Body mass estimation and locomotion of the Miocene pelecaniform bird *Macranhinga*

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The fossil darter *Macranhinga paranensis* (Aves: Pelecaniformes) from the late Miocene of Argentina is the largest of all known extinct or living Anhingidae. Its body mass is estimated at a mean value of 5.4 kg by using a scaling model derived from the logarithmic relationship between measurements of the least shaft circumference of the femur/ tibiotarsus and body masses. Predictions of body mass, as well as the analysis of anatomical evidence, are used to infer that *Macranhinga paranensis* would have probably had a powered flapping flight and an aquatic locomotion similar to that of cormorants. The morphology of the pelvis and the hind-limb would have allowed *Macranhinga paranensis* to catch fishes by means of pursuit-diving rather than stalking them in an anhinga-like manner. As determined by adaptations mainly of tarsometatarsal morphology, the species had well developed perching and climbing abilities.

Key words: Aves, Anhingidae, *Macranhinga*, Paleobiology, Miocene, Argentina.

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Introduction

The family Anhingidae nowadays comprises only one genus and four species, the American anhinga (*Anhinga anhinga*) and the Old World darters (*Anhinga melanogaster*, *A. rufa*, and *A. novaehollandie*). They are fairly large waterbirds with a very long slender neck and a straight, sharp and pointed bill. Darters are good fliers, alternating flapping flight with soaring glides in thermals of rising air. Their propulsion in water consists of swimming very low on the surface, with only the head and part of the neck emerging from the water, and slow dives, helped by their short legs and feet with webbed toes. However, darters are also well adapted for perching, and climbing about in vegetation (Owre 1967; Orta 1992).

Macranhinga paranenis is a fossil darter, belonging to the Anhingidae, which was described on the basis of complete tarsometatarsi and several dissociated skeletal elements (Noriega 1992, 1995). All the specimens come from a stratigraphic unit known as the 'Mesopotamian' (Ituzaingó Formation; upper Miocene) that outcrops discontinuously along the eastern cliffs of the Paraná river in Argentina. The most striking feature of this bird is its large size, much greater than in all other known fossil or extant anhingas (Noriega 1995). However, its actual body mass has not previously been estimated.

This contribution includes a quantitative approach in estimating the body mass of *Macranhinga paranensis* and makes comparisons with living darters and other American fossil representatives of the family; i.e. *Meganhinga chilensis* Alvarenga, 1995, *Anhinga fraileyi* Campbell, 1996, and *Anhinga grandis* Martin & Mengel, 1975. *Anhinga subvolans* (Brodkorb, 1956) is excluded because it is known only from a partial humerus.

Paleobiological aspects related to flying and swimming abilities, as well as arboreal locomotion in *Macranhinga paranensis*, are discussed on the basis of skeletal morphology and estimations of body mass.

Material and methods

The fossil material analyzed is housed in the collections of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and Museo de La Plata (MLP). They include a pelvic girdle (MLP 88-IX-20-5), two tarsometatarsi (MACN 13.507, 12.293), two femora (MACN 14.363, 13.299), two tibiotarsi (MLP 88-IX-20-3; MACN 14.378), four humeri (MLP 88-IX-20-1/2/10/11), and two carpometacarpi (MLP 88-IX-20-4; MACN 14.380).

Measurements. — Measurements were made with calipers and include: greatest length of the humerus from the head through the midpoint of the lateral condyle (GHL); greatest length of the carpometacarpus from most proximal portion of the carpal trochlea through facet for digit III (GCL); transverse width of distal end of humerus from the entepicondylar to the ectepicondylar prominence (HW); least shaft circumferences of the femora (LFC) and tibiotarsi (LTC).

The value of LTC in *Anhinga grandis* was estimated from measurements of width and depth of midshaft given by Becker (1987), assuming that a cross-section through the tibiotarsus has a nearly triangular shape and that LTC is the perimeter of a triangle. The supposed isosceles triangle is formed by two rectangled ones whose bases and altitudes are represented by the half width and depth of midshaft, respectively. The hypotenuse is calculated by the Pythagorean theorem. Comparisons between analogous estimates of LTC and direct measurements in *Anhinga anhinga* and *Anhinga fraileyi* gave an error of less than 3%.

Body mass estimation. — Measurements detailed above were used to estimate body masses by three different methods:

(1) Martin & Mengel (1975), assuming the proportions of fossil and living anhingas to be similar, state that the width of the distal end of the humerus is isometrically proportional to body mass raised to the 1/3 power.

(2) Prange *et al.*'s (1979) approach assumes that the length (in mm) of the humerus squared is nearly directly proportional to mass (in grams) in flying birds.

(3) Campbell & Marcus's scaling model (1992) is derived from the logarithmic relationship between measurements of the least shaft circumference of the femur or tibiotarsus and body masses in the overall data set analyzed by them (including 89 families of birds) and in taxonomically and morphologically determined subgroups of the data (Campbell & Marcus 1992: p. 397). Results for all their data are given in a table (Campbell & Marcus 1992: p. 405, table 2) that here is used for purposes of body mass estimation, selecting only those data for the subgroup of the 'Swimmers' (Subgroup SW including Gaviidae, Podicipedidae, Spheniscidae, Phalacrocoracidae, Anhingidae, and Phalaropodidae), the group into which *Macranhinga paranensis* would be classified, both taxonomically and morphologically. The scaling equation can be written as:

$$\frac{\text{Mean of } \log_{10}(\text{mass}) \text{ for SW}}{\text{Mean of } \log_{10}(\text{LFC or LTC}) \text{ for SW}} = \frac{\log_{10}(\text{mass}) \text{ of } M.\,paranensis}{\log_{10}(\text{LFC or LTC}) \text{ of } M.\,paranensis} \quad (1)$$

Locomotion. — The inferences of locomotion in *Macranhinga paranensis* related to flying abilities are more speculative than those concerning the hind-limb propulsion because its wing bones were not found associated with holotypical material. The lack of articulated specimens renders the exact proportions between fore- and hindlimb uncertains. However, the relative lengths of the available wing bones referred to *Macranhinga paranensis* (four humeri and two carpometacarpi), i.e., the intramembral proportions, are consistent and similar to those of *Anhinga anhinga*. Thus, estimates of wingspan, wing-loading, and surface area of the wing can be made if the proportions observed among all the wing bones referred to *Macranhinga paranensis* are supposed to be normal. In other words, if it is assumed that *Macranhinga paranensis* had small wings relative to its legs. A series of equations proposed by Greenewalt (1975) were used to calculate the wing parameters.

Results

Following Martin & Mengel (1975), the body mass of *Macranhinga paranensis* is estimated to have been 4.96 kg, considering that the mean of HW of seventeen *Anhinga anhinga* is 13.12 mm (Becker 1987: p. 362, table 1), the average mass of sixteen *Anhinga anhinga* is 1.21 kg (Owre 1967: p. 8), and the average of HW of four *Macranhinga paranensis* is 21.0 mm, with range of 19.2–21.75.

The predicted mass of *Macranhinga paranensis*, based on Prange *et al.* (1979), is 3.24 kg taking into account that GHL is 180 mm.

Finally, using Campbell & Marcus's equation, two mean estimates of body mass are obtained: 4.9 and 5.9 kg. They result from replacing in (1): mean of $\log_{10}$ (mass) for SW (2.938), mean of $\log_{10}$ (LFC) for SW (1.209) or mean of $\log_{10}$ (LTC) for SW (1.139), and LFC (33.00 mm; range, 32.7–33.3) or LTC (28.95 mm; range, 28.0–29.9) of *M. paranensis*, respectively. The three means of $\log_{10}$ measurements are from Campbell & Marcus (1992: p. 405, table 2).

These results, together with the predictions of body masses of other American fossil darters, are summarized in Table 1.

Wing parameters

(a) Wingspan
Assuming a similar ratio between the length of humerus and wingspan for both species (i.e. 1: 8.8), the wingspan of *Macranhinga paranensis* is calculated to be ca. 1.58 m.

(b) Wing surface area

$$b = \alpha \cdot S^{\beta} \quad (2),$$

where b is wingspan (in cm), α is a fitted value of Greenewalt (1975) or 2.221 which has slight variation among his different models (Campbell & Tonni 1983), S is wing surface area (in cm²), and β is another of Greenewalt's fitted value which is altered in this paper and adapted. In the case at hand, b or 0.5329 is derived from the same equation (2) by use of the observed mean wingspan (110 cm), the observed mean wing surface area (1515 cm²), and the observed mean mass of *Anhinga* was obtained from the data of Owre (1967). The wing surface of *Macranhinga paranensis* is estimated at 0.299 m².

(c) Wing-loading

$$WL = W/S \quad (3),$$

where WL is wing-loading, W is mass, and S is wing surface area. Wing-loading in *Macranhinga paranensis* is calculated at 16.3 and 19.7 kg/m², depending on which estimate of mass is used.

These results, together with data of total mass, wing area, and wing-loading for selected species of birds with different strategies of locomotion, are summarized in Table 2.

Discussion

Body mass. — The two first techniques applied have been used previously in estimating the body mass of the fossil darter *Anhinga grandis* (Martin & Mengel 1975; Becker 1987). In spite of its belonging to the same family, both methods seem 'a priori' to be inadequate in the case of *Macranhinga paranensis*. As indicated above, Martin & Mengel (1975) assume the proportions of the extant *Anhinga anhinga* and the fossil *Anhinga grandis* to be similar and propose an isometric scaling equation. Because *Macranhinga paranensis* is known from dissociated skeletal elements, proportions between fore- and hindlimbs cannot be known for certain. It must also be noted that the holotype is a tarsometatarsus.While there is a close correspondence in size and morphology between the remaining hindlimb bones assigned to *Macranhinga paranensis* (i.e., tibiotarsi and femora) and the holotype, the wing elements are referred with a lesser degree of certainty. In addition, the condition of isometric scaling of limb element width to body mass is supposed to occur rarely in birds (Prange *et al.* 1979; Becker 1987). Regardless of these strong constraints, it should be remarked that the value of body mass of *Macranhinga paranensis* predicted by Martin & Mengel's method is within the range of estimates calculated using Campbell & Marcus's equations.

Table 1. Predicted body-masses (in kg) of *Macranhinga paranensis, Anhinga grandis, Anhinga fraileyi, Meganhinga chilensis*, and *Anhinga anhinga*, following Martin & Mengel (1975) (A), Prange *et al.* (1979) (B), and Campbell & Marcus (1992) (C).

	A	B	C	
			Using LFC	Using LTC
Macranhinga paranensis	4.96^1	3.24^1	$4.9^{\,1}$	5.9^1
Anhinga grandis	2.42^2 2.19^3	2.25^4	–	1.76^5
Anhinga fraileyi	2.07^6	2.16^7	–	4.92^8
Meganhinga chilensis			–	3.25^9
Anhinga anhinga	–	1.56^{10}	1.54^{11}	1.49^{12}

1. See Results.
2. Prediction from Martin & Mengel (1975) based on the holotype.
3. Based on mean HW of *Anhinga grandis* = 15.98 mm, n = 5, with range of 15.0–17.2 mm, from Becker (1987); average mass of 16 *Anhinga anhinga* = 1.210 g, from Owre (1967); mean HW of 17 *Anhinga anhinga* = 13.12 mm, with range of 12.0–14.9 mm, from Becker (1987).
4. From Becker (1987) who estimates the length of the humerus = 150 mm.
5. Calculated for subgroup SW after estimating the value of LTC (18.14 mm) from data of mean width = 6.2 mm (5.9; 6.5) and mean depth = 5.1 mm (4.8; 5.4) of midshaft given by Becker (1987). See Material and methods.
6. Calculated by assuming the proportions of *Anhinga fraileyi* and *Anhinga anhinga* to be similar, and considering HW of *A. fraileyi* = 15.7 (Campbell 1996).
7. Calculated on the estimation of humerus length (ca. 147 mm) given by K.E. Campbell (personal communication).
8. Calculated for subgroup SW from data of LTC (27.0 mm) given by K.E. Campbell (personal communication).
9. Calculated for subgroup SW from data of LTC (23.0 mm) given by H. Alvarenga (personal communication).
10. Based on mean GHL of 17 *Anhinga anhinga* = 125.09 mm, with range of 113.2–137.6 from Becker (1987).
11, 12. Based on two specimens belonging to the Museo Nacional de Historia Natural de Paraguay (MNHNP). Mean LFC = 19.75 mm, with range of 19.0–20.5 mm. Mean LTC = 16.75, with range of 16.5–17.0 mm.

Table 2. Total mass (kg), wing area (m²), and wing loading (kg/m²) for selected species of birds with different strategies of locomotion (data from Campbell & Tonni 1983 and Livezey 1988).

	Total mass	Wing-area	Wing-loading
Pinguinus impennis	5.000	0.0154	325
Uria aalge	1.030	0.0500	20.6
Diomedea exulans	8.502	0.6206	13.7
Cygnus olor	11.602	0.6808	17.0
Branta canadensis	5.662	0.2820	20.1
Aquila chrysaetos	3.712	0.5382	6.9
Leptoptilus crumeniferus	7.030	0.8225	8.6
Gymnogyps californianus	9.500	1.3160	7.2
Phalacrocorax olivaceus	1.646	0.1581	10.4
Anhinga anhinga	1.209	0.1515	8.0
Macranhinga paranensis	4.900–5.900	0.2990	16.3–19.7

The equation developed by Prange *et al.* (1979) avoids isometric scaling, but is also based on a measurement of a forelimb element. So, this method has, in the case of *Macranhinga paranensis*, the same shortcomings as that of Martin & Mengel (1975).

On the other hand, Campbell & Marcus's scaling equation (1992) considers the relationship between body mass and functional morphology of the hind limb in birds. They noted that the femur, tibiotarsus, and tarsometatarsus are the skeletal elements that better reflect body mass in a scaling model because of their role in providing static support. Of these three bones, the femur appears to be the best indicator due to its almost exclusive function in supporting a bird's body mass. It is followed in importance by the tibiotarsus which also plays an additional locomotory function. Finally, Campbell & Marcus (1992) state that the tarsometatarsus adds an important feeding role to those of support and locomotion, being less accurate for predicting mass. In the case of darters, the tarsometatarsus is well adapted for perching and climbing rather than having a feeding role.

Taking into account these considerations, the mean of the two estimates obtained by Campbell & Marcus's equation (5.4 kg), using LFC and LTC for the subgroup SW (see Table 1), may be considered the best approach.

Locomotory mode. — The palaeobiological hypotheses concerning locomotion in *Macranhinga paranensis* are supported by anatomical evidence. Several morphological characters such as the shape and location of the iliac crests, the length of the preacetabular region of the pelvic girdle, the robustness of the femur shaft, the morphology of the tarsometatarsus, and the main associated muscular attachments of these bones, are clearly intermediate between the conditions typically observed in cormorants (Phalacrocoracidae) and anhingas. Although these characters have an unquestionable phylogenetic significance (Noriega & Alvarenga 2000), they also have an essentially adaptive and functional meaning related to flying, climbing, perching, and swimming abilities.

Estimations of wing-loading in *Macranhinga paranensis*, compared with those for selected species of birds with different strategies of locomotion (Table 2), make it possible to infer a sustained flapping flight for this darter as well-developed as in such large anserines as *Cygnus olor* and *Branta canadensis*. Its greater wing-loading compared to that of good soarers such as albatrosses (*Diomedea*), storks (*Leptoptilus crumeniferus*), and even extant anhingas, would probably be indicative of reduction in soaring capabilities. In addition, the posterior iliac crests in *Macranhinga paranensis* are more elevated than in cormorants, but less divergent than in *Anhinga anhinga*. This intermediate morphology, which implies a more reduced area of synsacral origin of *M. levator coccygis* and *M. levator caudae*, is indicative of a lesser ability to rotate and draw the tail laterally than *Anhinga anhinga* (Fig. 1). Consequently, the caudal muscles of *Macranhinga paranensis* would have been less adapted than those of *Anhinga anhinga* to effect constant adjustments of the tail typical of soaring or maneuvering flight (Owre 1967: p. 55). The narrower and more mesial surface of origin of these muscles in *Macranhinga paranensis* suggest a massive and directional power of elevation of the tail coincident with a cormorant-like heavy flapping flight and probably underwater steering.

Another important difference in the pelvic girdle of members of both pelecaniform families consists in the comparative development of the pre- and postacetabular re-
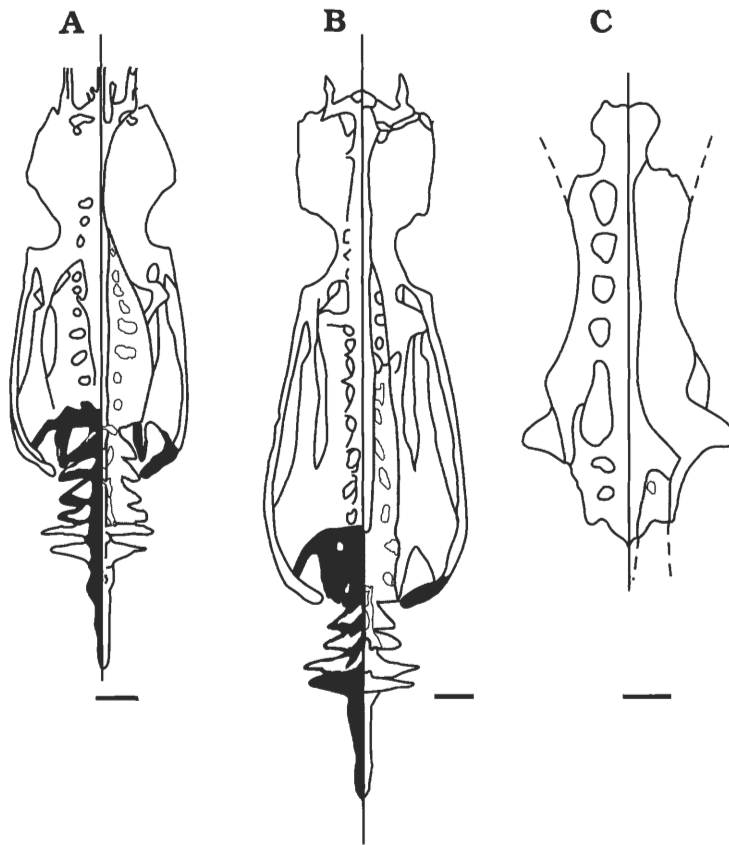
Fig. 1. Ventral (left) and dorsal (right) views of origins of muscles of the tail in *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and their inferred position in *Macranhinga paranensis* (**C**). *M. levator coccygis* and *M. levator caudae* are pointed in horizontal striped and *M. depressor coccygis* and *M. depressor caudae* in black. Modified from Owre (1967). Scale bars 1 cm.

gions, which in living anhingas differ markedly from those of cormorants in being longer and shorter, respectively. These osteological differences, mainly related to the extent and position of the areas of muscular attachments, are adaptations for different kinds of aquatic or arboreal locomotion in each family (Owre 1967). Again, the intermediate condition observed in *Macranhinga paranensis*, i.e., both pre- and postacetabular iliac bones relatively enlarged, is interpreted as an evidence of its having a more powered stroke of the leg than that possible for a living darter (Fig. 1). Muscles that draw the femur backward, e.g., m. flexor ischiofemoralis, are important in opposing the forward displacement produced by the force of propulsion (Owre 1967). The surface of attachment of this muscle in *Macranhinga paranensis* is cranially as large as in cormorants, i.e., comparatively greater than in *Anhinga anhinga*; however, its origin has a more lateral orientation than in cormorants due to the elevated extent of the posterior iliac crests, resembling the condition observed in darters (Fig. 2). Likewise, the insertions of mm. obturator internus, obturator externus, flexor ischiofemoralis, and caudofemoralis on the femur of *Macranhinga paranensis* are intermediate in shape
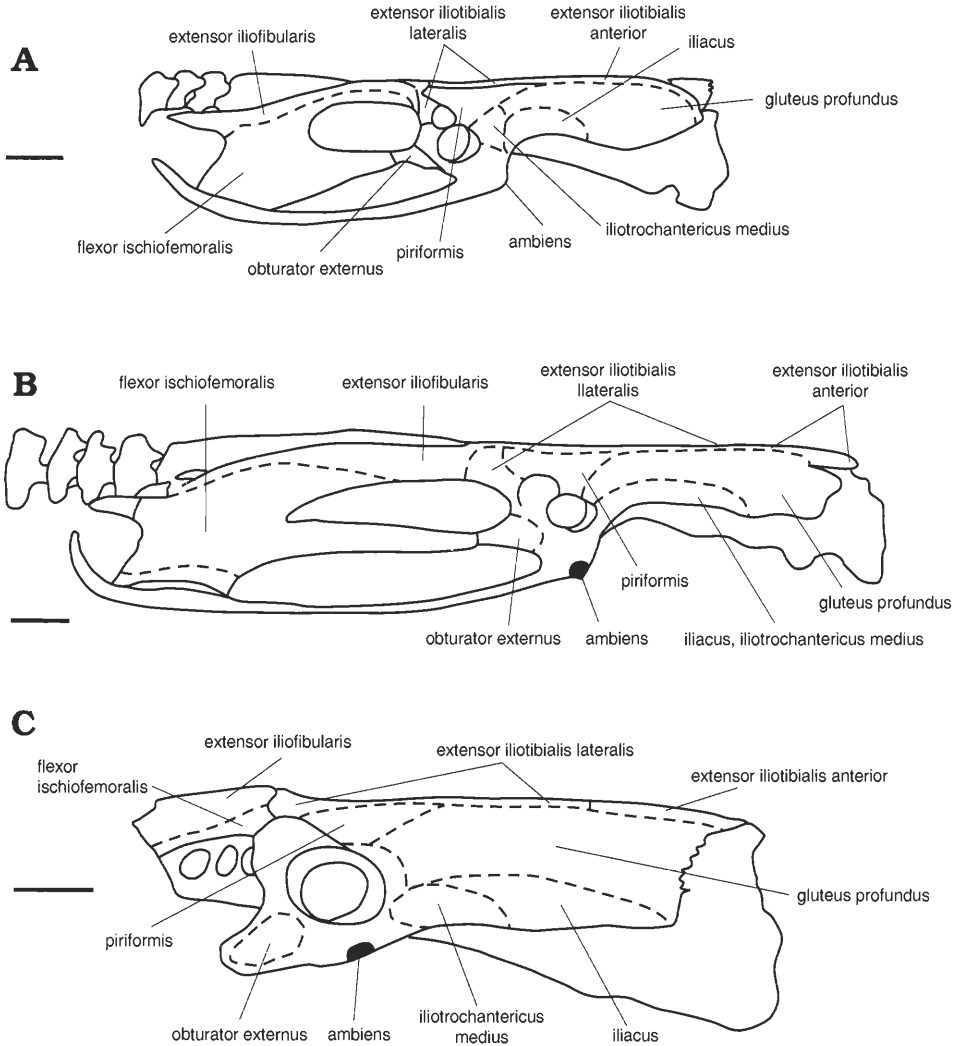
Fig. 2. Lateral views of muscle origins and insertions on the pelvic girdle of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.

and relative position to those of cormorants and anhingas (Fig. 3). These muscles are important in opposing the force of the swimming power-stroke and in rotating the femur posteriorly to produce a toe-out position of the foot. The latter action may be useful not only during swimming, but also in moving the foot-web into a more appropiate standing position (Owre 1967: p. 82).

On the other hand, muscles involved in flexion and anterior rotation of the femur (e.g., mm. gluteus profundus, iliacus, iliotrochantericus medius) are more important during non-swimming progression and consequently better developed in extant anhingas than in cormorants, reflecting the ability of anhingas to climb and perch on
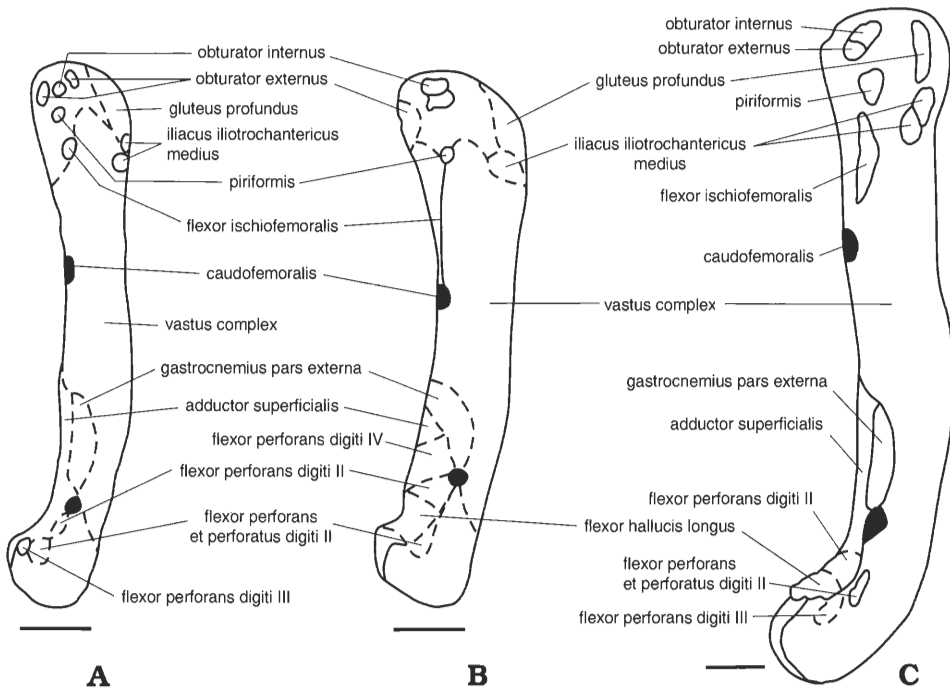
Fig. 3. Lateral views of muscle origins and insertions on the femur of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.

vegetation (Fig. 2). *Macranhinga paranensis* also exhibits conspicuous impressions of the pelvic origins and femoral insertions of this musculature (Figs. 2, 3).

The origin of m. extensor ilio-fibularis in *Macranhinga paranensis* is well-defined from the lateral surface of the posterior iliac crest as in the anhingas (Fig. 2). The functions of this muscle in tibiotarsal flexion and femoral extension are important in holding the anterior part of the body upright when standing and perching (Fisher 1946: p. 698; Owre 1967: p. 80).

Abduction of the femur is accomplished by m. piriformis and m. ambiens. The insertion of m. piriformis on the femur in *Macranhinga paranensis* is more proximal than in cormorants, but more distal than in the anhingas (Fig. 3). This condition may be indicative of an intermediate muscular function between the slow but powerful action in the former and the rapid but weak action in the latter.

M. ambiens, which also effects adduction of the tibiotarsus and augmentation of the force exerted by toe flexors lying along the shank, is better developed in darters than in cormorants (Owre 1967: p. 83). The pectineal process of *Macranhinga paranensis*, from which this muscle originates, lies midway between the cranial and ventral position to the acetabulum found in anhingas and cormorants respectively (Fig. 2). This position of origin may be interpreted as the development of an intermediate functional effectiveness of m. ambiens in *Macranhinga paranensis*.

The external head of m. gastrocnemius is very important in providing the propulsion stroke in swimming because it causes extension of the tarsometatarsus and flexion of the
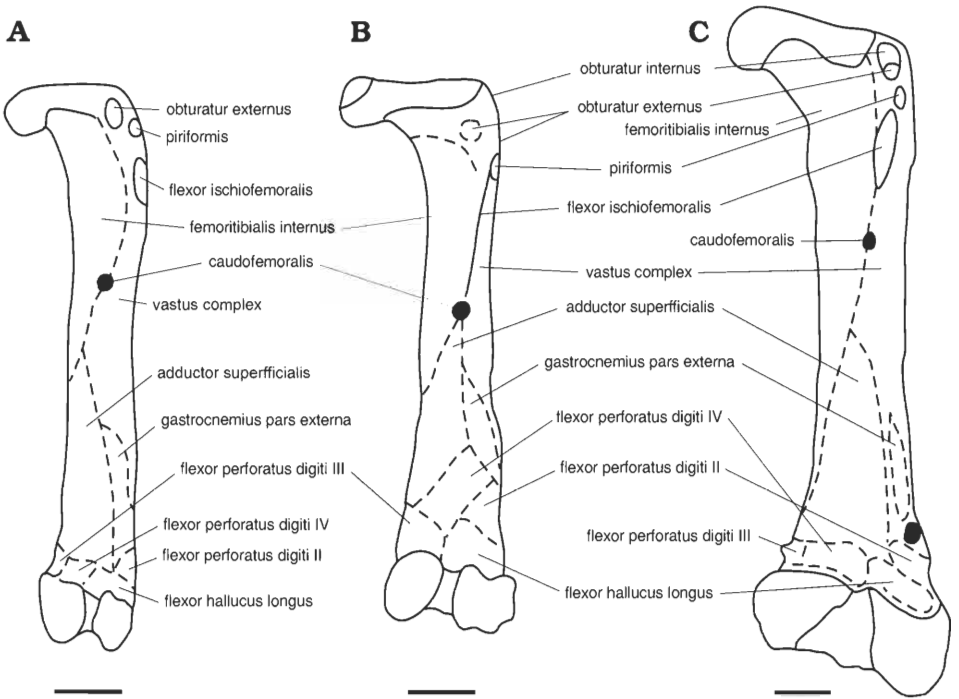
Fig. 4. Posterior views of muscle origins and insertions on the femur of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.
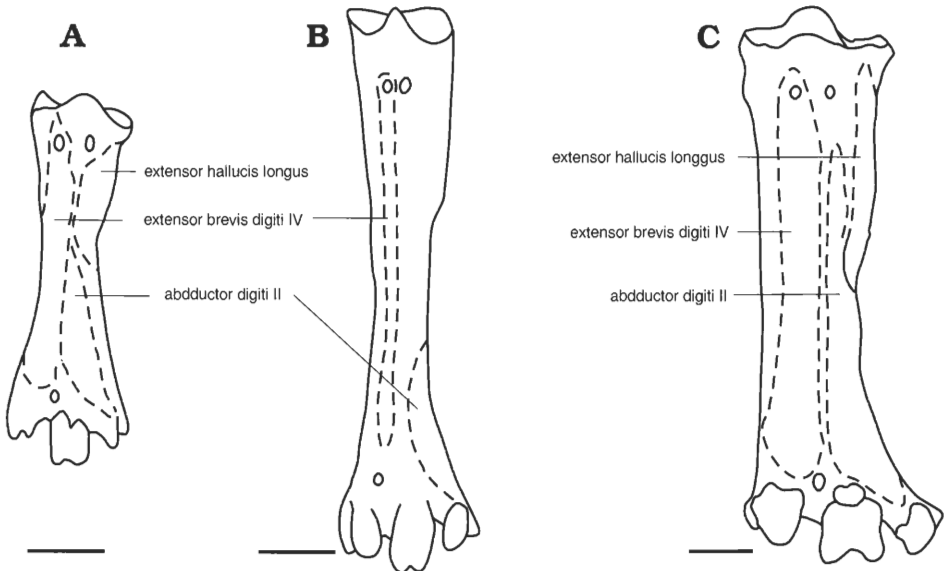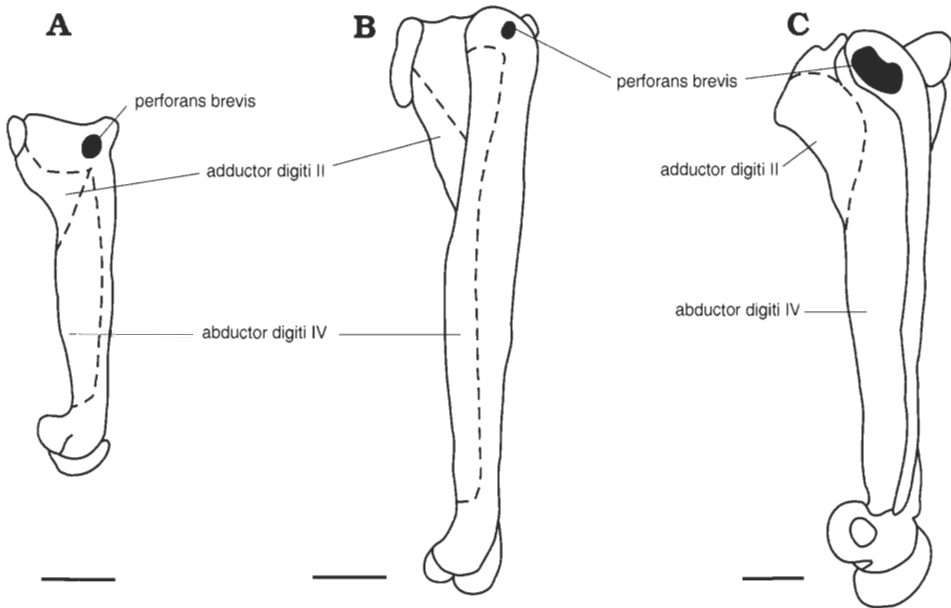

Fig. 5. Anterior views of muscle origins and insertions on the tarsometatarsus of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.

Fig. 6. Lateral views of muscle origins and insertions on the tarsometatarsus of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.

tibiotarsus. Its origin from the posterior surface of the femoral shaft is more proximal in *Macranhinga paranenis* than in *Anhinga* (Figs. 3, 4). In addition, the length of the surface of its insertion upon the hypotarsus, as well as the hypotarsal height, are proportionally somewhat longer than in anhingas but shorter than in cormorants.

Finally, the phalangeal musculature of *Macranhinga paranensis*, inferred through the origins from the femur and tarsometatarsus, is strikingly modified for arboreal locomotion. Likewise, the degree of modification of these muscles for aquatic locomotion is somewhat greater than in living darters, but clearly reduced in comparison with cormorants. The force of the water against the foot web is opposed during swimming by the flexors of the digits. Moreover, the toe flexors also provide thrust during walking and climbing. The different arrangements and development of these muscles in members of each family – Anhingidae and Phalacrocoracidae – are indicative of which of action is predominant in their locomotory habits. Thus, the origins of toe flexors from the popliteal fossa and surrounding areas of the posterior femoral side (e.g. m. flexor perforatus digiti III and IV, m. flexor perforans et perforatus digiti III) are smaller and more distal in *Macranhinga paranensis* than in cormorants (Fig. 4). However, according to the widths of the hypotarsal bony grooves for the passage of the tendons, the flexors inserting upon the hallux and the other ungual phalanges (mm. flexor hallucis longus and flexor digitorum longus) seem to have been as important in *Macranhinga paranensis* as in living anhingas but less so than in cormorants. This condition suggests a more independent positioning of the toes in order to perch and climb about on vegetation.

The attachments of the phalangeal muscles, where the origins on the tarsometatarsus of *Macranhinga paranensis* can be compared with living analogs, encompasses mm.
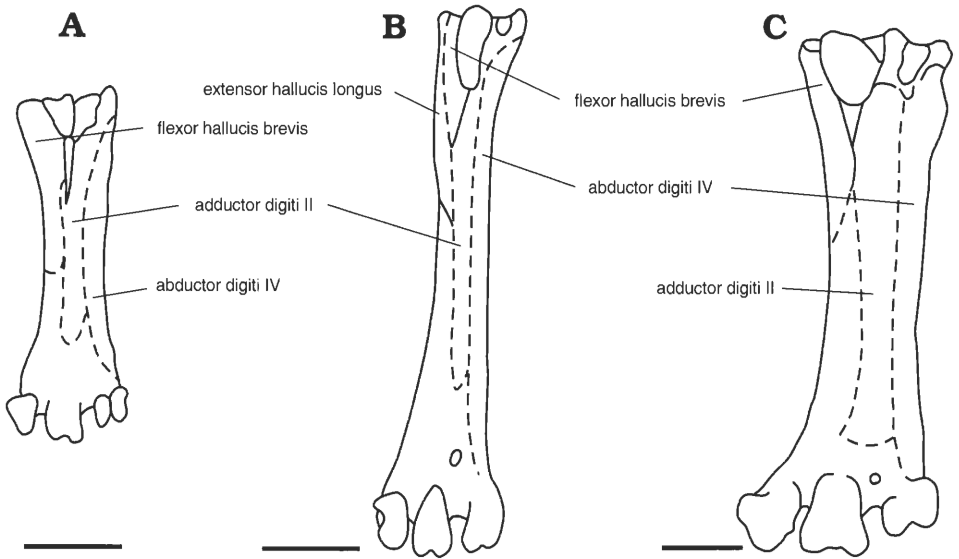
Fig. 7. Posterior views of muscle origins and insertions on the tarsometatarsus of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.
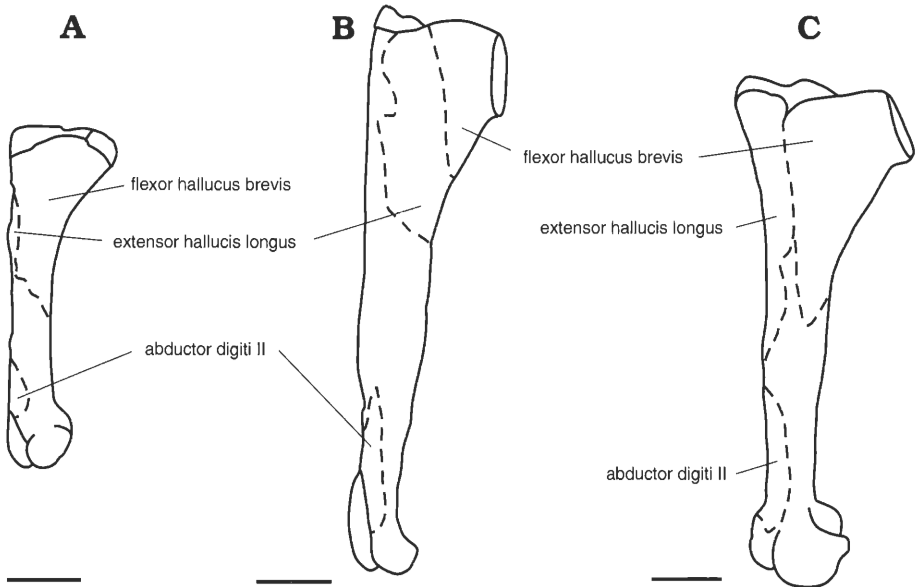

Fig. 8. Mesial views of muscle origins and insertions on the tarsometatarsus of *Anhinga anhinga* (**A**), *Phalacrocorax auritus* (**B**), and those inferred for *Macranhinga paranensis* (**C**). Modified from Owre (1967). Scale bars 1 cm.

extensor hallucis longus, adductor and abductor digiti II, abductor digiti IV, and flexor hallucis brevis. In all the cases, the development inferred for them is similar to that of the anhingas and significantly smaller than in cormorants (Figs. 5–8).

Conclusions

The body mass of *Macranhinga paranensis*, estimated to have in a mean value of 5.4 kg, confirms that this darter from the late Miocene of Argentina is the largest species of all known extinct or living Anhingidae. It is even larger than the two giant New World Tertiary anhingas – *Meganhinga chilensis* and *Anhinga fraileyi* – recently described (Alvarenga 1995; Campbell 1996). However, it will be necessary to find more associated material of all these taxa to make more accurate estimates of size.

Functional interpretation of morphological features makes it possible to infer that *Macranhinga paranensis* would have swum at the surface in a cormorant-like manner and have dived more quickly than extant darters. The morphology of the pelvic girdle and the hind-limb would have allowed *Macranhinga paranensis* to catch fishes by means of pursuit-diving rather than stalking them in an anhinga-like manner. Large body mass in diving birds is presumed to result in a reduction of buoyancy which makes a greater range of water depths for foraging available (Livezey 1988). Among cormorants and penguins, larger species are able to reach greater depths in their longer dives. The reduction of pneumaticity, as evidenced by the thick cortex and narrow marrow cavity of the ulna and the humerus of *Meganhinga chilensis* (Alvarenga 1995) and *Macranhinga paranensis*, respectively, would be also advantageous in avoiding buoyancy during submerged swimming. Likewise, numerous morphological adaptations of *Macranhinga paranensis*, observed mainly on its tarsometatarsus, are strongly indicative of its ability to perch and climb in an anhinga-like manner.

As discussed above, the fact that wing elements referred to *Macranhinga paranensis* were not found associated with holotype material makes the hypotheses concerning its flying abilities more speculative than those related to the hind-limb bones; i.e., those inferences of the biomechanics of swimming, perching and climbing, as well as predictions of body mass. However, the anatomical and phylogenetic studies based upon all the available material do support the proposed systematic assignment of these elements (Noriega 1992, 1994, 1995, 2000; Noriega & Alvarenga 2000).

It must be noted that *Meganhinga chilensis*, another giant darter from the Miocene of Chile closely related to *Macranhinga paranensis* (Noriega & Alvarenga 2000), is supposed to be flightless due to its proportionally very small ulna and carpometacarpus (Alvarenga 1995). This condition of having smaller than normal wings relative to its legs than in *Anhinga anhinga* is similar in *Macranhinga paranensis* if the assigned forelimb bones are assumed to belong to this species. However, the wing-loading of *Macranhinga paranensis* is far enough to pass the threshold of flightlessness of 25 kg/m^2 (Livezey 1988) and the morphology of the humerus and carpometacarpus is not suggestive of flightlessness. Rather, the anatomical evidence, together with the calculated wing parameters, are indicative of powerful flapping flight.

Acknowledgements

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