



BODY MASS ESTIMATIONS AND PALEOBIOLOGICAL INFERENCES ON A NEW SPECIES OF LARGE CARACARA (AVES, FALCONIDAE) FROM THE LATE PLEISTOCENE OF URUGUAY

WASHINGTON JONES,¹ ANDRÉS RINDERKNECHT,¹ RAFAEL MIGOTTO,² AND R. ERNESTO BLANCO^{1,3}

¹Museo Nacional de Historia Natural, CC. 399, 11.000, Montevideo, Uruguay, <wawijo@yahoo.com.ar>; <apaleorinder@yahoo.com>;
²Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão travessa 14, n.º 321, 05508–900, São Paulo, Brazil,
<rmigotto@usp.br>; and ³Instituto de Física, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11.400, Uruguay,
<ernesto@fisica.edu.uy>

ABSTRACT—The caracaras belong to a group of falconids with widespread geographical distribution in the Western Hemisphere, particularly in South America. Here we report fossil remains of a new species attributed to the genus *Caracara* from the late Pleistocene of Uruguay. This bird would have had an estimated body mass of 3700 grams, a value that greatly exceeds the maximum body mass reported for living falconids. Apparently, it would have had flying capabilities, in contrast to another paleospecies recently described from the Holocene of Jamaica. This fossil bird was found in association with mammal megafaunal remains and could offer new insights about the role of carnivorous birds in late Pleistocene environments of South America.

INTRODUCTION

CARACARAS, FOREST-FALCONS, falcons, and falconets comprise the family Falconidae, one of the four families of the traditional order Falconiformes, commonly referred to as the diurnal birds of prey (White et al., 1994). The 61 species allocated in ten genera are globally distributed except on the Antarctic continent. Falconids occur in a variety of habitats and exhibit a multiplicity of behaviors and body shapes, ranging from long-winged and fast-flying predatory birds (genus *Falco*) to forest inhabitants with great flight maneuverability (genus *Micrastur*) and to ground-dwelling scavenging birds (genera *Caracara* and *Phalcoboenus*). Based on a phylogenetic analysis of syringeal morphology and molecular data, Griffiths (1999) divided the Falconidae in two subfamilies: subfamily Herpetherinae—which includes the genera *Herpetheres* and *Micrastur*—, and subfamily Falconinae. The latter includes the tribe Caracarini with the genera *Milvago*, *Daptrius*, *Ibycter*, *Caracara* and *Phalcoboenus*; and the tribe Falconini with the genera *Spizapteryx*, *Falco*, *Microhierax* and *Polihierax*. Attempts to reconstruct the evolutionary biogeography of the family suggested that the origin and early diversification of the group may have occurred in South America (Griffiths, 1999); and most of the diversity of extant genera (seven of 10) is concentrated in this part of the world (Ferguson-Lees and Christie, 2001).

The living members of the genus *Caracara* (formerly *Polyborus*, but see Banks and Dove, 1992) are represented by: *Caracara plancus* from Amazon River to Peru, south to Straits of Magellan; and *Caracara cheriway* from southern North America, Cuba, Central America to northern South America (Dove and Banks, 1999). A third and insular species, *Caracara lutosus* from Guadalupe Island, became extinct in the early twentieth century (Greenway, 1967; Dove and Banks, 1999).

The earliest record of the Falconidae family in South America is represented by *Badiastes patagonicus* Ameghino, 1895 from the early Miocene of Patagonia (Ameghino, 1895; Brodkorb, 1964). Recently, the systematic position of two early-middle Miocene species of genus *Thegornis* Ameghino, 1895 was rearranged from Accipitridae to Falconidae (Noriega et al., 2011). There are several fossil species described from Pleistocene–Holocene deposits of North America and West Indies, most of which are referred to the genus *Caracara*. Wetmore (1920) described *Caracara latebrosus* from Holocene

cave of Puerto Rico. *Caracara prelutosus* have been described based on several remains from Pleistocene deposits of Rancho La Brea, California (Howard, 1938). *Caracara creightoni* Brodkorb, 1959, is another paleospecies reported from Pleistocene and probable Holocene deposits of Cuba and the Bahamas (Olson and Hilgartner, 1982; Suárez and Olson, 2001, 2003; Steadman et al., 2007). More recently, Olson (2008) described *Caracara tellustris*, reported from Holocene caves of Jamaica as a conspicuous bird characterized by the presence of several non-flying features.

In this context, we describe herein a large specimen of a new *Caracara* species from the late Pleistocene of southern Uruguay, with a body mass estimation that exceeds the range of any known living species of Falconidae. The material consists of a nearly complete coracoid and femur and other skeletal elements belonging to a single individual.

GEOLOGICAL AND BIOSTRATIGRAPHIC SETTING

The described material was recovered in southern Uruguay (Fig. 1) in fluvial deposits of brown mudstones with calcium carbonate concretions. A nearly complete skeleton of *Glyptodon* sp. was found in association with the fossil bird material studied here. The remains of several mammals including *Glyptodon clavipes* Owen, 1839, *Propaopus* sp., *Eutatus seguini* Gervais, 1867, *Lestodon* sp., *Toxodon* sp., *Macrauchenia patachonica* Owen, 1838, Cervidae indet., *Lagostomus* sp., *Galea* sp. are summarized by Rinderknecht (2006). Rinderknecht (1998) also reported a material of an indeterminate Colubridae from the same site. The bearing sediments of this fauna have been assigned to the late Pleistocene and included in Libertad Formation (Ubilla and Rinderknecht, 2001; Rinderknecht, 2006), although based on lithography it is not possible to rule out that they belong to Dolores Formation, also assigned to the late Pleistocene (Ubilla and Perea, 1999; Ubilla, 1999; Martínez and Ubilla, 2004).

MATERIALS AND METHODS

The allometric relationships obtained by Alexander (1983), Anderson et al. (1985), and Campbell and Marcus (1992) were applied to estimate body masses of the new taxon described here and for *Thegornis musculosus* MPM-PV-3443 using femoral measurements. From the same authors, although using tarso-

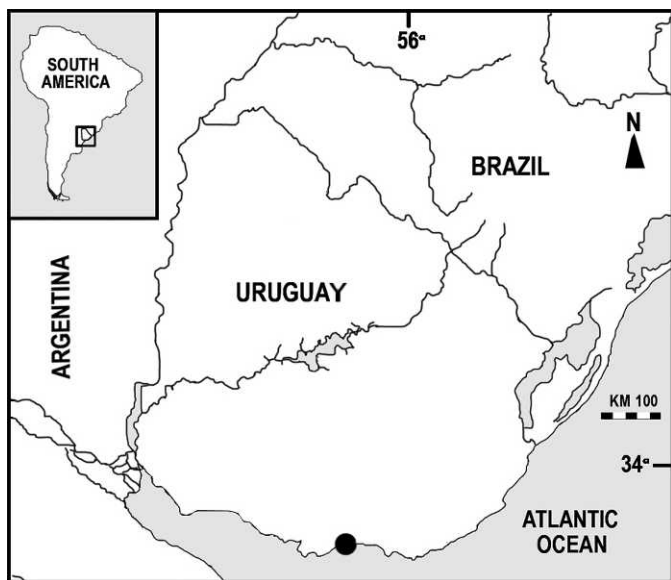


FIGURE 1—Map of Uruguay with solid circle indicating the locality where the holotype of *Caracara major* n. sp. (MNHN 615) was collected.

metatarsal measurements, the body masses of *Thegornis musculosus* MPM-PV-3443 and *Caracara tellustris* USNM 535727 were also estimated. We calculated the circumference of an elliptical cross-section of the femoral mid-shaft of *Thegornis musculosus* by using the width and deep measures (major and minor axes respectively) at that point. The measurements of the coracoidal sternal end width, defined as the distance between the processus lateralis and the angulus medialis coracoidei, were used for body mass estimation from reduced major axis regression with log-transformed data from 28 specimens of 19 species of Falconiformes. The distance from the coracoidal foramen (at proximal rim) to the procoracoidal rim at the base of the procesus procoracoideus and from the angulus medialis coracoidei to the coracoidal foramen (at proximal rim), were measured to calculate the relative position of the coracoidal foramen among extant Caracarini species in comparison to the specimen described here. All measurements were taken with dial calipers.

Taxonomic arrangement and anatomical terminology were based on revision of Griffiths (1999) and White et al. (1994), and Howard (1929) and Baumel and Witmer (1993) respectively. Comparative specimens are listed in Appendix 1; measurements are provided in Table 1 and Appendix 2; measurement data and plot regression are provided in Appendix 2.

TABLE 1—Comparison of coracoidal measurements (in mm) between *Caracara major* n. sp. (MNHN 615) and living species of falconid (mean and range).

| Species (N=number of specimens) | Sternal end width (SW) | Distance of angulus medialis to coracoidal foramen (DAMF) | Distance of coracoidal foramen to procoracoidal rim (DFPR) | DFPR/DAMF |
|--|------------------------|---|--|---------------------|
| <i>Caracara major</i> n. sp. | 35.01 | 60.81 | 9.56 | 0.16 |
| <i>Caracara plancus</i> (N=3) | 23.78 (24.94–22.64) | 44.13 (44.62–43.52) | 9.97 (10.60–9.65) | 0.23 (0.24–0.22) |
| <i>Milvago chimango</i> (N=2) | 12.13 (12.58–11.67) | 23.87 (24.25–23.48) | 5.15 (5.33–4.96) | 0.22 (0.23–0.2) |
| <i>Ibycter americanus</i> | 15.71 | 30 | 6.43 | 0.21 |
| <i>Phalcoeboenus australis</i> (N=3) | 23.63 (24.52–22.68) | 43.26 (43.84–36.76) | 11.91 (13.15–11.29) | 0.28 (0.32–0.26) |
| <i>Herpetotheres cachimanns</i> (N=2) | 17.18 (17.29–17.06) | 35.71 (36.71–34.7) | 6.85 (7.35–6.35) | 0.2 (0.21–0.18) |
| <i>Micrastur semitorquatus</i> (N=2) | 18.01 (19.09–16.92) | 39.01 (42.09–35.93) | 6.96 (7.90–6.01) | 0.18 (0.19–0.17) |

Institutional acronyms.—AMNH, American Museum of Natural History, New York; MHNT, Museu Historia Natural do Taubaté, Sao Paulo-Brazil; MNHN, Museo Nacional de Historia Natural, Montevideo-Uruguay; MPM-PV, Museo Regional Provincial Padre M. J. Molina, Río Gallegos, Argentina; LACMHC, Los Angeles County Natural History Museum, U.S.A.; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A.; WS, William Suárez collection, La Habana, Cuba.

SYSTEMATIC PALEONTOLOGY

Class AVES Linnaeus, 1758
 Order FALCONIFORMES (Sharpe, 1874)
 Family FALCONIDAE Leach, 1820

Remarks.—The fossil material described here is referred to the family Falconidae based on the following characters: the sternal end of coracoid does not strongly flare out as it does in Accipitridae, Cathartidae, Pandionidae and Saggitaridae. The medial angle is acuted or blunt, and the processus lateralis is rounded and thus not forming a distinct sternocoracoid process, this being the typical condition observed in falconids (Jollie 1976).

Genus CARACARA Merrem, 1826

Remarks.—The following character states observed in the material are typical of Caracarini representatives: 1) a wide width of sternal end; 2) the curved shape of distal portion of the linea intermuscularis ventralis; 3) a deep muscular impression of the m. supracoracoideus in dorsal view; 4) the presence of a well marked tuberculum on the processus lateralis coracoidei; 5) the medial direction of the muscular line from the margo supra angularis in coracoidal ventral view.

The stoutness of the coracoidal shaft of the fossil coracoid is comparable to the observed in the species of the genus *Caracara*. Concerning this particular feature, a remarkable difference occurs between the genera *Phalcoeboenus* and *Caracara*, as *Phalcoeboenus*'s coracoidal shaft is more robust and shorter than *Caracara* species. This relative stoutness of the genus *Phalcoeboenus* can also be observed in other skeletal elements (see Olson, 2008, figs. 1–3). The “*impressio musculi obturatorius*” is large and similar in shape to that observed in the other species of the genus *Caracara*.

CARACARA MAJOR new species
 Figures 2–4

Diagnosis.—Remarkable great size; out-of-size range of any known living *Caracara* species and only comparable with fossil species *Caracara tellustris* Olson, 2008. Femoral shaft cross-section expanded mediolaterally, lateral and medial tubercula of muscle gastrocnemialis are leveled at the proximal border of the fossa poplitea, in contrast to other Caracarini species, where the

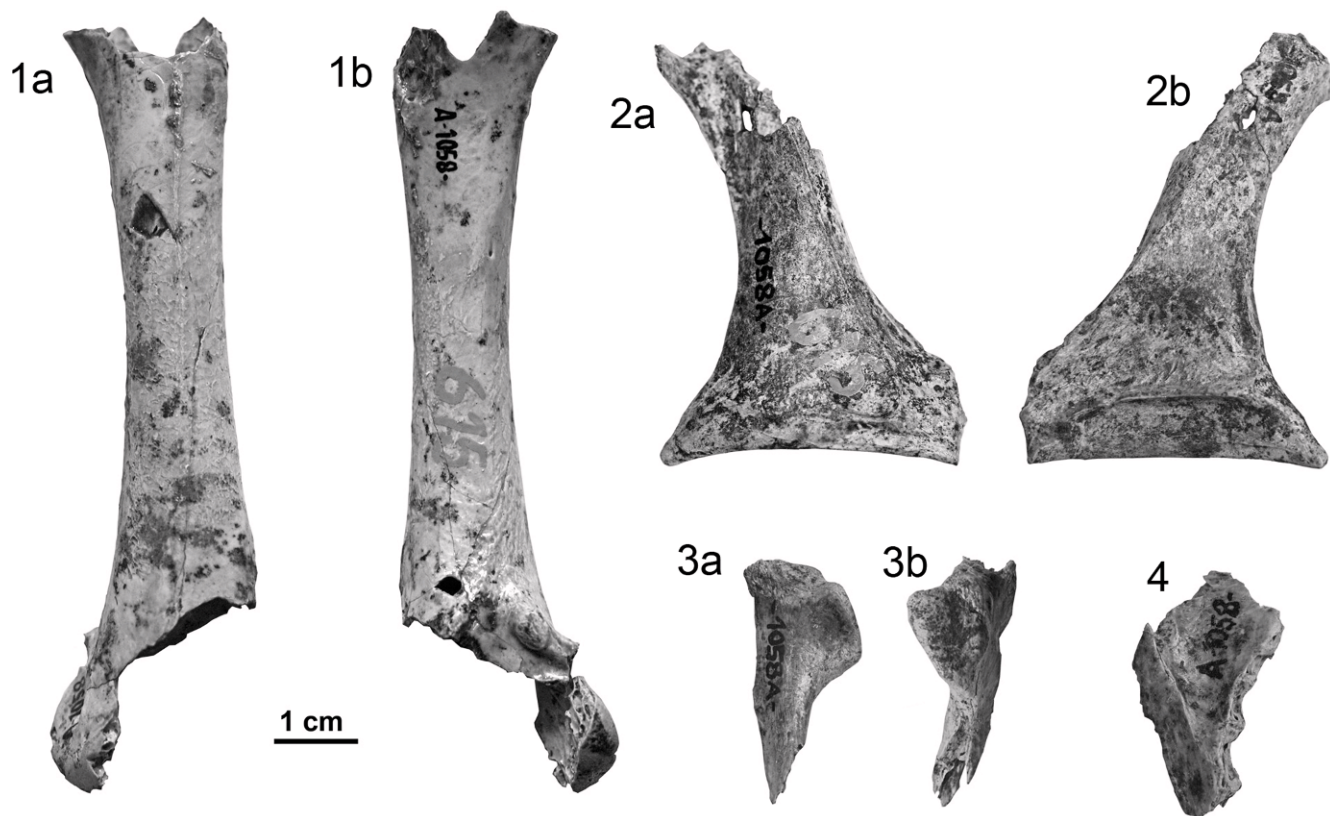


FIGURE 2—Skeletal elements of *Caracara major* n. sp. (MNHN 615) from late Pleistocene of Uruguay. 1a, 1b, anterior and posterior views of left femur, respectively; 2a, 2b, dorsal and ventral views of left coracoid, respectively; 3a, 3b, ventral and dorsal views of proximal end of right scapula, respectively; 4, fragment of left costal margin of sternum. Scale bar=1 cm.

tuberculum m. gastrocnemialis lateralis is more proximally positioned (Fig. 5); coracoidal distal end very expanded in relation to its proximo-distal length; distance of coracoidal foramen to procoracoidal rim shorter than the observed on other Caracarini species (see Fig. 6).

Description.—The omal end of the coracoid is missing. There is a coracoidal foramen rather than a coracoidal fenestra. This condition is typically observed in Herpetotherinae and Caracarini

genera and different from the exhibited in Falconini representatives (Friedmann, 1950).

In contrast to Herpetotherinae genera the procoracoidal process of the coracoid is roughly perpendicular to the coracoidal shaft

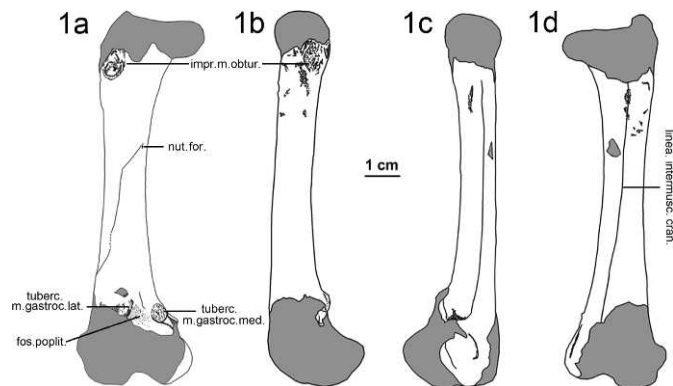


FIGURE 3—Femur views of *Caracara major* n. sp. (MNHN 615). 1a–1d, posterior, lateral, medial, and anterior views, respectively. Gray parts in *C. major* n. sp. are reconstructed assuming geometric scaling with *Caracara plancus*. Abbreviations: fos. poplit.=fossa poplitea; impr.m. obtur.=impression musculi obturatorius; lin. intermusc. cran.=linea intermuscularis cranialis; nut.for.=nutrient foramen; tuberc. m. gastroc. lat.=tuberculum musculi gastrocnemius, pars lateralis; tuberc. m. gastroc. med.=tuberculum musculi gastrocnemius, pars medialis. Scale bar=1 cm.

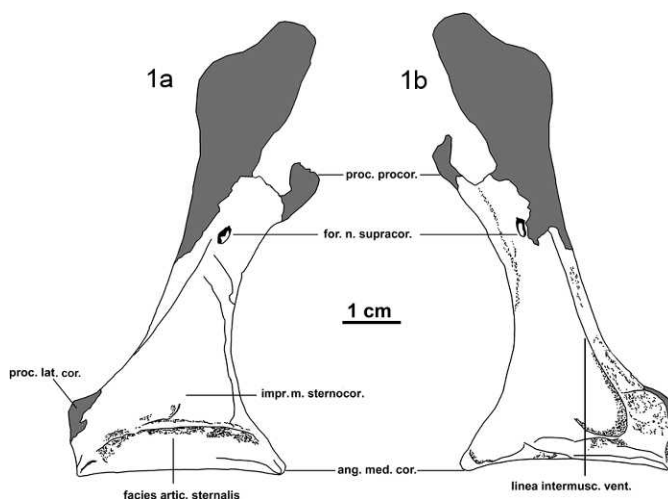


FIGURE 4—1a, 1b, ventral and dorsal views, respectively, of left coracoid of *Caracara major* n. sp. (MNHN 615). Gray parts in *C. major* n. sp. are reconstructed assuming geometric scaling with *Caracara plancus*. Abbreviations: ang. med. cor.=angulus medialis coracoidei; facies artic. sternalis=facies articularis sternalis; for. n. supracor.=foramen nervi supracoracoidei; impr.m. sternocor.=impressio musculi sternocoracoidei; linea intermusc. vent.=linea intermuscularis ventralis; proc. lateralis=processus lateralis coracoidei; proc. procor.=processus procoracoideus. Scale bar=1 cm.

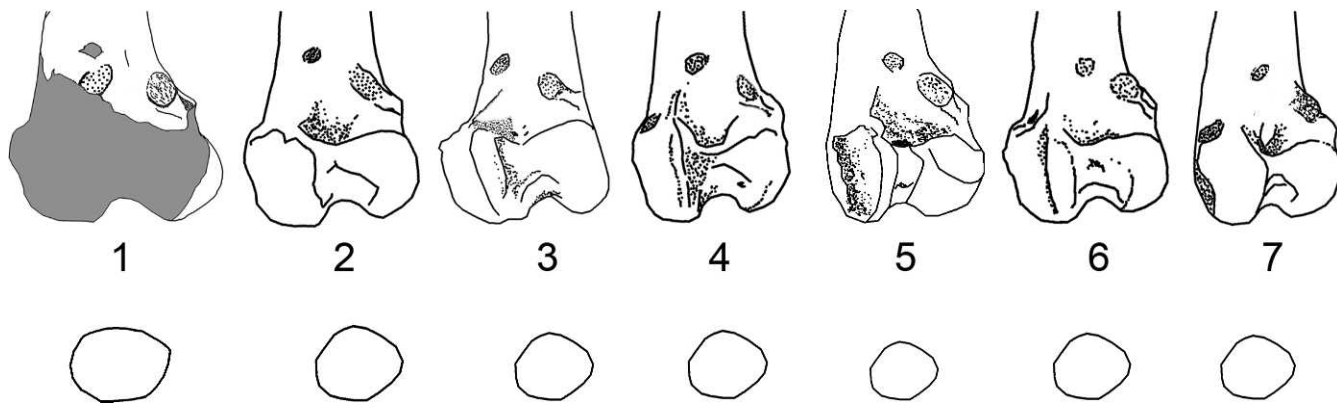


FIGURE 5—Distal portion of left femora of Caracarini species in posterior views (not to scale) and the corresponding cross-sections at mid-shaft. 1, *Caracara major* n. sp. (MNHN 615); 2, *Caracara plancus* (MNHN 6254); 3, *Caracara lutosus* (USNM 19916); 4, *Caracara prelutosus* from late Pleistocene of United States (NHMLAC 4587); 5, *Caracara creightoni* from Holocene of Cuba (WS 1933); 6, *Caracara cheriway* (USNM 553229); 7, *Phalcoboenus australis* (USNM 557987). Views 3–7 based on its depth and width measures and on *C. plancus* cross-section shape; gray parts in *C. major* n. sp. are reconstructed assuming geometric scaling with *Caracara plancus*.

(Baumel and Witmer, 1993; curved shape in *Herpetotherinae*; see Jollie, 1976, fig. 155). The distance of the coracoidal foramen from the procoracoidal rim is comparable to that observed in *Herpetotherinae* genera (see Table 1; Fig. 6). However, the fossil foramen has a more medial position in relation to coracoidal shaft, a condition observed in all Caracarini species.

Scapula.—The corpus after the collum scapulae is missing. The absence of a pneumatic foramen on the sulcus supracoracoideus confirms the impossibility of the fossil belonging to the genera *Herpetotheres* or *Micrastur*.

Sternum.—A fragment of left costal margin of sternum where three intercostal spaces and their respective costal processes can be observed.

Femur.—The epiphyses of the femur are missing. There is a small, shallow nutrient foramen at the third distal portion of the caudal side of shaft. Relative position and shape of the lateral and medial tubercula of the muscle gastrocnemialis on the caudal side are characters cited by several authors in phylogenetic studies of avian groups (Livezey and Zusi, 2006 and references therein). In

C. major n. sp., these tubercula are very pronounced and have an oval shape. Their shape resembles those of Caracarini species. These tubercula are leveled at the proximal border of popliteal fossa. Although intraspecific variation on the position of these tubercula occurs, especially in *Caracara* species (i.e., see Howard, 1938, figs. 6–9), in our extensive examination of extant Caracarini species the particular condition on *C. major* femur (Fig. 5) regarding this feature was never observed. On cranial view, the intermuscular cranial line has the same orientation as in *Caracara* species.

The mediolateral diameter of the femoral shaft of *C. major* is larger relative to anteroposterior diameter, a condition observed only in *Thegornis musculosus* Ameghino, 1895. In contrast, the femoral shaft cross-section of the other falconids has a more circular shape (Fig. 5).

Etymology.—From the Latin word *major*, meaning greater.

Holotype.—MNHN-615: a diaphysis of left femur, a left incomplete coracoid, articular portion of right scapula, a fragment of left costal margin of sternum, and shaft fragments of long

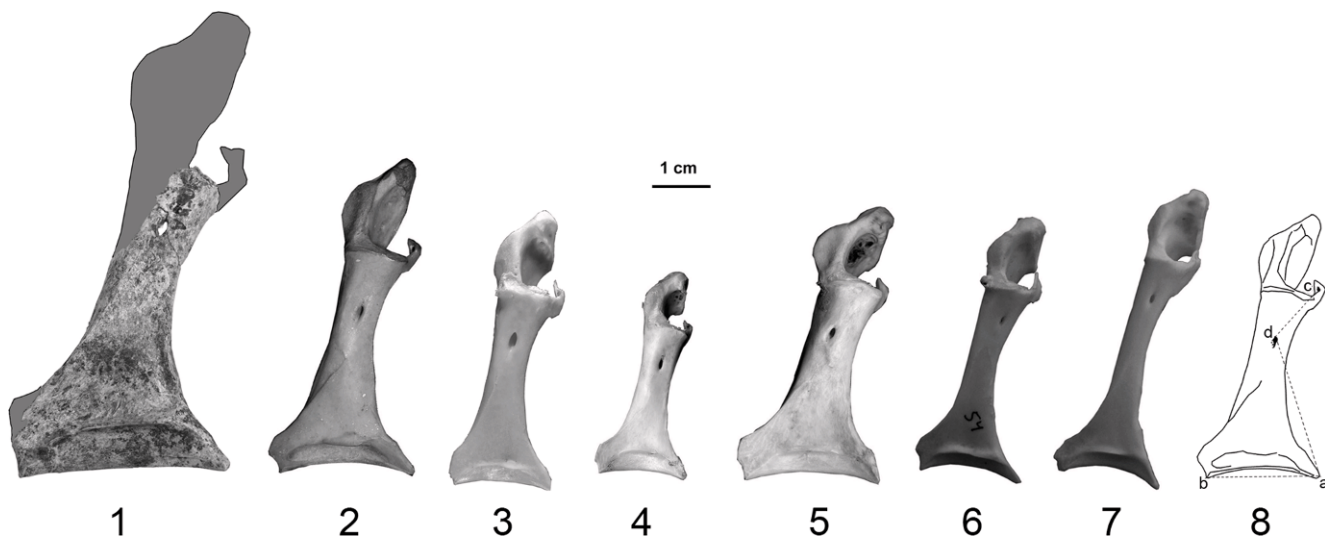


FIGURE 6—Ventral views of left coracoids of falconid species. 1, *Caracara major* n. sp. (MNHN 615); 2, *Caracara plancus* (MNHN 6254); 3, *Caracara cheriway* (USNM 553229); 4, *Ibycter americanus* (USNM 621943); 5, *Phalcoboenus australis* (USNM 557987); 6, *Herpetotheres cachinnans* (MHNT 54); 7, *Micrastur semitorquatus* (MHNT 1463); 8, scheme showing the measurements on the coracoid: segment b–a: coracoidal sterna end width (SW); segment a–d: distance of angulus medialis to proximal rim of coracoidal foramen (DAMF); segment d–c: distance of proximal rim of coracoidal foramen to procoracoidal rim at the base of procoracoidal processes (DFPR). Gray parts in *C. major* n. sp. are reconstructed assuming geometric scaling with *Caracara plancus*. Scale bar=1 cm.

TABLE 2.—Measurements (in mm) of *Caracara major* n. sp. (MNHN 615), *Caracara tellustris* Olson, 2008 and *Thegornis musculosus* Ameghino, 1895. Body mass estimation (in grams) based on different methods as noted below.

| Species | Femoral midshaft sagittal diameter | Femoral midshaft antero-posterior diameter | Femoral minimum mid-shaft circumference/body mass estimation from flying bird sample ^a (range estimation) | Femoral shaft least circumference estimation/body mass estimation from general avian sample—reduced major axis ^b (range estimation) | Femoral shaft least circumference estimation/body mass estimation from bird of prey sample—reduced major axis ^b (range estimation) | Body mass estimation from femoral midshaft sagittal diameter—flying bird sample—Model 1 ^c (range estimation) | Tarsometatarsal midshaft sagittal diameter/body mass estimation from flying bird sample—Model 1 ^c (range estimation) | Tarsometatarsal length/body mass estimation from of flying bird sample—Model 1 ^c (range estimation) |
|------------------------|------------------------------------|--|--|--|---|---|---|--|
| <i>C. major</i> n. sp. | 11.24 | 9.87 | 34/3351 (4768–2355) | 34/4240 (4518–3980) | 34/3274 (7447–1550) | 3862 (4639–3216) | 8.6 ^d /4063 (7156–2307) | 115.4 ^d /3567 (4848–2624) 95.04 ^e /2015 (2739–1483) |
| <i>C. tellustris</i> | — | — | — | — | — | — | — | — |
| <i>T. musculosus</i> | 10.8 ^e | 7.54 ^e | 29/2332 (3265–1665) | 29/2055 (2627–1607) | 29/2154 (4721–1055) | 3512 (4218–2924) | — | — |

^a Anderson et al. (1985)
^b Campbell and Marcus (1992)
^c Alexander (1983)
^d After Olson (2008)
^e After Noriega et al. (2011)

bones. The type material described here is housed in Museo Nacional de Historia Natural, Montevideo, Uruguay. Measurements on Tables 1 and 2.

Occurrence.—El Bagre Creek, at its mouth into the Río de la Plata estuary, San Luis town, Canelones Department, southern Uruguay (S 34°46'17", W 55°36'07"; see Fig. 1); late Pleistocene, Libertad Formation (or Dolores Formation, see above).

DISCUSSION

Despite the fragmentary appearance of the material described herein, the anatomical condition of the bones—regarding its structures as well as the muscular lines, crests and impressions—are strikingly well-preserved. The excellent preservation allows comparison with almost all extant genera of Falconidae in detail, offering a sufficient anatomical framework to erect a new species within the genus *Caracara*.

Body mass estimations from the femoral cross-section measurements yield an average body mass estimate of 3,700 (see Table 2). The estimation from the width of the coracoidal sternal end could reflect a questionable result, due that the dimension of this bone is severely constrained by the flying capabilities (Feduccia, 1999). However, the proportions and deep muscular impressions of the coracoid suggest a developed flight condition for *Caracara major* n. sp., and for a regression sample we chose only flying Falconiformes species (see Appendix 2 data). The obtained result (3,767 grams) based on width measure of coracoidal sternal end (SW of graphic regression, see Appendix 2) falls within the estimated range from all other body mass estimations (7,447 grams–1,550 grams; Table 2). The body mass estimation of *Caracara tellustris* from the Holocene of Jamaica (Olson, 2008), obtained here from tarsometatarsal diameter and length resulted in an average of 3,815 grams (see Table 2). However, these estimations should be considered as questionable. Certainly, this species was a large caracara but its nearly flightless and terrestrial condition previously suggested (Olson, 2008), could have affected its tarsometatarsal dimensions. This tarsometarsus is much enlarged and robust in comparison to the other *Caracara* species, and the overall weak aspect of its incomplete humerus and coracoid clearly reinforce the flightless hypothesis. The coracoidal and humeral dimensions are strongly related to the flight muscle mass (Feduccia, 1999). These muscles represent approximately 20% of total body mass in flying birds (Greenewalt, 1962; Rayner, 1988). The Caracarini species are active fliers (Brown and Amadon, 1968; White et al., 1994) and the supracoracoideus and pectoralis muscles have a considerable relative mass. These features must be taken into account when applying an allometric equation for flying birds (Alexander, 1983) in order to estimate the body mass. Therefore, it seems that *C. major* would have been larger than the Jamaican species. Although our results regarding *C. tellustris* body mass estimations could be overestimated, it is likely that it would have exceeded the body mass range of actual Caracarini species.

Body mass estimations of early Miocene species *Thegornis musculosus* obtained from femoral and tarsometatarsal dimensions have an average of 2,500 grams (see Table 2), a value far smaller than these two Pleistocene species.

The maximum of body mass range of an extant falconid corresponds to the female gyrfalcon (*Falco rusticolus*), with a reported body mass of 2,000 grams (Brown and Amadon, 1968). The new species described here almost doubles this mass (see Table 2). Therefore, it is reasonable to consider *C. major* as an unusually large falconid species, probably the largest known.

The great body size of *C. major* might have reinforced the scavenging dominance that is observed in extant crested caracaras

with other avian scavengers (Wallace and Temple, 1987; White et al., 1994). The living crested caracara is an accomplished avian kleptoparasite; they have an opportunistic feeding behavior, taking food from other raptors, marine and wader birds (White et al., 1994; Fergusson-Lees and Christie, 2001). The increased size of this new *Caracara* species might have resulted in the piracy of a broad range of other birds, even in flight persecution. The apparent well-developed flying capabilities and the greater body size of *C. major* could have implied better gliding performance and larger territory size than extant Caracarini species (Rayner, 1988; Palmqvist and Vizcaíno, 2003).

The large amount and size of megafaunal carrion that probably would have existed during late Pleistocene environments could have favored the large body size of *C. major*. We think that the significant size difference rules out a possible clinal variety of living crested caracara (*Caracara plancus*) with a reported maximum body mass of 1,600 in Chile and Peru (White et al., 1994).

The great body size of *C. major* is comparable with large buteonines and other accipitrids. Its significantly larger body size could imply higher predatory skills when comparing with living caracara species. The mean estimated body mass of *C. major* exceeds, for example, that of the black-chested buzzard-eagle (*Geranoaetus melanoleucus*), which has a maximum reported body mass of 3200 grams (report for a female specimen, Fergusson-Lees and Christie, 2001). This living species is fairly common in southern South America habitats and it is a large carnivorous bird that mainly predates mid-sized mammals (Thiollay, 1994; Fergusson-Lees and Christie, 2001). Based on the roughly similar body masses of both species, we suggest that *C. major* probably could have predated on mid-sized mammals that thrived during the late Pleistocene of Uruguay (Ubilla, 2007). Due primarily to its great size, the ecological role of *C. major* may have been distinct from any extant caracara species.

ACKNOWLEDGMENTS

For the photographic material we are greatly indebted to B. Schmidt and J. Dean, members of curatorial staff of Smithsonian National Museum of Natural History. For the same reasons we give thanks to S. Claramunt of American Museum of Natural History, A. Farrell of Los Angeles County Natural History Museum, W. Suárez and Y.W. García Lavín of Museo Nacional de Historia Natural de Cuba. H. Alvarenga of Museo de Historia Natural de Taubaté provided access of comparative material essential to this study. We are indebted to M. Pavia for his valuable review and to E. Lindsay and S. Sensale for improvement of English grammar. We also thank to Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq, Brazil and CAPES Foundation, Ministry of Education of Brazil, for doctoral research grants of RM (respectively processes 142462/2009–8 and BEX 9190/11–2), Agencia Nacional de Investigación e Innovación (ANII) and Programa de Desarrollo de Ciencias Básicas (PEDECIBA).

REFERENCES

- ALEXANDER, R. M. 1983. Allometry of the leg bones of moas (Dinornithes) and other birds. *Journal of Zoology*, 200:215–31.
- AMEGHINO, F. 1895. Sur les oiseaux fossiles de Patagonie et la faune mammalogique des couches à *Pyrotherium*. *Boletín del Instituto Geográfico Argentino*, 15:501–660.
- ANDERSON, J. F., A. HALL-MARTIN, AND D. A. RUSSELL. 1985. Long bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology*, 207:53–61.
- BANKS, R. C. AND C. J. DOVE. 1992. The generic name for crested caracaras (Aves: Falconidae). *Proceedings of Biological Society of Washington*, 105: 420–425.
- BAUMEL, J. J. AND L. M. WITMER. 1993. Osteology, p. 45–132. In J. J. Baumel, A. S. King, J. E. Brazile, H. H. Evans, and J. C. Vanden Berge (eds.), *Handbook of Avian Anatomy: Nomina Anatomica Avium*, second edition. Publications of Nuttall Ornithological Club, Cambridge, Massachusetts.
- BRODKORB, P. 1959. Pleistocene birds from New Providence Island, Bahamas. *Bulletin of the Florida State Museum, Biological Science*, 4:349–371.
- BRODKORB, P. 1964. Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). *Bulletin of the Florida State Museum, Biological Sciences*, 8: 201–335.
- BROWN, L. AND D. AMADON. 1968. *Eagles, Hawks and Falcons of the World*, two volumes. New York, McGraw-Hill, 759 p.
- CAMPBELL, K. E. AND L. MARCUS. 1992. The relationship of hindlimb bone dimensions to body weight in birds, p. 395–412. In K. E. Campbell (ed.), *Papers in Avian Paleontology Honoring Pierce Brodkorb*, Science Series Natural History Museum of Los Angeles City, 36.
- DOVE, C. J. AND R. C. BANKS. 1999. A taxonomic study of crested caracaras (Falconidae). *Wilson Bulletin*, 111:330–339.
- DUNNING JR., J. B. 2008. *Handbook of Avian Body Masses*, second edition. CRC Press, Taylor and Francis Group, 655 p.
- FEDUCCIA, A. 1999. *The Origin and Evolution of Birds*, second edition. Yale University Press, 466 p.
- FERGUSON-LEES, J. AND D. A. CHRISTIE. 2001. *Raptors of the World*. Boston, Houghton Mifflin Company, 992 p.
- FRIEDMANN, H. 1950. The birds of North and Middle North America, Part XI. *Bulletin of United States National Museum*, 50:1–793.
- GERVAIS, P. 1867. Sur une nouvelle collection d'ossements fossiles de mammifères recueillies par M. F. Seguin dans la Confédération Argentine. *Comptes Rendus de l'Académie des Sciences*, 65:279–282.
- GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. *Smithsonian Miscellaneous Collections*, 144:1–46.
- GREENWAY JR., J. C., 1967. *Extinct and Vanishing Birds of the World*. Dover, 520 p.
- GRIFFITHS, C. S. 1999. Phylogeny of the Falconidae inferred from molecular and morphological data. *Auk*, 116:116–130.
- HOWARD, H. 1929. The avifauna of Emeryville Shellmound. *University of California Publications in Zoology*, 32:301–394.
- HOWARD, H. 1938. The Rancho La Brea caracara: a new species. *Carnegie Institution of Washington Publication*, 487:217–240.
- JOLLIE, M. 1976. A contribution of the morphology and phylogeny of Falconiformes. *Evolutionary Theory*, 1:285–296.
- LEACH, W. E. 1820. *Systematic catalogue of the Specimens of the Indigenous Mammalia and Birds that are preserved at the British Museum*. London, 42 p+2.
- LINNAEUS, C. 1758. *Systema Naturae per Regna Tria Naturae*. Tenth edition, Vol. I: *Regnum Animale*. L. Salvii, Holmiae, Sweden, 824 p.
- LIVEZEY, C. B. AND R. L. ZUSI. 2006. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: 1. Methods and characters. *Bulletin of Carnegie Museum of Natural History*, 37:1–544.
- MARTÍNEZ, S. AND M. UBILLA. 2004. El Cuaternario de Uruguay, p. 195–228. In G. Verolavsky, M. Ubilla, and S. Martínez (eds.), *Cuencas sedimentarias de Uruguay. Geología, paleontología y recursos naturales. Cenozoico*. DIRAC, Facultad de Ciencias, Montevideo.
- MERREM, B. 1826. *Allgemeine Encyclopadie der Wissenschaften und Kunste in alphabetischer Folge von genannten Schriftstellern bearbeitet und hrsg. von J. S. Ersch und J. G. Gruber*. Leipzig, 15:159–160.
- NORIEGA, J. I., J. I. ARETA, S. F. VIZCAÍNO, AND S. M. BARGO. 2011. Phylogeny and taxonomy of the patagonian Miocene falcon *Thegornis musculosus* Ameghino, 1895 (Aves: Falconidae). *Journal of Paleontology*, 85:1089–1104.
- OLSON, S. L. 2008. A new species of large, terrestrial caracara from holocene deposits of in Southern Jamaica (Aves, Falconidae). *Journal of Raptor Research*, 42:265–272.
- OLSON, S. L. AND W. B. HILGARTNER. 1982. Fossil and subfossil birds from the Bahamas, p. 22–56. In S. L. Olson (ed.), *Fossil vertebrates from the Bahamas*. Smithsonian Contribution to Paleobiology, 48.
- OWEN, R. 1838. Fossil Mammalia, 1, p. iv+1–40. In C. Rarwin (ed.), *The Zoology of the Voyage of H. M. S. Beagle*.
- OWEN, R. 1839. Description of a tooth and part of the skeleton of the *Glyptodon*, a large quadruped of the edentate order, to which belongs the tessellated bony armour figured by Mr. Clift in his memoir on the remains of the *Megatherium*, brought to England by Sir Woodbine Parish, F. G. S. *Proceedings of the Geological Society of London*, 3:108–113.
- PALMQVIST, P. AND S. F. VIZCAÍNO. 2003. Ecological and reproductive constraints of body size in the gigantic *Argentavis magnificens* (Aves, Theratornithidae) from the Miocene of Argentina. *Ameghiniana*, 40:379–385.
- RAYNER, J. M. V. 1988. Form and function in avian flight. *Current Ornithology*, 5:1–66.
- RINDERKNECHT, A. 1998. Nuevos microvertebrados fósiles para el Pleistoceno superior del Uruguay (Amphibia, Reptilia, Aves). *Comunicaciones Paleontológicas del Museo de Historia Natural de Montevideo*, 2:133–144.

- RINDERKNECHT, A. 2006. Vertebrados fósiles de la costa uruguaya, p. 343–349. In R. Menafrá, L. Rodríguez-Gallego, F. Scarabino, and D. Conde (eds.), Bases para la conservación y el manejo de la costa uruguaya. Vida Silvestre Uruguay, Montevideo.
- SHARPE, R. B. 1874. Catalogue of the birds in the British Museum. British Museum, London, 1:1–480.
- STEADMAN, W. D., R. FRANZ, G. S. MORGAN, N. A. ALBURY, B. KAKUK, K. BROAD, S. E. FRANZ, K. TINKER, M. P. PATEMAN, T. A. LOTT, D. L. JARZEN, AND D. M. DILCHER. 2007. Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas. Proceedings of National Academy of Science, 104:19897–19902.
- SUÁREZ, W. AND S. L. OLSON. 2001. Further characterization of *Caracara creightoni* Brodkorb based on fossils from the Quaternary of Cuba (Aves: Falconidae). Proceedings of Biological Society of Washington, 114:501–508.
- SUÁREZ, W. AND S. L. OLSON. 2003. A new species of caracara (*Milvago*) from Quaternary asphalt deposits in Cuba, with notes on new material of *Caracara creightoni* Brodkorb (Aves: Falconidae). Proceedings of Biological Society of Washington, 116:301–307.
- THIOLLAY, J. M. 1994. Family Accipitridae (Hawks and Eagles), p. 52–205. In J. del Hoyo, A. Elliot and J. Sargatal (eds.), Handbook of the Birds of the World. New World Vultures to Guinea Fowls, 2. Lynx Editions, Barcelona.
- UBILLA, M. 1999. Dataciones radiocarbónicas (C14) para la Fm. Dolores (Río Santa Lucía, Dpto. de Canelones, y A° Gutiérrez Chico, Dpto. de Río Negro) y comentarios sobre la fauna de vertebrados asociada. Revista de la Sociedad Uruguaya de Geología, 6:48–53.
- UBILLA, M. 2007. Late Pleistocene of South America. Vertebrate Records, p. 3175–3189. In S. Elías (ed.), Encyclopedia of Quaternary Science, 4. Elsevier.
- UBILLA, M. AND D. PEREA. 1999. Quaternary vertebrates of Uruguay: a biostratigraphic, biogeographic and climatic overview. Quaternary of South America and Antarctic Peninsula, 12:75–90.
- UBILLA, M. AND A. RINDERKNECHT. 2001. Consideraciones sobre el género *Galea* Meyen, 1831 (Rodentia, Caviidae), su registro en el pleistoceno de Uruguay y descripción de una nueva especie extinguida. Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica), 96:111–122.
- WALLACE, M. P. AND S. A. TEMPLE. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk, 104:290–295.
- WETMORE, A. 1920. Five new species of birds from cave deposits in Puerto Rico. Proceedings of Biological Society of Washington, 33:77–82.
- WHITE, C. M., P. D. OLSEN, AND L. F. KIFF. 1994. Family Falconidae (Falcons and Caracaras), p. 216–275. In J. del Hoyo, A. Elliot and J. Sargatal (eds.), Handbook of the Birds of the World. New World Vultures to Guinea Fowls, 2. Lynx Editions, Barcelona.

ACCEPTED 27 JUNE 2012

APPENDIX 1

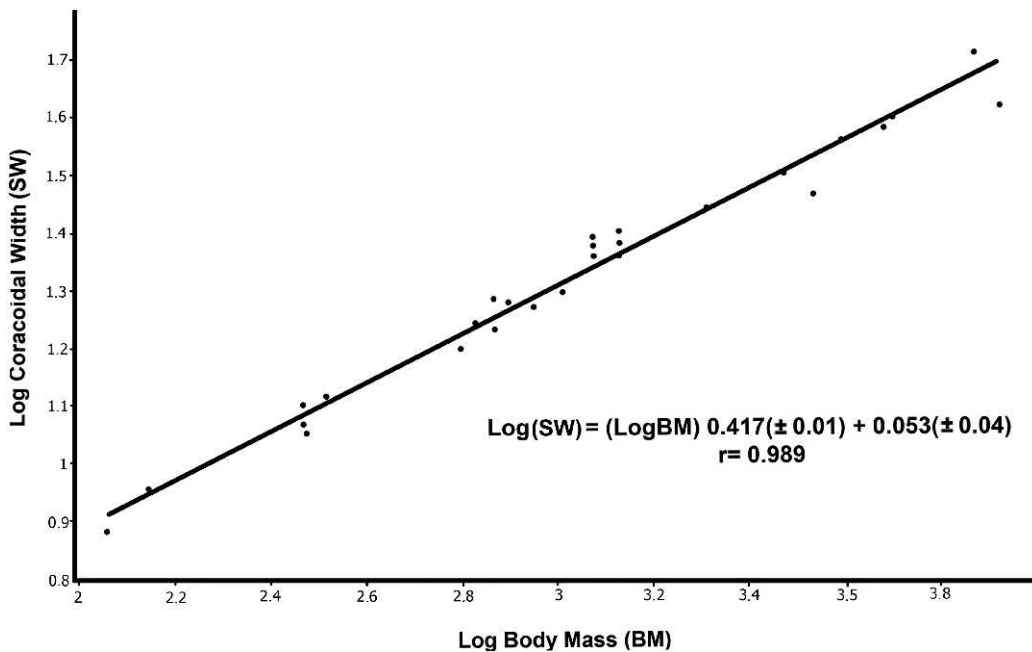
The coracoids, femora, and scapulae of the following specimens were used for morphological comparisons, morphometrics, and body mass estimations.

Caracara plancus: MNHN 6254, –6390, –6391; *Caracara cheriway*: USNM 553229, AMNH 11526, –13817, –27191; *Caracara lutosus*: USNM 19916; *Caracara prelutosus*: LACMHC H 4587, -E 651, -E 4236; *Caracara creightoni*: WS 1933; *Caracara tellustris*: USNM 535727; *Thegornis musculosus*: MPM-PV-3443; *Phalcoboenus australis*: USNM 557987, –490979, AMNH 28200; *Phalcoboenus megalopterus*: USNM 500273, AMNH 4960; *Ibycter americanus*: USNM 621943; *Milvago chimachima*: MNHN 6264, MHNT 53; *Milvago chimango*: MNHN 5637, –5638; *Micrastur semitorquatus*: MHNT 1125, –1463; *Herpetotheres cachinnans*: MHNT 54, –1959; *Falco sparverius*: MNHN 5639; *Falco peregrinus*: MHNT 1245; *Spizapteryx circumcinctus*: USNM 319444; *Harpyhaliaetus coronatus*: MHNT 1815; *Haliaeetus vocifer*: MHNT 1935; *Haliaeetus leucocephalus*: MHNT 520; *Aquila chrysaetus*: MHNT 514; *Harpya harpyja*: MHNT 1862, –4824; *Necrosyrtes monachus*: MHNT 49; *Gyps fulvus*: MHNT 917.

APPENDIX 2—Data used in lineal regression for body mass (BM) estimation of *Caracara major* n. sp. (MNHN 615) from coracoid sternal end width (SW). Mean body masses taken from Dunning (2007 and references therein). When sex of specimen is identified the correspondent mean body mass is considered.

| Species | Coracoid sternal end width (mm) | Mean body mass (g) |
|---|---------------------------------|--------------------|
| Falconidae | | |
| <i>Milvago chimachima</i> MNHN 6264 ♀ | 13.03 | 329 |
| <i>Milvago chimachima</i> MHNT 53 | 11.29 | 299.5 |
| <i>Milvago chimango</i> MNHN 5637 | 12.58 | 296 |
| <i>Milvago chimango</i> MNHN 5638 | 11.67 | 296 |
| <i>Caracara plancus</i> MNHN 6254 | 22.64 | 1,348 |
| <i>Caracara plancus</i> MNHN 6390 | 24.94 | 1,348 |
| <i>Caracara plancus</i> MNHN 6391 | 23.75 | 1,348 |
| <i>Caracara cheriway</i> ¹ USNM 553229 | 18.45 | 893.5 |
| <i>Herpotheres cachimans</i> MHNT 54 | 17.06 | 672 |
| <i>Herpotheres cachimans</i> MHNT 1959 | 17.29 | 672 |
| <i>Phalcoboenus australis</i> USNM 490979 ♀ | 24.52 | 1,187 |
| <i>Phalcoboenus australis</i> USNM 557987 | 22.68 | 1,187 |
| <i>Phalcoboenus australis</i> AMNH 28200 ♀ | 23.7 | 1,187 |
| <i>Phalcoboenus megalopterus</i> USNM 500273 | 18.86 | 788 |
| <i>Ibycter americanus</i> USNM 621943 | 15.71 | 624 |
| <i>Micrastur semitorquatus</i> MHNT 1463 | 16.92 | 739 |
| <i>M. semitorquatus</i> MHNT 1125 | 19.09 | 739 |
| <i>Spizapteryx circumcinctus</i> USNM 319444 ♂ | 9.06 | 141 |
| <i>Falco sparverius</i> MNHN 5639 | 7.59 | 115.5 |
| <i>Falco peregrinus</i> MHNT 1245 | 19.7 | 1,025 |
| Accipitridae | | |
| <i>Harpyhaliaetus coronatus</i> MHNT 1815 ♂ | 31.5 | 2,950 |
| <i>Haliaeetus vocifer</i> MHNT 1935 ♀ | 29 | 3,400 |
| <i>Haliaeetus leucocephalus</i> MHNT 520 | 39.1 | 5,019 |
| <i>Aquila chrysaetos</i> MHNT 514 ♂ | 35.8 | 3,900 |
| <i>Harpya harpyja</i> MHNT 4824 ♂ | 37.5 | 4,800 |
| <i>Harpya harpyja</i> MHNT 1862 ♀ | 41 | 8,300 |
| <i>Necrosyrtes monachus</i> MHNT 49 | 27.5 | 2,043 |
| <i>Gyps fulvus</i> MHNT 917 | 50.3 | 7,436 |

¹Specimen belongs to Southern population of *C. cheriway* (see Dunning, 2007).



Graphic of linear regression using reduced major axis (RMA) of coracoidal sternal end width (in mm) plotted against body mass (in grams). Regression equation (error of regression coefficients) and Pearson’s r correlation have been calculated from 28 specimens of Falconiformes species (data above). Axes expressed in decimal logarithms.