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Body mass estimation for †*Cyonasua* (Procyonidae, Carnivora) and related taxa based on postcranial skeleton

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ABSTRACT

Procyonidae were the first northern placental carnivorans that reached the Neotropics. They are represented by two extinct genera: †*Cyonasua* and †*Chapalmalania* (late Miocene – early Pleistocene). Postcranial elements are only known for †*Cyonasua* and related taxa (†*Parahyaenodon argentinus* and †*Tetraprothomo argentinus*). To obtain highly reliable allometric equations for body mass estimations of fossil procyonids, we performed least squares regressions (multiple and bivariate lineal models) using 51 postcranial linear measurements. The extant sample included 124 taxa corresponding to nine families of Carnivora, with body mass data from the literature. We obtained about 63 equations from diverse combinations of postcranial measurements; 14 of them were selected using several reliability indexes as criteria. Our results show that body masses calculated for †*Cyonasua* range between 12.63 and 28.45 kg, †*P. argentinus* was estimated at 14.41 kg, while †*T. argentinus* at 25.31 kg. Thus, the body mass of †*Cyonasua* would have been at least twice as high as the mean of the extant procyonid *Procyon cancrivorus*. †*Cyonasua* was probably able to fend off predators and quite capable of climbing slowly on thick-enough branches. Other palaeoecological and palaeobiological inferences are discussed.

Introduction

The family Procyonidae comprises six extant genera, five of which, *Bassaricyon* Allen 1876, *Nasuella* Hollister 1915, *Potos* Geoffroy Saint-Hilaire & Cuvier 1795, *Procyon* Storr 1780 and *Nasua* Storr 1780, inhabit South America. *Procyon* and *Nasua* are also recorded as fossils in South America (late Pleistocene–Holocene) at several localities in Argentina, Brazil and Bolivia (Paula-Couto 1970; Soibelzon et al. 2010; Rodriguez et al. 2013). In addition, this family comprises two South American extinct genera: †*Cyonasua* and †*Chapalmalania*, both recorded from the late Miocene to early Pleistocene (Bond 1986; Soibelzon & Prevosti 2007, 2012; Soibelzon 2011). †*Cyonasua* encompasses ten species, †*C. argentina* Ameghino 1885, †*C. brevirostris* (Moreno & Mercerat 1891), †*C. longirostris* (Rovereto 1914), †*C. pascuali* Linares 1981, †*C. groeberi* Kraglievich & Reig 1954, †*C. lutaria* (Cabrera 1936), †*C. clausa* (Ameghino 1904), †*C. robusta* (Rovereto 1914), †*C. argentinus* (Burmeister 1891), and †*C. meranii* (Ameghino & Kraglievich 1925); whereas †*Chapalmalania* includes two species: †*Ch. ortognatha* Ameghino 1908a and †*Ch. altaefrontis* Kraglievich & Olazábal 1959 (Soibelzon 2011).

Procyonids were the first northern placental carnivorans that reached the Neotropics, where they successfully became part of the composite and complex communities formed by ancient South American lineages (marsupials, xenarthrans, notoungulates, litopterns and astrapotheres), New World primates and caviomorph rodents (Reig 1981). They remained as the only placental carnivorans in South America until the late Pliocene, when few new Mustelidae and Canidae taxa are first recorded; the diversity of Carnivora remained low until the Ensenadan, when it was increased by numerous new immigrant taxa and local speciation events (Prevosti & Soibelzon 2012; Soibelzon & Prevosti 2012). For this reason, some authors (e.g. Simpson 1950, 1980; Patterson & Pascual 1972; Werdelin 1987, 2009) proposed that procyonids were responsible for the extinction of South American hypercarnivorous metatherians (Sparassodonta) through competitive displacement, given that the sparassodonts were somewhat similar to fossil procyonids in body size. In contrast, others authors have suggested that sparassodonts were simply undergoing a gradual decline at the time of the arrival of procyonids (Marshall 1977; Forasiepi et al. 2007; Prevosti et al. 2013). Furthermore, most of these metatherians were hypercarnivorous and some were larger than †*Cyonasua*; thus, the former likely occupied different ecological niches and could even have preyed upon the latter, not supporting a replacement scenario (Forasiepi et al. 2007; Soibelzon 2011; Prevosti et al. 2013). Thus, reconstructing the palaeoecology of fossil procyonids is very important for understanding the evolution of South American mammal communities. Despite this, published

paleobiological studies about fossil South American procyonids are relatively scarce (Soibelzon & Prevosti 2007, 2012; Soibelzon 2011; Prevosti & Soibelzon 2012; Prevosti et al. 2013; Tarquini et al. 2017).

According to the palaeoecological reconstruction protocol outlined by Vizcaíno et al. (2010, 2012, 2016), autoecological characterisation of extinct taxa should include at least three key biological features: body size, dietary habits, and substrate use and preference (including posture and locomotion). Body size is one of the most important variables in biological systems, given its correlation with numerous physiological (e.g. metabolic rates, energy cost of locomotion, body temperature, pregnancy duration, age of sexual maturity, number of offspring) and ecological factors (population density, behavioural adaptation, home range size, prey size) (McNab 1973; Peters & Wassenberg 1983; Peters & Raelson 1984; Schmidt-Nielsen 1984; Gittleman 1985; Hildebrand 1988; Johnson 2002; Van Valkenburgh et al. 2004; Vizcaíno et al. 2016). Thus, it is one of the most ecologically significant variables to be estimated for extinct forms.

Although traditionally, dental and cranial measurements have been used for inferring body size, the latter may also be estimated on the basis of information from the postcranial skeleton. Indeed, limb bones are the main elements that support the body and may therefore be more closely correlated to body mass; therefore, not surprisingly they have received more attention in ecomorphological studies (Anyonge 1993; Egi 2001; Andersson 2004; Christiansen & Harris 2005; Ercoli & Prevosti 2011; Figueirido et al. 2011; Toledo et al. 2014; among others). For fossil procyonids, estimations of body mass are almost nonexistent, with few previous attempts based on the dental equation of Van Valkenburgh (1990) (in Wroe et al. 2004; Prevosti & Soibelzon 2012; Prevosti et al. 2013) or dimensional comparison of the skulls (Soibelzon & Prevosti 2007). According to these analyses, average body mass was estimated at around 3–24 kg for †Cyonasua species and about 25–93 kg for †Chapalmalania.

In this context, here we provide allometric equations obtained from a sample of carnivorans with very good representation of procyonids, and the first body mass estimations for South American fossil procyonids (assigned to †Cyonasua or related to them) based on postcranial skeletal elements. Because at present no postcranial remains of †Chapalmalania have been found, this study is focused on specimens of †Cyonasua and related taxa, such as †Parahyaenodon argentinus and †Tetraprothomo argentinus that have been regarded as procyonids (Bordas 1942; Forasiepi et al. 2007).

Material and methods

Institutional abbreviations

AMNH, American Museum of Natural History, Department of Mammalogy, NY, USA. MACN-PV, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', División Paleontología de Vertebrados, Capital Federal, Argentina. MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', División Mastozoología. MLP, Museo de La Plata, Buenos Aires, Argentina. MMP, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia', Mar del Plata, Buenos Aires, Argentina. MNHN, Museo Nacional de História Natural de Montevideo, Uruguay. MNRJ, Museu Nacional, Universidade Federal do Rio do Janeiro, Brasil. USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. ZOOBA-M, Zoológico de Buenos Aires, Colección de biomateriales, Capital Federal, Argentina. ZVC-M, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

Extinct taxa

The fossil specimens studied here are housed in Argentinean institutions, and were recovered from sediments ranging in age from late Miocene to late Pliocene in Argentina. They correspond to adult specimens of †Cyonasua and related taxa such as †Parahyaenodon argentinus, which has been reassigned by Forasiepi et al. (2007) to the Procyonidae. In the same way, †Tetraprothomo argentinus, originally described by Ameghino (1908b) as a hominid, was reassigned as a procyonid by subsequent discussions of its systematic position (Bordas 1942; Forasiepi et al. 2007).

The fossil procyonid taxa referred to †Cyonasua and related taxa included in this study are listed below:

MACN-PV 2352 †Cyonasua sp. Location and Age: Catamarca province, Argentina. Huayquerian (late Miocene). Skeletal elements: right astragalus and calcaneus, and a phalanx.

MACN-PV 6229 †Cyonasua sp. Location and Age: La Pampa province, Argentina. Huayquerian (late Miocene). Skeletal elements: incomplete skull, mandible with canine and molars and a complete left astragalus.

MACN-PV 6237 †Cyonasua sp. Location and Age: Buenos Aires province, Argentina. Chapadmalalan (late Pliocene). Skeletal elements: complete right femur.

MACN-PV 8209: †C. longirostris (Holotype of †Amphinasua longirostris) Catamarca province, Argentina. Huayquerian (late Miocene). Skeletal elements: skull and mandible with almost complete teeth. Proximal and distal epiphysis of right femur, fragments of pelvis, sacrum and 12 vertebrae and fragments.

MLP 04-VI-10-1. †Cyonasua sp. Location and Age: Miramar area, Buenos Aires province, Argentina. Chapadmalalan (late Pliocene). Skeletal elements: almost complete skull, mandible and dental series. Axis, and other vertebral fragments. Right incomplete scapula, fragments of right and left humerus, left radius lacking the proximal epiphysis, left elements of ulna; hamate; pisiform; metacarpal and two phalanges.

MLP 35-X-04-4 †Cyonasua sp. (Procyonidae indet.). Location and Age: Miramar area, Buenos Aires province, Argentina. Chapadmalalan (late Pliocene). Skeletal elements: distal epiphysis of right humerus.

MLP 29-X-08-18 †Cyonasua sp. Location and Age: Catamarca province, Argentina. Huayquerian (late Miocene). Skeletal elements: distal epiphysis of right humerus.

MMP 5178 †Cyonasua sp. Location and Age: Miramar area, Buenos Aires province, Argentina. Chapadmalalan (late Pliocene). Skeletal elements: partially complete pelvic girdle, right femur and tibia, almost complete left fibula, right astragalus and calcaneus.

MACN-PV 4339 †Tetraprothomo argentinus. Location and age: Monte Hermoso area, Buenos Aires province, Argentina. Montehermosan (late Miocene-early Pliocene). Skeletal elements: distal half of left femur.

MACN-PV 8073 †*Parahyaenodon argentinus*. Location and Age: Monte Hermoso area, Buenos Aires province, Argentina. Montehermosan (late Miocene-early Pliocene). Skeletal elements: incisor, upper and lower left canine, premolar. Proximal radius, uncompleted ischium, two caudal vertebrae. Elements of left foot including calcaneus, astragalus, tarsal elements, metatarsals and phalanges.

Extant taxa

The extant sample utilised in this study includes 124 adult and subadult individuals corresponding to nine families and 21 species of Carnivora (see Appendix 1) spanning the range of terrestrial-cursorial to arboreal habits. Previous authors (Diniz-Filho & Vieira 1998; Egi 2001; Diniz-Filho & Tôrres 2002) have suggested a strong phylogenetic pattern regarding body size for many carnivorans; consequently, to take this into account and minimise the bias introduced by phylogeny, our sample includes the closest living relatives of the extinct genera studied, as well as a wide spectrum of body mass values and taxonomic diversity, as suggested by Mendoza et al. (2006) and Figueirido et al. (2011).

Average body mass was taken from the literature and ranges between 0.25 and 103 kg in this sample (Table 1). In most cases, body mass was calculated as the average of several values mentioned in the literature and between sexes, except in the case of *Tremarctos ornatus* in which only females were included. Among procyonids, *Nasuella olivacea* was excluded from the analyses due to the insufficient number of available specimens.

Measurements and abbreviations

Fifty-one postcranial measurements were selected on the basis of their availability given the fragmentary nature of the fossil materials; all measurements were taken with digital calipers. Body mass estimations were calculated from measurements of the scapula, humerus, ulna, femur, tibia, astragalus and calcaneus (Figures 1 and 2). For comparison purposes, we also calculated the postcranial equations for carnivorans proposed by Anyonge (1993) and Figueirido et al. (2011). Furthermore, we computed a cranio-dental equation proposed by Van Valkenburgh (1990) based on m1 mesio-distal length for a few fossil taxa in which this element was preserved.

Equations, both new to this work and previously published, are designated with an initial letter followed by a number: astragalus, a1-2, calcaneus, c1-2; femur, f1–f5; humerus, h1–h3; scapula, s1-2; skull, sk1-3; tibia, t1-2; ulna, u1.

Statistical procedures

The variables (mean body mass and limb measurements) were log10-transformed prior to the analysis to reduce dimensionality and ensure linear relationship. Allometric equations were obtained by least squares regression, through multiple and bivariate lineal models for each postcranial element from the extant sample.

Considering that the coefficients of correlation (r) or determination (r^2) may not be sufficient to evaluate the predictive power of the regression equations, we calculated the Percent Prediction Error (%PE) to select the most reliable equations among those

Table 1. Extant species used in the statistical analyses with indication of body mass average values taken from the literature.

Taxon	BM (kg)	References
Procyonidae		
Procyon cancrivorus	8.5	Canevari and Vaccaro (2007)
Potos flavus	3	Grzimek (1990)
Nasua narica	4.7	Gompper (1995)
Nasua nasua	4.3	Gompper and Decker (1998)
Procyon lotor	6.4	Jones et al. (2009)
Bassaricyon	1.4	Helgen et al. (2013)
Bassariscus astutus	1.01	Jones et al. (2009)
Ailuridae		
Ailurus fulgens	4.5	Wilson and Mittermeier (2009)
Mustelidae		
Eira barbara	4.13	Jones et al. (2009)
Conepatus chinga	2	Kasper et al. (2012)
Galictis cuja	1.37	Jones et al. (2009), Wilson and Mittermeier (2009)*
Lyncodon patagonicus	0.225	Jones et al. (2009)
Meles meles	11.88	Jones et al. (2009)
Gulo gulo	15.1	Grzimek (1990), Pasitschniak-Arts and Larivière (1995)*
Ursidae		
Melursus ursinus	103.7	Jones et al. (2009), Wilson and Mittermeier (2009)*
Tremarctos ornatus	70 f.	Wilson and Mittermeier (2009)
Viverridae		
Arctictis binturong	13	Jones et al. (2009)
Paradoxurus hermaphroditus	3.2	Jones et al. (2009)
Nandinidae		
Nandinia binotata	2.17	Jones et al. (2009)
Felidae		
Leopardus geoffroyi	4.8	Wilson and Mittermeier (2009), Lucherini et al. (2006)*
Canidae		
Lycalopex gymnocercus	5	Jones et al. (2009), Wilson and Mittermeier (2009)*

Abbreviations: BM, body mass average including females and males; f, body mass for females only. The asterisk (*) indicates body mass averaged from listed literature sources.

calculated. This indicator was computed using raw data (weight in kg.) as follows: %PE = [observed−predicted]/predicted × 100 (Smith 1981). To assess the possible bias stemming from the use of log-transformed variables, we applied the 'Ratio Estimator' (RE) of Snowdon (1991).

All calculations were performed using the statistical software Past 3.09 (Hammer et al. 2001) and MS Excel 2013.

Analysis of phylogenetic signal

In order to evaluate the possible existence of phylogenetic pattern regarding body mass, two phylogenetic comparative methods were performed on the log-transformed variables: Orthonormal decomposition analysis (Ollier et al. 2006) using the R package ade4 (Dray & Dufour 2007) and Abouheif C-mean test (Abouheif 1999) using the R package adephylo (Dray & Jombart 2008). Neither method requires branch lengths and the null hypothesis (H_0) is complete absence of phylogenetic dependence.

For this purpose, a phylogenetic tree for extant taxa was built according to the phylogenetic hypotheses of Nyakatura and Bininda-Emonds (2012) and Koepfli et al. (2007) (see Supplemental Material).
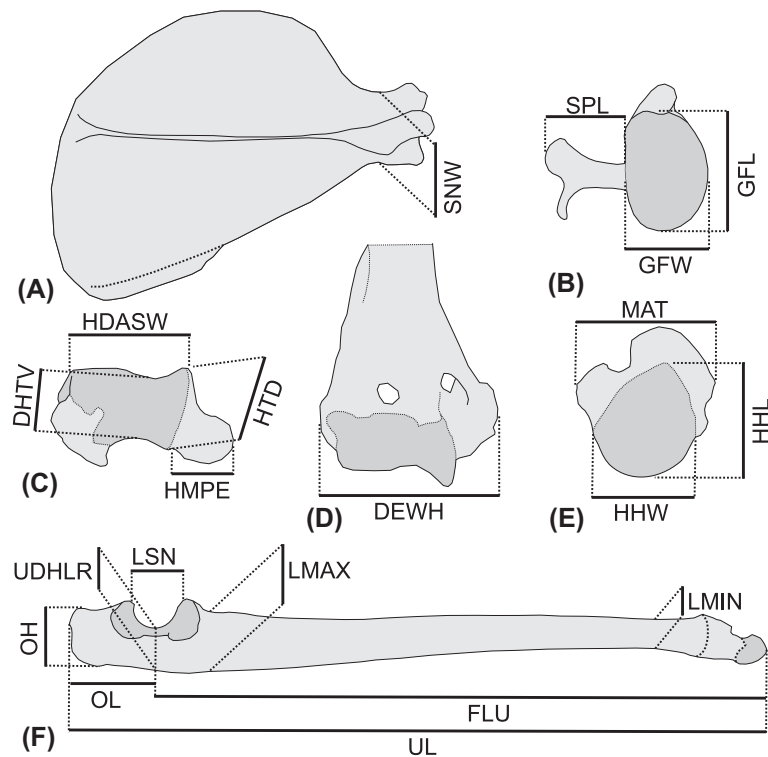
Figure 1. Abbreviations and definitions of forelimb osteological measurements used in the regression analyses. Illustrations based on *P. cancrivorus*. A: lateral view of right scapula, SNW scapula neck width, B: glenoid fossa view of right scapula, GFL glenoid fossa length, GFW glenoid fossa width, SPL scapular spine length. C: distal view of humeral distal epiphysis, HDASW humeral distal articular surface width, HTD humeral trochlea depth, DHTV depth of humeral trochlear valley, HMPE medial protrusion of humeral medial epicondyle. D: anterior view of distal epiphysis of right humerus, DEWH distal epiphysis width of humerus. E: right humerus, proximal view with anterior aspect upward, HHL humeral head length, HHW humeral head width, MAT maximum breath between tubercles. F: lateral view of right ulna, UL ulnar length, OL olecranon length, OH olecranon height, LSN proximo-distal length of semilunar notch, LMAX antero-posterior maximum length of ulnar diaphysis, LMIN antero-posterior minimum length of ulnar diaphysis, UDHLR depth of ulnar diaphysis at middle of lunate recess, FLU functional length of ulna.

Results

Both phylogenetic tests were not significantly different from the null hypothesis, therefore indicating low or absent correlation between tree topology and the variables studied herein (see Supplemental Material for these results). Thus, we conclude that the carnivoran data sample used in this work is not biased by phylogeny, making the application of phylogenetic correction methods unnecessary. We obtained 63 equations from diverse combinations of postcranial measurements. Of these, we selected 14 on the basis of two criteria: those with better statistical fit (lower %PE and high r/r^2) and those allowing estimation of body mass for all specimens of the sample (Table 2 includes these selected equations plus six additional ones from the literature). Thus, all the selected predictive equations presented high correlation and determination coefficient ($r/r^2 > 0.96$), highly significant p values, and RE values that were very close to 1 (Table 2); the latter suggests that the logarithmic conversion of the variables had not necessarily produced a bias. As expected, the equations with best fit and lowest %PE were those obtained from multiple regressions that included several variables. In general terms, almost all limb elements showed low %PE values, with lowest for the femur (11.35), followed by the tibia (11.85) and ulna (12.38). Conversely, the calcaneus and scapula were the estimators with generally highest %PE values (%PE ~15.5–16.6).

Body mass estimations for fossil procyonids obtained both from our postcranial equations and those presented by other authors (using postcranial and cranial variables) are shown in Table 3. This table shows that more than one equation was used to estimate body mass for some specimens; this procedure allowed comparison of results obtained from different bones that yielded similar %PE, taking advantage of the fact that for some fossil specimens several postcranial elements were available.

The body masses calculated for †*Cyonasua* range between 12.63 and 28.45 kg (average ~19.53 kg; see Table 3), with the lowest values corresponding to †*Cyonasua* sp. MACN-PV 2352 (estimated from astragalus and calcaneus) and the highest in the range, to †*Cyonasua* sp. MLP 29-X-08-18 (estimated from a distal humeral fragment). †*Parahyaenodon argentinus* MACN-PV 8073 (also estimated using astragalus and calcaneus) yielded a value of 14.41 kg, similar to that of the smallest †*Cyonasua* (12.63 kg), while the body mass of †*Tetraprothomo argentinus* MACN-PV 4339 was estimated (from a distal femur only) at 25.31 kg.

Our results closely resemble estimated body mass values based on postcranial equations of Anyonge (1993) and Figueirido et al. (2011), except for equation f4 (Anyonge 1993), which presented lower values compared to our results (see Table 3). Body mass estimated from cranio-dental measurements through the equation of Van Valkenburgh (1990) was calculated only for two fossil specimens (see Table 3). Total skull-length (SKL) and occiput-to-orbit length (OOL) estimations were computed for †*Cyonasua* MACN-PV 8209 and do not differ greatly from those calculated based on postcranial measurements. On the other hand, the first lower molar length (MIL) equation calculated for †*Cyonasua*
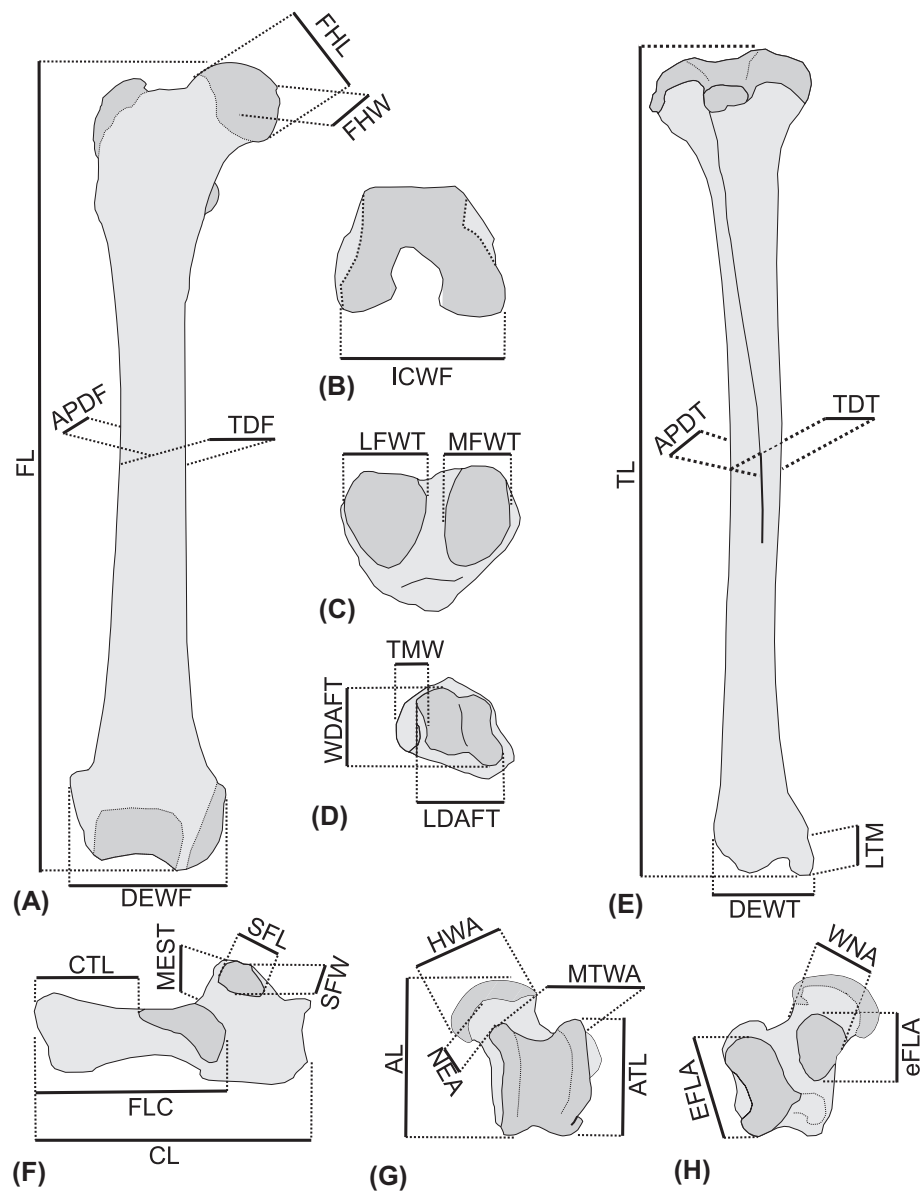
Figure 2. Abbreviations and definition of hindlimb osteological measurements used in the regression analysis. Illustration are based on *P. cancrivorus*. A: anterior view of right femur, FL femur length, TDF transverse diameter of femur (= Fdml of Figueirido et al. 2011), APDF antero-posterior diameter of femur, FHW femoral head width, FHL femoral head length, DEWF distal epiphysis width of femur. B: distal view of right femur epiphysis, ICWF Intercondylar maximum width between lateral and medial edge of both femoral condyles. C: proximal view of tibia epiphysis, LFWT lateral facet width of tibia, MFWT medial facet width of tibia. D: distal view of tibia epiphysis, LDAFT latero-medial length of distal articular facet of tibia, WDAFT anteroposterior width of distal articular facet of tibia, TMW tibia malleolus width. E: anterior view of right tibia, TL tibia length, APDT anterior-posterior diameter of tibia (= Tedap of Figueirido et al. 2011), TDT transverse diameter of tibia (= Tdml of Figueirido et al. 2011), DEWT distal epiphysis width of tibia, LTM length of tibial malleolus. F: dorsal view of right calcaneus, CL calcaneal length, FCL functional length of calcaneus, MEST medial extension of sustentaculum tali, CTL calcaneal tuber length, SFL sustentaculum tali facet length, SFW sustentaculum tali facet width. G: dorsal view of right astragalus, AL astragalar length, ATL astragalar trochlear length, MTWA maximum trochlear width of astragalus, NEA neck extension of astragalus, HWA head width of astragalus. H: plantar view of right astragalus, EFLA ectal facet length of astragalus, eFLA ental facet length of astragalus, WNA width of astragalar neck.

MLP 04-VI-10-1 yielded a body mass value far from expected (see Table 3).

Discussion

Reliability of estimators

While all the equations yielded low %PE values and showed fairly good fit (*i.e.* greatest precision), the best estimators were the equations derived from femur measurements, which supports previous proposals for carnivorans (e.g. Anyonge 1993; Christiansen & Harris 2005; Soibelzon & Tarantini 2009; Figueirido et al. 2011).

Results from the few estimations feasible to be calculated using the postcranial equations of Anyonge (1993) and Figueirido et al. (2011) were similar to our values. On the other hand, the results obtained through Van Valkenburgh's (1990) equations calculated from first lower molar measurements (MIL) were well below the values obtained by us, probably because molar dimensions would be more influenced by dietary adaptations (Van Valkenburgh 1989; Meiri et al. 2005; Soibelzon & Tarantini 2009). Body mass estimations obtained through equations involving SKL and OOL measurements resulted closer to the values obtained from postcranial measurements (see Table 3, specimen MACN-PV 8209).

Table 2. Predictive equations and statistics for each of the studied elements of the postcranial skeleton. In most cases, more than one equation was selected; these were identified by a letter (initial of postcranial element) and a number.

Element	Abbrev.	Equation	%PE	RE	r	r^2
Scapula	s1	−1.9614 + 0.20948 GFL + 1.8567 GFW −0.2583 SPL + 0.70319 SNW	15.12	1.017	0.9905	0.98109
	s2	−2.0401 + 0.63998 GFL + 1.9933 GFW	15.58	1.018	0.9896	0.97923
Humerus	h1	−2.6904 + 1.9899 HHL −2.3998 HHW + 1.2168 HDASW + 0.52229 DHTV −0.17138 HTD + 0.043976 HMPE + 1.5261 MAT	12.52	1.011	0.9934	0.98693
	h2	−2.5976 + 0.82211 HDASW + 0.35023 DHTV + 0.50813 HTD −0.30029 HMPE + 1.2911 DEWH	13.34	1.013	0.9922	0.98455
	h3	−2.3417 + 0.67593 DHTV + 2.0473 HDASW	15.5	1.016	0.9912	0.98255
Ulna	u1	−4.5323 + 12.383 UL + 1.0297 LMIN −0.31909 LMAX + 0.65108 UDHLR −0.92334 OH −1.9129 OL −9.6178 FLU + 1.2824 LSN	12.38	1.01	0.9937	0.98754
Femur	f1	−2.4789 −0.20326 FL + 0.31599 TDF −0.55793 APDF + 0.01156 AFHW + 1.5955 FHL + 0.67657 DEWF + 0.87924 ICWF	11.35	1.01	0.99332	0.98668
	f2	−0.71198−0.90875 FL + 1.3219 TDF + 2.2731 APDF	19.61	1.031	0.9827	0.96565
	f3	−2.9812 + 2.7776 DEWF	14.73	1.016	0.9908	0.98173
	f4	−5.27 + C132.92 FL	25	−	0.95	−
	f5	−1.742 + 2.659 Fdml	14.06	−	0.994	−
Tibia	t1	−1.6787 −0.76495 TL −0.37421 TDT + 0.020557 APDT + 2.0147 DEWT + 0.18901 MFWT + 0.44141 LFWT + 1.376 WDAFT −0.1553 LDAFT + 0.32343 LTM −0.31257 TMW	11.85	1.009	0.995	0.99009
	t2	−2.284 + 1.922 Tdml + 1.229 Tedap	26.45	−	0.983	−
Astragalus	a1	−2.2867 + 2.5721 MTWA −0.25736 ATL + 0.68736 AL + 0.88136 EFLA −0.52812 eFLA −0.34824 HWA + 0.20567 WNA −0.338 NEA	12.95	1.013	0.9928	0.98563
	a2	−1.864 + 2.79 MTWA + 0.11318 ATL −0.36418 HWA + 0.48078 WNA −0.30987 NEA	15.34	1.015	0.9914	0.98298
Calcaneus	c1	−2.7225 −0.053755 CL + 3.3871 FLC + 1.839 MEST −1.604 CTL−0.01703 SFL−0.66563 SFW	16.5	1.003	0.9894	0.97898
	c2	−2.7465 + 3.3601 FLC + 1.8528 MEST−1.6299 CTL−0.020859 SFL−0.67588 SFW	16.63	1.018	0.9894	0.97897
Skull	sk1	−2.27 + 2.97 M_1L	97	−	0.83	−
	sk2	−5.59 + 3.13 SKL	47	−	0.95	−
	sk3	−5.74 + 3.44 OOL	42	−	0.95	−

Notes: Gray rows indicate equations taken from the literature: f4, from Anyonge (1993); f5 and t2, from Figueirido et al. (2011); sk1-3, from Van Valkenburgh (1990). Abbreviations: %PE, Percent Prediction Error of the estimate; r^2, coefficient of determination; RE, 'Ratio Estimator'; SKL total skull length, OOL occiput-to-orbit length and M_1L total length of lower first molar of Van Valkenburgh (1990). Other abbreviations as in Figures 1 and 2.

Table 3. Body mass estimated for each studied specimen on the basis of allometric equations (Table 2).

Element	Eq.	†Cyonasua 1	2	3	4	5	6	7	8	Related taxa 9	10
Scapula	s1	−	17.89	−	−	−	−	−	−	−	−
	s2	−	20.82	−	−	−	−	−	−	−	−
Humerus	h1	−	15.53	−	−	−	−	−	−	−	−
	h2	−	−	**17.63**	−	−	−	−	−	−	−
	h3	−	16.83	19.81	−	−	−	−	28.45	−	−
Ulna	u1	−	**16.25**	−	−	−	−	−	−	−	−
Femur	f1	−	−	−	−	−	−	18.93	−	−	−
	f2	−	−	−	−	19.82	−	22.43	−	−	−
	f3	−	−	−	−	−	21.91	24.57	−	−	**25.31**
	f4	−	−	−	−	18.06	−	15.83	−	−	−
	f5	−	−	−	−	20.99	−	25.01	−	−	−
Tibia	t1	−	−	−	−	20.68	−	−	−	−	−
	t2	−	−	−	−	18.59	−	−	−	−	−
Astragalus	a1	**12.63**	−	−	**19.8**	−	−	−	−	**14.41**	−
	a2	12.66	−	−	20.7	15.76	−	−	−	14.36	−
Calcaneus	c1	15.1	−	−	−	−	−	−	−	13.8	−
	c2	14.87	−	−	−	14.8	−	−	−	13.56	−
Skull	sk1	−	5.94	−	−	−	−	−	−	−	−
	sk2	−	−	−	−	−	23.73	−	−	−	−
	sk3	−	−	−	−	−	22.33	−	−	−	−
Mean body mass					19.53					14.41	25.31

Notes: Gray rows indicate equations taken from the literature: f4, from Anyonge (1993); f5 and t2, from Figueirido et al. (2011); sk1-3, from Van Valkenburgh (1990). Bold font indicates most reliable results. †Cyonasua specimens: 1 MACN-PV 2352; 2 MLP 04-VI-10-1; 3 MLP 35-X-04-4; 4 MACN-PV 6229; 5 MMP 5178; 6 MACN-PV 8209; 7 MCN-PV 6237; 8 MLP 29-X-08-18. Related to †Cyonasua: 9 †Parahyaenodon argentinus MACN-PV 8073; 10 †Tetraprothomo argentinus MACN-PV 4339.

Thus, using these equations could be considered when postcranial remains are not available. In this context, the body mass estimated in Wroe et al. (2004) for †Cyonasua by means of SKL Van Valkenburgh's equation would be the most reliable among those previously calculated by other authors (see Introduction). However, we do not know which specimen of †Cyonasua was used by Wroe et al. (2004) (no collection number was provided)

and whether it also has presents postcranial elements that could be used to corroborate those results.

According to our results, and in agreement with previous works (e.g. Egi 2001; Soibelzon & Tarantini 2009; Figueirido et al. 2011; Toledo et al. 2014), the hindlimb long bones femur and tibia are more reliable than forelimb bones in order to predict body mass. This may be related to the fact that hindlimbs are

influenced mainly by stresses related to supporting body weight (Egi 2001), while forelimb morphology is influenced by diverse factors including locomotor mode and substrate preference (the forelimb participates in numerous functions, such as climbing, digging, grappling of prey, defense, etc.; see Smith & Savage 1955; Taylor 1974; Lynch 2012).

Previous body mass estimations of †*Cyonasua* through dimensional comparisons of the skull or Van Valkenburgh's (1990) dental equations have yielded values ranging from 3 to 13 kg (Soibelzon & Prevosti 2007; Prevosti & Soibelzon 2012). The mass estimates reported in this work do not agree with those obtained from dental measurements (see sk1 in Table 2), a fact that may not be surprising when considering that Van Valkenburgh (1990) used equations with high %PE values and with a data-set that was not focused on predicting procyonid body mass.

The wide range of estimated body mass values for †*Cyonasua* could be expected given the great diversity observed within the genus. Beyond this, it is noteworthy that within this diversity, the highest value of body mass corresponds to specimen MLP

29-X-8-18, which consists only of a distal humeral epiphysis, with a corresponding equation (h3) that presented the highest %PE value among all equations derived for this bone (h1, h2 and h3). Thus, such extreme values should be considered with caution.

Palaeoecological implications

Taxa studied here are diverse not only in estimated body size, but also in stratigraphic and geographical provenance. Our analyses do not show any straightforward biogeographical or biostratigraphical pattern related to body size among them (Figure 3).

As previously mentioned, body size is a major factor in biological systems, strongly correlated to numerous biological characteristics. Many of the relationships between a given ecological variable (home range, metabolic rate, etc.) with body mass can be described by allometric scaling equations derived of the 'quarter-power scaling' (Lindstedt et al. 1986; West et al. 1997). In this context, we explore some palaeoecological implications of our results.
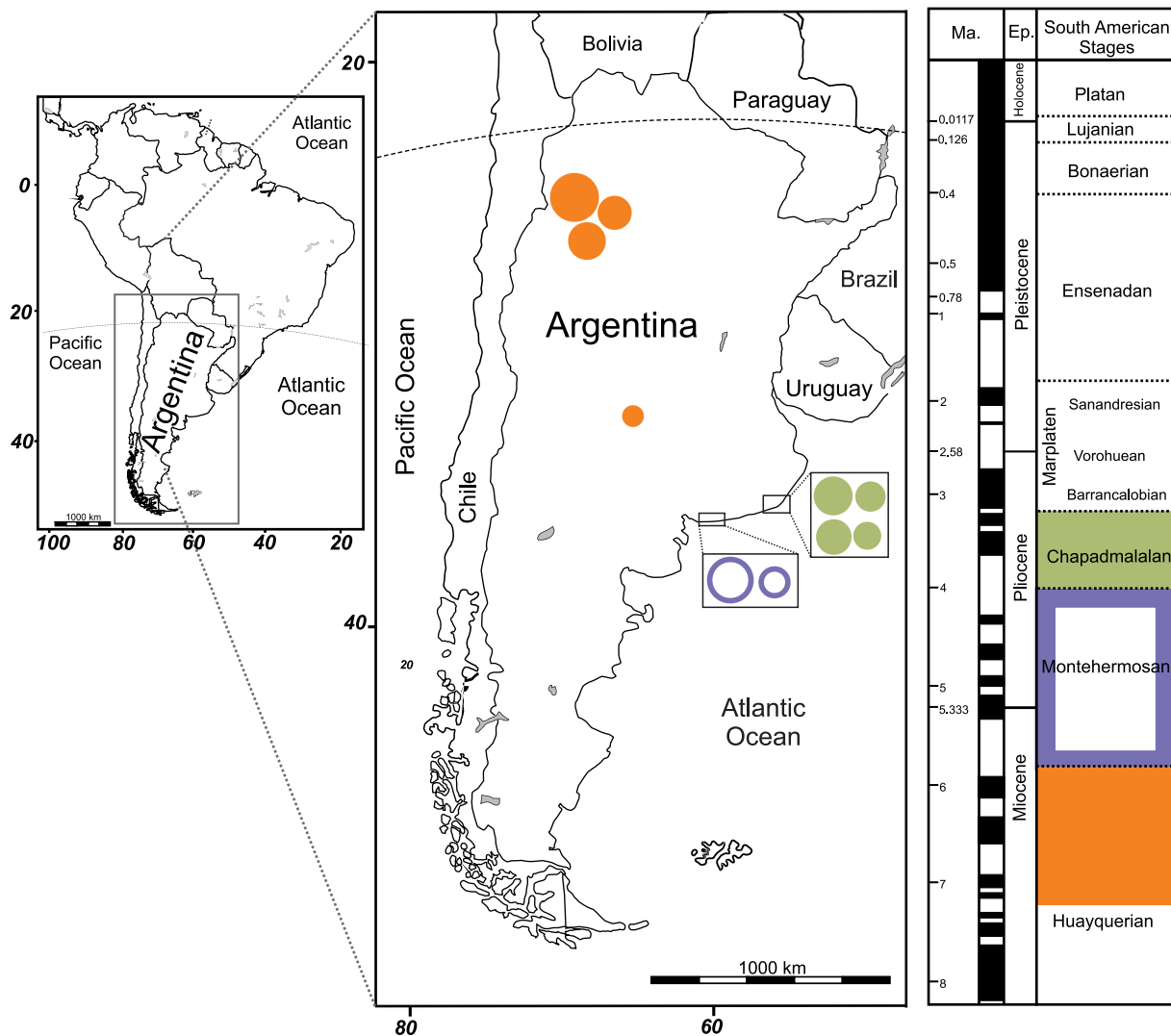

Figure 3. Stratigraphy, geochronology and geographical provenance of fossil materials studied in this work. For stratigraphy and geochronology we followed Cione et al. (2015). Map corresponds to South America and Argentina depicting sites where fossil materials where found. Full circles represent †*Cyonasua* records and open circles indicate related taxa; size differences of circles indicate relative body masses and colors are associated to age.

According to McNab (1980, 2008), body mass is probably the most important factor influencing basal metabolic rate (BMR), and the correlation between them can be described by the allometric equation of Kleiber's Law (Kleiber 1932, 1947), which predicts that total BMR is proportional to mass raised to the ¾ power. In this regard, †*Cyonasua* would have had in average a BMR twice as high as the mean of an extant procyonid of about one-third of its body size (221.75 kJ/d for *P. cancrivorus*, Muñoz-García & Williams 2005). Beyond this, providing a more robust characterisation of this trait would require taking into account the complex interactions of BMR with other factors such as phylogeny, dietary habits, climate, etc.

Home range is another important ecological variable that is positively correlated with body mass (Gittleman & Harvey 1982; Jetz et al. 2004); the slope of allometric equations for home range area vs. body mass approximates isometry, while intercept values vary with latitude and habitat productivity (Lindstedt et al. 1986). Home range is also influenced by other factors such as age, sex and/or diet (see below), among others (Peters & Raelson 1984; Desy et al. 1990; Ottaviani et al. 2006). In extant procyonids, body mass has been found to be positively correlated with home range extent (Wilson & Mittermeier 2009); accordingly, the home range area of †*Cyonasua* would have been larger, possibly twice as large or more, than that of its relatively smaller living counterparts (1.14 km² for *Procyon lotor*, Harestad & Bunnel 1979; similar values were found for *P. cancrivorus*, Arispe et al. 2008).

Body mass of a species is also tightly linked to its trophic status; in general terms, predators are between one and three orders of magnitude larger than their prey (Woodward et al. 2005). †*Cyonasua* and its relatives would have been mesocarnivores (i.e. omnivores with 50–70% of meat in their diet, Van Valkenburgh 2007) given the more trenchant teeth morphology of †*Cyonasua* compared to that of *Procyon* (Soibelzon 2011). This characteristic combined with their comparatively larger body mass and putative climbing capabilities (see below), would have allowed them to exploit diverse trophic resources including a wider variety of prey compared to their living relatives (hypocarnivores, according to Van Valkenburgh 2007) as well as items unavailable on the ground. Furthermore, as previously mentioned, diet type is also related to home range size; thus, animals that consume larger proportions of meat generally have relatively larger home ranges than insectivores and folivores/frugivores (Gittleman & Harvey 1982; Gittleman 1985), also supporting the estimation of a larger home range.

Concerning substrate preference, a previous morphofunctional analysis (Tarquini et al. 2017) suggested that †*Cyonasua* would be a capable climber, but with poorly-developed grasping ability. According to this, these capabilities coupled with its larger size could have restricted agile arboreal locomotion, especially climbing on thin branches. †*Cyonasua* was probably quite capable of climbing slowly on thick-enough branches, similarly to the case of extant medium- to large-sized climbing carnivorans, such as the binturong and the Andean bear. These species (*Arctictis binturong*, ~13 kg, Jones et al. 2009; *Tremarctos ornatus* 60 kg for females and 140 kg for males, Wilson & Mittermeier 2009) spend time on trees, resting or foraging (Goldstein 1991; Nowak 2005; Widmann et al. 2008). †*Cyonasua*, due to its more generalised forelimb morphology (Tarquini et al. 2017), likely did not spend as much time on trees as the abovementioned carnivorans, but could have been able to climb occasionally, possibly to rest or avoid predators, the latter also aided by its relatively large body size (Gittleman 1985; Hildebrand 1988; Van Valkenburgh et al. 2004). Thus, †*Cyonasua* was probably able to fend off predators such as the 'terror birds' (Phorusrhacidae) and some large Sparassodonta, which were the predominant carnivores in South America until the late Neogene (Pascual 1966; Tambussi & Noriega 1996; Tambussi et al. 1999; Tambussi & Degrange 2013; Degrange et al. 2015). Conversely, hypercarnivorous carnivorans are not recorded in South America until the late Pliocene (Prevosti & Pardiñas 2009; Prevosti & Soibelzon 2012; Soibelzon & Prevosti 2012), and they probably did not pose a threat for these extinct procyonids until later times.

Conclusions

- Equations obtained through postcranial measurements were highly reliable, with hindlimb long bones such as the femur and tibia being more reliable than forelimb ones for predicting body mass in procyonids.
- Body mass values for †*Cyonasua* and relatives were in a range between 12.63 and 28.45 kg. Thus, they were at least twice as large as the mean for the largest extant species of the family, *P. cancrivorus*.
- †*Cyonasua* would have had higher BMR and a home range area possibly twice as large as that of its living relatives.
- Their larger body mass coupled with its more carnivorous diet and climbing abilities would have allowed them to exploit a wider variety of prey, as well as avoid some predators.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix 1. List of specimens of extant taxa used in this work.

AMNH: American Museum of Natural History, Department of Mammalogy, NY, USA. MACN Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Col. Mamíferos, Div. Mastozoología. MLP: Col. Mastozoología, Div. Zoología Vertebrados, Secc. Mastozoología, Museo de La Plata, Buenos Aires, Argentina. MNHN: Museo Nacional de História Natural de Montevideo, Uruguay. MNRJ: Museu Nacional do Rio de Janeiro, RJ, Brasil. USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA. ZOOBA-M: Zoológico de Buenos Aires, Colección de biomateriales, Capital Federal, Argentina. ZVC-M: Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

Taxon	Collection number
Procyonidae	
Procyon cancrivorus	MACN 32254, MLP 2110, 1.I.03.25, 1957; MNHN 1229, 3146, 3285, 1268, 2714, 3264; MNRJ 5503.
Potos flavus	AMNH 266597, 266599, 267050, 267607, 267608; MLP 1740; MNRJ 55500, 68610; ZVC-M 5730.
Nasua narica	AMNH 14062, 91173; USNM A 22810, A 49644, 257314.
Nasua nasua	AMNH 30203, 134007, 255871; MACN 5.12, 25862, 33269; MNRJ 79184, 79293, 799349; ZOOBA-M- 0084, -0085.
Procyon lotor	AMNH 135185, 237438, 238271, 245498, 245620; MACN 23573.
Bassaricyon	AMNH 184985; USNM 305748, 305749, 307037, 310666, 395837, 396992, 598996, 598997.
Bassariscus astutus	USNM 135963, 135965, 135966, 137030, 137053.
Ailuridae	
Ailurus fulgens	AMNH 35433, 119474, 119675, 146682, 146778.
Mephitidae	
Conepatus chinga	MACN 28.20, 24007, 24941; MLP 19.XII.02.2.
Mustelidae	
Eira barbara	MLP 1013; MNHN 5518, 95374, 133953.
Galictis cuja	MACN 23519, MLP 15.V.97.42, 2020; MNHN 1158, 2548, 2696, 3233.
Lyncodon patagonicus	MACN 21982; MLP 6.III.36.32, 29.XII.00.17.
Meles meles	AMNH 70604; MACN 5.36; USNM A 22253, 534227.
Gulo gulo	AMNH 149692, 165766; USNM 248216, 265588, 272316.
Viverridae	
Arctictis binturong	AMNH 22906, 35469, 90279, 119600; USNM 197252.
Paradoxurus hermaphroditus	AMNH 35780, 113032, 113771, 113772; USNM 458891.
Nandinidae	
Nandinia binotata	AMNH 35440, 51461, 51469, 55799; USNM 467628.
Ursidae	
Melursus ursinus	AMNH 22896, 35602, 54464, 54467, 150205.
Tremarctos ornatus	MLP 1.I.03.62, 2329.
Felidae	
Leopardus geoffroyi	MLP 9.X.92.1, 27.XII.01.17, 27.XII.01.18, 27.XII.01.22, 20.V.02.1, 1884, 1998.
Canidae	
Lycalopex gymnocercus	MACN 23.910, 24.259, 33.267, 34.317; MLP 15.V.96.5, 190, 1967.