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A giant darter (Pelecaniformes: Anhingidae) from the Upper Miocene of Argentina and weight calculation of fossil Anhingidae

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With 2 figures and 3 tables

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Abstract: Darters are fresh-water birds presently distributed in tropical regions all over the world. Fossil darters were only known from North America, Europe, and Africa, but description in the last decade of various genera and paleospecies revealed an unsuspected diversity of large-bodied taxa of Anhingidae in the Tertiary of South America. We report the finding of the largest specimen of Anhingidae known to date, for which we estimate a mass of 17.7 kg. Specific assignment is precluded both on morphological and stratigraphical grounds. We tentatively assign this form to the genus cf. *Giganhinga*. The non-monophyletic "Miocene radiation of giant darters" is set in perspective, showing the existence of both dwarf and giant forms. The femur in birds is usually little influenced by locomotion and feeding adaptations, which makes it the best hindlimb element to predict body-weight. Due to the existence of flightless forms, we recommend caution when estimating mass from fore-limbs in the fossil anhingas.

Key words: Giant darter, Anhingidae, Late Miocene, Argentina, South America.

1. Introduction

Darters, also known as snakebirds or anhingas, are fairly large fresh-water birds presently distributed in tropical regions on all continents except Antarctica. Two to four allopatric species are currently recognized: *A. anhinga* from the New World and *A. melanogaster* from the Old World, which includes the subspecies *rufa* and *novaehollandiae* sometimes recognized as distinct species (ORTA 1992).

Although divergence from a common ancestor with the Phalacrocoracidae is estimated to have begun at approximately 30 ma during the Oligocene (BECKER 1986; ORTA 1992), the fossil record of darters extends only to the Miocene where some forms intermediate between actual darters and cormorants are found (NORIEGA, 2002). The status of *Protoplotus beauforti* LAMBRECHT, 1931 from the Paleogene of Sumatra as Anhingidae is uncertain.

Until recently, fossil darters were mainly known from North America, Europe, Africa and probably Asia (LAMBRECHT 1931; RINDERKNECHT & NORIEGA 2002). Three fossil species are known from North America: *Anhinga grandis* MARTIN & MENGEL, 1975, *Anhinga subvolans* (BRODKORB, 1956), and *Anhinga beckeri* EMSLIE, 1998; and seven fossil species have been described from South America: *Macranhinga paranensis* NORIEGA, 1992, *M. ranzii* ALVARENGA &

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Table 1. Precedence, stratigraphy and body mass estimation for Tertiary fossil giant darters of South America.

	Locality	Horizon	Age	Body mass (kg)	Source
Meganhinga chilensis	Rucananco, Malleco Province, Chile	CuraMallín Formation	Early Miocene	3.2	ALVARENGA (1995)
Macranhinga paranensis	Paraná, Entre Ríos Province, Argentina	Ituzaingó Formation	Late Miocene	5.4	NORIEGA (1992)
Macranhinga ranzii	Niteroi, Acre State, Brazil	Solimões Formation	Late Miocene – Early Pliocene	7.8	ALVARENGA & GUILHERME (2003)
Giganhinga kiyuensis	Kiyú, San José Department, Uruguay	San José Formation	Pliocene – Pleistocene	12.8	RINDERKNECHT & NORIEGA (2002)
cf. *Giganhinga*	Paraná, Entre Ríos Province, Argentina	Ituzaingó Formation	Late Miocene	17.7	This contribution

GUILHERME, 2003, *Meganhinga chilensis* ALVARENGA, 1995, *Giganhinga kiyuensis* RINDERKNECHT & NORIEGA, 2002, *Anhinga fraileyi* CAMPBELL, 1996, *A. minuta* ALVARENGA & GUILHERME, 2003, and cf. *A. grandis* MARTIN & MENGEL, 1975 (RASMUSSEN & KAY 1992; NORIEGA 2002; RINDERKNECHT & NORIEGA 2002; ALVARENGA & GUILHERME 2003).

In the last decade, description of four paleospecies in three different genera (*Meganhinga, Macranhinga*, and *Giganhinga*) revealed an unsuspected morphological and ecological diversity of large-bodied darters in the Tertiary of South America (Table 1). Two of the largest species, *Macranhinga paranensis* and *M. ranzii*, came from Upper Miocene and Miocene-Pliocene localities of Argentina and Brazil, respectively. A third one, *Giganhinga kiyuensis*, was recorded in a Pliocene-Pleistocene geological unit in Uruguay. *Meganhinga chilensis* is only known from the Early Miocene of Chile. The group has been recently reviewed by NORIEGA & ALVARENGA (2002) and ALVARENGA & GUILHERME (2003).

In this contribution, we report the finding of a fifth giant darter which is the largest specimen of Anhingidae known to date and briefly analyze its ecological and evolutionary significance. We set the "Miocene radiation of giant Anhingas" (NORIEGA & ALVARENGA 2002) in perspective and comment on the validity and procedures of weight calculation in fossil darters.

2. Systematic paleontology

Class Aves LINNAEUS, 1758
Order Pelecaniformes SHARPE, 1891
Family Anhingidae RIDGWAY, 1887
cf. *Giganhinga* RINDERKNECHT & NORIEGA, 2002
Fig. 1

Material: The material, housed in the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" of Buenos Aires (MACN 12179), consists of a well preserved distal end of a left femur (Fig. 1).

Horizon and locality: The specimen comes from the basal part of the Ituzaingó Formation, informally known as the "Mesopotamian" (FRENGUELLI 1920), which outcrops discontinuously along the eastern cliffs of the Paraná River in the Entre Ríos Province of Argentina, South America (NORIEGA 1995; Fig. 2). These beds are biochronologically assigned to the Late Miocene (Huayquerian age) which is correlated with the Tortonian of the Geologic Time Scale (GRADSTEIN & OGG 1996; see PASCUAL & ODREMAN RIVAS 1971; MARSHALL et al. 1983, and CIONE et al. 2000 for details about stratigraphic correlation).

Description: MACN 12179 is clearly distinguished from the Phalacrocoracidae by having the distal portion of the shaft straighter; the fibular condyle less protruding laterally; the posterior intercondylar fossa not as deep; the crista supracondylaris medialis more developed and sharper. It can be distinguished from the genus *Anhinga* and resembles *Macranhinga* by presenting some characters with an intermediate condition between those observed in cormorants (Phalacrocoracidae) and those typical of living darters:

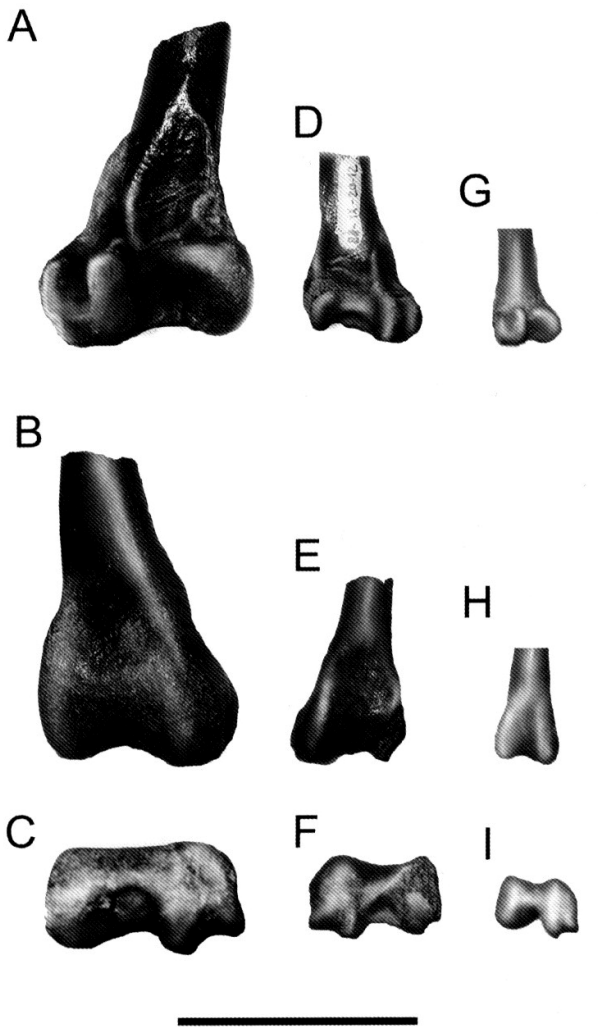


Fig. 1. Distal ends of femora of cf. *Giganhinga* (MACN 12179), *Macranhinga paranensis*, and *Anhinga anhinga*, in posterior (A, D, and G), anterior (B, E, and H), and distal (C, F, and I) views, respectively. Scale bar: 5 cm.

shaft more robust; distal end wider and more produced posteriorly; origin of the external head (Pars lateralis) of M. gastrocnemius located more proximally, with the tuberculum M. gastrocnemialis lateralis correspondingly greater and located more proximally.

The most striking feature of the specimen here described is its large size, much greater than in all other known fossil or extant anhingas (RINDERKNECHT & NORIEGA 2002: table 2; Table 2). The specimen cannot be directly compared with *Giganhinga kiyuensis* because the latter is known only by a pelvis with its fused synsacrum. The femur of *Meganhinga chilensis* is also unknown.

The distal width of the femur MACN 12179 is 40.6 mm and its least shaft circumference is 56 mm; the depth of the condylus medialis is 22.85 mm, and the depth of the condylus lateralis is 23.90 mm.

3. Discussion

Specific assessment: Direct assignment of MACN 12179 to any previously described fossil species is difficult based on morphological and stratigraphical grounds. There is no clear diagnostic character of the femur herein described that makes it mandatory to refer it to any known fossil species. As stated in the above description, the femora of *Meganhinga*

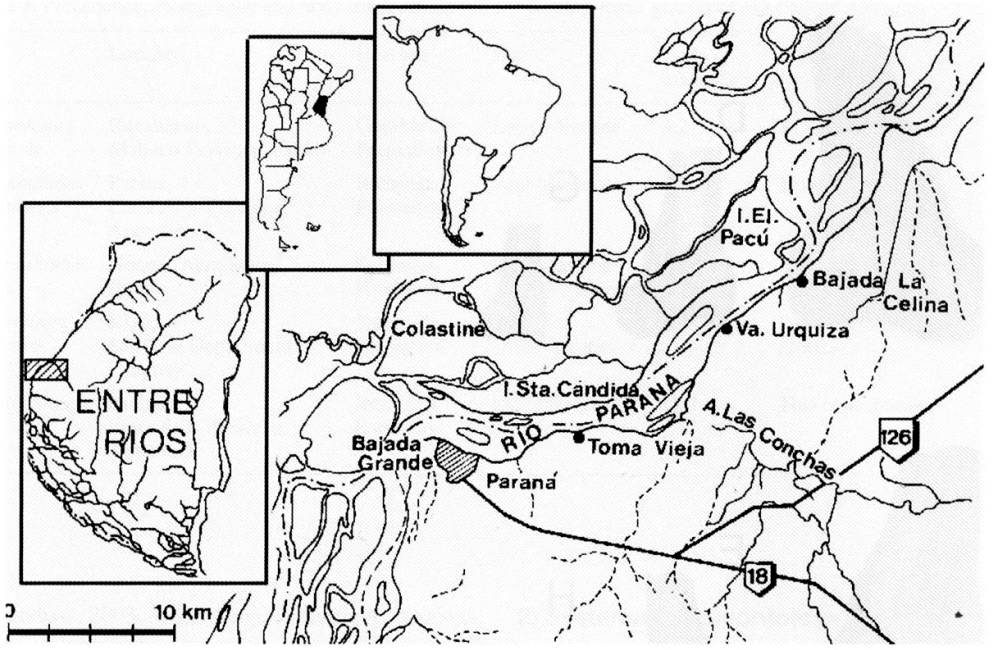


Fig. 2. Location map representing the fossiliferous site at the area of the Paraná city, Entre Ríos Province, Argentina.

chilensis and *G. kiyuensis* are not available for direct comparison with MACN 12179. Although morphologically similar, *Macranhinga paranensis* is far from the size of MACN 12179. Despite arguments against using size as a useful diagnostic character (CAMPBELL 1996), there is no single known case of such extreme size variation in any living species of Phalacrocoracidae or Anhingidae (ORTA 1992). Faced with morphological similarity we feel that size is, in this case, a proper character that clearly shows that MACN 12179 does not belong to any described fossil *Anhinga, Meganhinga* or *Macranhinga* species.

Generic assessment: Generic assessment of MACN 12179 is difficult because of both size variation parameters in the family and lack of morphological differentiation. Living darters show little variation in body weight and are not useful for comparison due to their low actual diversity. However, fossil giant darters can offer a possible basis for generic assessment. Size differences between known members of *Macranhinga* are around 30% (5.4 kg / 7.8 kg = 0.69). On the other hand, size differences between the smallest *Macranhinga* and the only known *Meganhinga* reaches 40 % (3.2 kg / 5.4 kg = 0.59). This suggests that a 30 % ratio could be used as a tool for generic assignment based on size. A c. 30% size proportion is also observed between *G. kiyuensis* and MACN 12179 (12.8 kg / 17.7 kg = 0.72, see below). As concepts and objects without a name cannot be properly inserted in lines of thought and tend to be ignored, we propose to tentatively assign this darter to cf. *Giganhinga,* which is consistent with known generic level size parameters in other giant darters.

Size and mass estimation: The mass of fossil anhingas has been traditionally estimated following any of three approaches. 1) MARTIN & MENGEL (1975), assuming constant proportions between compared taxa, stated that the width of the distal end of the humerus (femur in our case) is isometrically proportional to body mass raised to 1/3 power. 2) PRANGE et al. (1979) proposed that the length of the

humerus squared is nearly directly proportional to the mass of flying birds. 3) CAMPBELL & MARCUS (1992) calculated average relationships between linear dimensions and body weights of functional and taxonomic groupings.

We used two methods to estimate the body mass of MACN 12179, considering the least shaft circumference (LFC) of the femur and its distal width (W-dist). The femur in birds is used as a cantilever to support their weight and is usually little influenced by locomotion and feeding adaptations, which makes it the best hindlimb element to predict body-weight (CAMPBELL & MARCUS 1992), unlike the tibiotarsus which is influenced by locomotory use and the tarsometatarsus which is generally important for both locomotion and feeding (NORIEGA 2001).

MARTIN & MENGEL's model (Model 1) is a good mass predictor only if isometry (= proportional growth) is guaranteed between comparative material. Accuracy of mass estimations using this model depends directly on the existence of allometric differences along evolutionary lineages, i.e., as shape changes estimations are prone to be mistaken or to increase their error. This source of error in mass estimations should be corrected by taking into account more complex equations that include scaling indexes intended to represent differential growth in the parts being compared. Scaling indices can be calculated only if enough osteological data is available but in the absence of such information rough estimations should be done by referring to the most precise source and, preferably, always to the same one. This would make the error to be at least internally consistent, for other disturbing factors are not added in the estimation. The following equation shows this isometric scaling relation:

Mass of MACN 12179 / Mass of *A. anhinga* = (W-dist MACN 12179 / W-dist *A. anhinga*)^3 (1)

Estimation of body mass calculated for MACN 12179 by this method is 40.7 kg. It results from replacing in (1): Mass of *A. anhinga* = 1.245 kg (OWRE 1967: 8; Table 1), greatest width of distal end of femur (W-dist) of MACN 12179 = 40.6 mm, and greatest width of distal end of femur (W-dist) of *A. anhinga* = 12.7 mm (ALVARENGA & GUILHERME 2003: 617; Table 1). This model has an important caveat: it can only be applied in certain cases and when size difference among compared organisms is not far from an acceptable error threshold. If size difference is huge between any two related organisms, allometry will, as a rule, appear almost necessarily. In this sense, estimation of MACN 12179 mass from *A. anhinga* data is far from accurate due to obvious scaling effects, and should be considered an overestimation. This leads to an important conclusion for mass estimation in giant fossil anhingas: as there are no ecological or morphological equivalents for them, mass estimation is always made against a weak comparison background. The error in mass estimation should be greater as differences in size and ecology between fossil and living darters increase.

Table 2. Femur measurements (in mm) for comparison between cf. *Giganhinga* and closely related pelecaniforms.

	Femur Length	Head diameter	Distal width	Proximal width
cf. Giganhinga	–	–	40.6	–
M. paranensis	87	12.0	24.7	22.5
M. ranzii	–	–	28	25.2
A. anhinga	59.1	6.0	12.7	14.3
P. olivaceus	60.2	6.9	17.0	16.9

RINDERKNECHT & NORIEGA (2002), using the latter procedure, greatly overestimated the mass of *G. kiyuensis* at 25.7 kg. This was due to a cumulative error which resulted from having used a previous mass estimation (that of *M. paranensis*) to estimate *G. kiyuensis* body mass, instead of using the known weight of *A. anhinga*. When corrected, the estimated mass of *G. kiyuensis* drops to 12.8 kg (i.e., approximately half of the previous calculation).

The approach of PRANGE et al. (1979) (Model 2) is impossible to follow, because there is no fossil humerus available of MACN 12179.

CAMPBELL & MARCUS' model (Model 3) is derived from the logarithmic relationship between measurements of the least shaft circumference of the femur (LFC) or tibiotarsus (LFT) 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: 397). Results for all their data are given in a table (CAMPBELL & MARCUS 1992: 405; Table 2). For purposes of mass estimation we selected only those data for the "Swimmers" subgroup (Subgroup SW including Gaviidae, Podicipedidae, Spheniscidae, Phalacrocoracidae, Anhingidae, and Phalaropodidae), the group into which cf. *Giganhinga* would be classified, both taxonomically and

morphologically. This model was previously applied to estimate the body mass of *Macranhinga paranensis* (NORIEGA, 2001). The scaling equation can be written as:

Mean of $\log_{10}$ (mass) for SW/Mean of $\log_{10}$ (LFC) for SW = Log_{10} (mass) of MACN 12179/Log_{10} (LFC) of MACN 12179 (2).

The estimation of body mass obtained for MACN 12179 is 17.7 kg. It results from replacing in (2): mean of $\log^{10}$ (mass) for SW (= 2.938), mean of $\log_{10}$ (LFC) for SW (= 1.209), and Log_{10} (LFC) of MACN 12179 (= 1.748), being LFC = 56 mm. This model might also not be accurate when estimating masses of birds that greatly exceed the average weight of actual swimmers. Nevertheless, as this equation takes into account some scaling effects of mass estimation and is calculated for a functional ecological group, we concede priority to this calculation over the one estimated by using MARTIN & MENGEL's model (Model 1).

At least two giant anhingas, *M. ranzii* and *M. chilensis*, show marked reduction of their flight apparatus (NORIEGA & ALVARENGA 2002). So any giant darter mass estimation based on forelimb proportions must be taken with care and, if we assume reduced flight capacity, almost certainly as an underestimation of the actual weight. This underestimation is predicted based on several facts: 1) flightless birds usually have reduced forelimbs and 2) they also are allowed to be heavier due to the loss of flight constraints (CARROLL 1997; FEDUCCIA 1999); and 3) a third factor exists in the case of diving birds: being heavy is advantageous as it reduces energy expenditure and enhances diving (NORIEGA 2001).

A test can be performed in order to assess how misleading a mass estimation based on forelimb can be. All we need is a couple of closely related species, also allied to darters. One of them must be flightless or with a notable reduction of flight muscles and forelimbs, and the other one must be fully volant. Luckily we can test this scenario not in evolutionary terms but by means of evaluating the case of the Flightless Cormorant (*Phalacrocorax harrisi* or *Nannopterum harrisi*) and the Olivaceus Cormorant (*Phalacrocorax olivaceus*). Since the living species of Phalacrocoracidae, are traditionally considered the sister group of the Anhingidae (OLSON 1985; SIEGEL-CAUSEY 1988), they can be properly used to test error in weight estimation. The Flightless Cormorant is the biggest living cormorant and among the heaviest (probably the heaviest). As its vernacular name implies, it has lost its flying capacity and has notably reduced wings. The Olivaceus Cormorant is an average sized cormorant with the habitual flying capacities present in most members of the genus.

Table 3. Average weight, average wing length, weight/size ratio and reciprocal mass estimation for two *Phalacrocorax* cormorants (*P. harrisi* and *P. olivaceus*). Data from ORTA (1992).

	Average Weight (AW)	Average Wing Length (AWL)	AW/AWL	Reciprocal mass estimation
P. harrisi	3.25 kg	250 mm	7.7	0.25 kg
P. olivaceus	1.8 kg	480 mm	26.7	23 kg

If we are to calculate the weight of *P. harrisi* based on the proportional relation of average length wing to body mass in *P. olivaceus* we would obtain a mass estimation of 0.25 kg, which is actually over ten times lower than its actual mass (Table 3). The opposite also is true: a mass estimation of *P. olivaceus* from *P. harrisi* proportions grossly overestimates its mass from the actual 1.8 kg to an astonishing 23 kg. Clearly, such allometric differences lead to totally misleading estimations. Close phylogenetic position, ecology and morphology indicate that this comparison may also hold true for darters, and hence the importance of using hindlimb measurements when estimating fossil specimen body masses. Finally, and as a generalization, masses of fossil short-winged anhingas estimated from comparison with the mass of any living flying anhinga are in all likelihood underestimated, i.e. fossil giant darters were probably heavier than calculated.

All living darters are similar in size and flying habits, thus any mass estimation of fossil anhingas have to cope with the shortcoming of having a reduced variational basis from which calculate alometric equations to predict body mass of considerable smaller or larger forms.

4. Conclusions

The existence of such an enormous darter necessarily raises some questions on the ecology of darter's bauplan: which is the size limit for the evolution of darters? Is the specimen herein described a giant darter or are the living darters just dwarfs? Which were the evolutionary triggers of such a change?

NORIEGA & ALVARENGA (2002) suggested the existence of a "Miocene radiation of giant darters" but they did not mention that this radiation must be understood only in morphological and ecological terms and not as a single phylogenetic event. Their cladogram clearly shows that the "Miocene giant darters" considered in the analysis (*M. chilensis* and *M. paranensis*) do not constitute a monophyletic group, but a polyphyletic one (NORIEGA & ALVARENGA 2002: 46, fig. 4). This reasoning has important consequences for the interpretation of the evolution within the group as it would mean that there was not only one, but at least two "gigantization" events, or conversely, that there was at least one dwarfization event in the node of *A. anhinga* (NORIEGA & ALVARENGA, 2002: 46, fig. 4). The evolutionary basis of size and shape change in darters can only be explained against an evolutionary tree that considers all the newly described forms to include the full morphological and size spectrum, which now ranges from the tiny *A. minuta* to the giant cf. *Giganhinga* herein described.

Developmental studies in darters and cormorants will shed light on the evolutionary pathways that led to the change and loss of their flying capabilities. Findings of new and more complete materials are necessary in order to broaden the knowledge of giant South American darters and explain their radiation and phylogeny.

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