); Garuva: MHNCI3864 (skin and skull); Jaraguá do Sul: ZMB21081 (skull), ZMB21097 (skull), ZMB21120 (skull), ZMB 21122 (skull). **São Paulo:** Bragança Paulista: MZUSP27683 (skin, skull and skeleton); Campos do Jordão: MZUSP2137 (skin); Conchas: MZUSP13796 (skin and skull); Dourado: MZUSP24234 (skin); Eugênio Lefèvre, Santo Antônio do Pinhal: MZUSP9912 (skin and skeleton); Franca: MZUSP810 (skin and skull); Guareí, Fazenda Fortaleza: UFMT26 (skin); Iguape: MZUSP2740 (skin and skull); Iporanga (Lajeado): MZUSP6549 (skin and skull); Itaquaquecetuba: MZUSP32633 (skin, skull and skeleton); Itararé: MZUSP1168 (skull); Itatiba: MZUSP3724 (skin); Ituverava: MZUSP2971 (skull); Lins: MZUSP6262; Paranapiacaba: MZUSP401 (skull); Piedade: MZUSP6457 (skin); Ponte Alta: MZUSP6456 (skin); Ribeirão Fundo: FMNH94319 (skin, skull and skeleton); Rio Grande: MZUSP2321 (skin and skull), MZUSP2360 (skin and skull), MZUSP2362 (skull); São Paulo (Santo Amaro): MZUSP6459 (skin and skull); Serra da Bocaina: MNRJ50821 (skin); Tamanduá (Rio Ipiranga), Descalvado: MZUSP10425 (skin and skeleton); Ubatuba: MZUSP1877 (skull), MZUSP1878 (skin and skull); Valparaíso: MZUSP3799 (skin and skull), MZUSP3811 (skin and skull); **Unknown locality:** MZUSP1090 (skull), MZUSP1393 (skull), MZUSP1395 (skull), MZUSP2438 (skin and skull), MZUSP6728 (skin and skull). **Unknown locality:** FMNH296 (mounted), ZMB58116 (skull). **PARAGUAY:** **Caaguazú:** Rio Yuqueri: MCZ30269 (skin), MCZ30270 (skin; melanistic); **Ñeembucú:** Rio Yguazú: MCZ28678 (skin and skull); **Unknown locality:** MACN31.191 (skin).

APPENDIX II

Gazetteers

***Leopardus tigrinus* (Schreber, 1775)** – The numbers in the map (Fig. 8) refer to the following localities: **1.** Caracas, 9.4 km N. Hotel Humboldt, District Federal, Venezuela; **2.** 100 m Reactor RV-1 Del Ivic, Miranda, Venezuela; **3.** Autopista Coche-Tejerías, Distribuidor Los Totumos, Miranda, Venezuela; **4.** Carrillo, S Llano (Llanuras) de Santa Clara, San Jose, Costa Rica; **5.** Yamayaujaina, Rio Negro, Serranía de Perijá, Zulia, Venezuela; **6.** Cartago, Cartago, Costa Rica; **7.** Pozo Azul, Pirris, Costa Rica (type locality of *Felis carrikeri* Allen, 1904); **8.** Montes de la Sierra, Merida, Venezuela; **9.** near Merida, páramo de San Antonio (3,000 m), Merida, Venezuela; **10.** Sierra Nevada, Merida, Venezuela; **11.** Porto Ordaz, Bolívar, Venezuela; **12.** Páramo El Zumbador, Táchira, Venezuela; **13.** 2 km NW Represa Guri 1 km & Alcabala Obra, Bolívar, Venezuela; **14.** El Manteco, 28 km SE, Los Patos, Bolívar, Venezuela; **15.** Serranía de Los Pijiguas 140 km SW de Caicara, Bolívar, Venezuela; **16.** Sierra de Lema km 753, Bolívar, Venezuela; **17.** Villa de Leyva, Mamarramos, Boyacá, Colombia; **18.** Onoribo, on Para River, 5 km of Paranam, about 25 km S of Paramaribo, Para District, Suriname; **19.** Coper, Boyacá, Colombia; **20.** cuenca alta del rio Tapias, Neira, Caldas, Colombia; **21.** Cayenne, French Guiana (type locality of *Felis tigrina* Schreber, 1775); **22.** Saramaca District, Suriname; **23.** Reserva Florestal Bremen, Circasia, Quindío, Colombia; **24.** Bogotá, Cundinamarca, Colombia; **25.** Villavecencia, Meta, Colombia; **26.** Río Chili, South of Manizales, Tolima, Colombia; **27.** Rio Negro frente Isla Chicharral, Amazonas, Venezuela; **28.** Leticia, Moscopán, Cauca, Colombia; **29.** Las Pabas (= Valle de Las Papas), near San Antonio, Cauca, Colombia (type locality of *Margay caucensis* Allen, 1915); **30.** Santa Elena, Antioquia, Colombia (type locality of *Margay tigrina elenae* Allen, 1915); **31.** Aproximado 3 km S San Carlos de Rio Negro, Amazonas, Venezuela; **32.** Uribe, Cauca, Colombia; **33.** Dadanawa Ranch, 60 mi. E, Rupununi, Guyana; **34.** Malvatá, Cauca, Colombia; **35.** Charguayaco, Cauca, Colombia; **36.** Sabanetas, Cauca, Colombia; **37.** Totoro, Cauca, Colombia; **38.** La Quintana, Cauca, Colombia; **39.** La Plata, Vereda La Segoviana, Huila, Colombia; **40.** Huila, Andalucía, Colombia; **41.** Almaguer, Cauca, Colombia; **42.** Charguayaco, Cauca, Colombia; **43.** San Adolfo, Huila, Colombia; **44.** Florencia, Caquetá, Colombia; **45.** El Tambo, Cauca, Colombia; **46.** P.N.N. Volcan Galeras, Nariño, Colombia; **47.** Estrada Campo Verde, Porto Peaton, Amapá, Brazil; **48.** Alonguineho, Mojanda (south), Pichincha, Napo, Ecuador; **49.** Mt. Pichincha, Napo, Ecuador; **50.** Puerto Leguizamo, Río Putumayo, Amazonas, Colombia; **51.** Rio Chalpichico entre Papallacta y Cuyuja, Napo, Ecuador; **52.** San Francisco de Las Pampas, Cotopaxi, Ecuador; **53.** Pozuzo, Oxapampa, Pasco, Peru; **54.** Chanchamayo, Chanchamayo, Junín, Peru; **55.** La Florida (región Alto Yurinaki), Junín, Peru; **56.** San Juan, Sandia, Puno, Peru; **57.** Río Carapari, Angostuta, Salta, Argentina.

***Leopardus emiliae* (Thomas, 1914)** – The numbers in the map (Fig. 11) refer to the following localities: **1.** Óbidos, Pará; **2.** Fazenda Carrapato (João Cativo), Itapipoca, Ceará, Brazil; **3.** Sítio Novo, Boa Lembrança, Grajaú, Maranhão, Brazil; **4.** Rio Jamari, Terra Santa, Pará, Brazil; **5.** Tijuco, Aquiraz, Ceará, Brazil; **6.** Macapá, São Benedito, Ceará, Brazil; **7.** Comunidade Balança, Caridade, Ceará, Brazil; **8.** Serra do Baturité, Mulungu, Ceará, Brazil; **9.** Ipu, Ceará, Brazil (type locality of *Felis emiliae* Thomas, 1914); **10.** Cratéus, Ceará, Brazil; **11.** Barra do Corda, Maranhão, Brazil; **12.** Iguatu, Ceará, Brazil; **13.** Jaguaribe, Ceará, Brazil; **14.** Fazenda Juazeiro, Santana do Matos, Rio Grande do Norte, Brazil; **15.** Aldeia do Ponto, Maranhão, Brazil; **16.** Cuité, Paraíba, Brazil; **17.** Várzea (Sítio Coreia), Paraíba, Brazil; **18.** REBIO Guaribas, Área II, Estrada de Jacaraú, 300 m da sede, Mamangape, Paraíba, Brazil; **19.** Tabuleiro de Patrocínio, Usina São João, Paraíba, Brazil; **20.** São Mamede, Paraíba, Brazil; **21.** Olivados, Paraíba, Brazil; **22.** Comunidade Soledade, Paraíba, Brazil; **23.** Juazerinho, Paraíba, Brazil; **24.** Pocinhos, Paraíba, Brazil; **25.** Estrada de Lucena a Santa Rita, Paraíba, Brazil; **26.** Distrito de Socorro, Olho d'Água, Paraíba, Brazil; **27.** Serra do Araripe, Crato, Ceará, Brazil; **28.** Uruçuí, Piauí, Brazil; **29.** São João do Cariri, Paraíba, Brazil; **30.** Fazenda Genipapo, Exu, Pernambuco, Brazil; **31.** BR 232, Distrito de Varzinha, Serra Talhada, Pernambuco, Brazil; **32.** Ladeira do Timbó, BR 232, km 29, Moreno, Pernambuco, Brazil; **33.** Carnaubeira (= Carnaubeira da Penha), Pernambuco, Brazil; **34.** São Caetano, Pernambuco, Brazil; **35.** vicinity of the REBIO Serra Negra, Inajá, Pernambuco, Brazil; **36.** Quebrângulo, Alagoas, Brazil; **37.** Fazenda São Manuel, Viçosa, Alagoas, Brazil; **38.** between the municipalities of Pilar and Atalaia, Alagoas, Brazil; **39.** BR 153, Paraíso do Tocantins, Tocantins, Brazil; **40.** Senhor do Bonfim, Bahia, Brazil; **41.** Barreiras, Bahia, Brazil; **42.** Palma, Goiás, Brazil; **43.** BR 101, km 397, ponte Rio Ouriço, Bahia, Brazil; **44.** Agroceres, Moçam-

binho, Município de Manga, Minas Gerais, Brazil; **45.** BR 101, km 645, 36 km S do Rio Pardo, Bahia, Brazil; **46.** Rio das Garças, Mato Grosso, Brazil; **47.** Aragarças, Goiás, Brazil.

Leopardus guttulus (Hensel, 1872) – The numbers in the map (Fig. 16) refer to the following localities: **1.** Pantanal, Mato Grosso, Brazil; **2.** São Lourenço, near the border between States of Mato Grosso and Mato Grosso do Sul; **3.** Reserva Florestal de Linhares ES CVRD final da estrada do Parajá, Espírito Santo, Brazil; **4.** Colatina, Espírito Santo, Brazil; **5.** Serra do Mamão, São Roque do Canaã, Espírito Santo, Brazil; **6.** Santa Teresa, Espírito Santo, Brazil; **7.** Rio do Norte, Santa Leopoldina, Espírito Santo, Brazil; **8.** BR 262-MG (near the border of the states of Minas Gerais and Espírito Santo), Minas Gerais, Brazil; **9.** Ituverava, São Paulo, Brazil; **10.** Rio Caparaó, Serra do Caparaó, Minas Gerais, Brazil; **11.** Franca, São Paulo, Brazil; **12.** Viçosa, Minas Gerais, Brazil; **13.** Valparaíso, São Paulo; **14.** Lins, São Paulo, Brazil; **15.** Tamanduá (Rio Ipiranga), Descalvado, São Paulo, Brazil; **16.** Dourado, São Paulo, Brazil; **17.** Nova Friburgo, Rio de Janeiro, Brazil; **18.** Teresópolis, Rio de Janeiro, Brazil; **19.** Ponte Alta, São Paulo, Brazil; **20.** Estação Ecológica do Caiuá, Diamante do Norte, Paraná, Brazil; **21.** Campos do Jordão, São Paulo; **22.** Eugênio Lefèvre, Santo Antônio do Pinhal, São Paulo, Brazil; **23.** Serra da Bocaina, próximo Rio Paca Grande, São Paulo, Brazil; **24.** São Francisco, Jacarepaguá, Rio de Janeiro, Rio de Janeiro, Brazil; **25.** Bragança Paulista, São Paulo, Brazil; **26.** Itatiba, São Paulo, Brazil; **27.** Angra dos Reis, Rio de Janeiro, Brazil; **28.** Sertãozinho, Paraná, Brazil; **29.** Conchas, São Paulo, Brazil; **30.** Fazenda Fortaleza, Guaré, São Paulo, Brazil; **31.** Itaquaquecetuba, São Paulo, Brazil; **32.** Ubatuba, São Paulo, Brazil; **33.** Santo Amaro, São Paulo, São Paulo, Brazil; **34.** Piedade, São Paulo, Brazil; **35.** Paranapiacaba, São Paulo, Brazil; **36.** Rio Grande, São Paulo, Brazil; **37.** Itararé, São Paulo, Brazil; **38.** Horto São Nicolau, Arauco Florestal, Arapoti, Paraná, Brazil; **39.** Ribeirão Fundo, São Paulo, Brazil; **40.** Iporanga (Lajeado), São Paulo, Brazil; **41.** Iguape, São Paulo, Brazil; **42.** Fazenda Lagoa, Castro, Paraná, Brazil; **43.** Relógio, Prudentópolis, Paraná, Brazil; **44.** Rio Yuqueri, Caaguazú, Paraguay; **45.** Paraná, Brazil; **46.** Campina Grande do Sul, Paraná, Brazil; **47.** Palmeira, Paraná, Brazil; **48.** Fazenda Piraf-Guarapuava, Capão Rico, Paraná, Brazil; **49.** Represa do Passaúna, Curitiba, Paraná, Brazil; **50.** Estrada do Encantamento, Rio Iraí, Piraquara, Paraná, Brazil; **51.** Fazenda Banestado, Cajuru, Jaquariaíva, Paraná, Brazil; **52.** Bela Vista, Morretes, Paraná, Brazil; **53.** Parque Nacional da Foz do Iguazu, Foz do Iguazu, Paraná, Brazil; **54.** Parque Nacional Iguazú, Misiones, Argentina; **55.** Colombo, Paraná, Brazil; **56.** Candió, Paraná, Brazil; **57.** Pinhão, Paraná, Brazil; **58.** Arroyo Uruguai, km 10, Misiones, Argentina; **59.** Agudos do Sul, Paraná, Brazil; **60.** Garuva, Santa Catarina, Brazil; **61.** Paulo de Frontim, BR 153, Paraná, Brazil; **62.** Arroyo Aguaray Guazú Inferior, Misiones, Argentina; **63.** Arroyo Aguaray Guazú Superior, Misiones, Argentina; **64.** Departamento General Manuel Belgrano, Misiones, Argentina; **65.** Corupá, Santa Catarina, Brazil; **66.** Jaraguá do Sul, Santa Catarina, Brazil; **67.** Ruta Nacional N° 14, 5 km al N de San Pedro, Misiones, Argentina; **68.** Rio Iguazu, Ñeembucú, Paraguay; **69.** Cuartel Río Victoria, Departamento Guaraní, Misiones, Argentina; **70.** Dos de Mayo, Departamento Cainguás, Misiones, Argentina; **71.** Arroyo Doradito, Departamento Montecarlo, Misiones, Argentina; **72.** Pinambi, Rio Grande do Sul, Brazil; **73.** Caxias do Sul, Rio Grande do Sul, Brazil; **74.** Rio Pardo, BR 290, km 141, Rio Grande do Sul, Brazil; **75.** São Lourenço, Rio Grande do Sul, Brazil; **Question mark.** Rio Grande do Sul, Brazil [precise locality unknown; Hensel (1872) did not give a precise locality where the type specimens were collected].