

New fossil anhingids from the upper Acre River (Late Miocene of southwestern Amazon)

Edson Guilherme¹  | Carlos D'Apolito¹  | Fellipe Muniz^{2,3} |
Silvia Oliveira Lomba^{2,3} | Leonardo Aldrin¹ | Annie Schmaltz Hsiou^{2,3} 

¹Laboratório de Pesquisas Paleontológicas, Centro de Ciências Biológicas e da Natureza, UFAC, Rio Branco, AC, Brazil

²Laboratório de Paleontologia, Departamento de Biologia, FFCLRP/USP, Ribeirão Preto, SP, Brazil

³Programa de Pós-graduação em Biologia Comparada, FFCLRP/USP, Ribeirão Preto, SP, Brazil

Correspondence

Edson Guilherme, Laboratório de Pesquisas Paleontológicas, Centro de Ciências Biológicas e da Natureza, UFAC, Rio Branco, AC, Brazil.
Email: edson.guilherme@ufac.br

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Abstract

Four extant species of anhingids are found worldwide, all belonging to a single genus (*Anhinga*). However, the fossil record reveals a much greater diversity of this group in the past. The oldest known anhingids date back to the upper Oligocene period in Australia, but during the Miocene epoch in South America, they achieved their most remarkable diversity. This study describes newly discovered anhingid fossils from the Late Miocene period in South America. These fossils were extracted from the Acre conglomerate member, part of the Upper Miocene deposits in the southwestern Amazon region. The described fossils consist of two fragments of pelvic girdles, two femora, and two vertebrae belonging to a giant anhingid (*Macranhinga* sp.), as well as a vertebra from *Anhinga minuta*, the smallest of all darters. The examination of these fossils suggests the presence of potentially three distinct anhingid taxa within the same locality. The environment in which the conglomerate deposits were formed was ecologically complex. It is likely that these three species coexisted within the same ecosystem but avoided direct competition for food and reproductive sites by not fully exploiting their fundamental niche.

KEYWORDS

Anhinga minuta, fossil, *Macranhinga*, Solimões formation

1 | INTRODUCTION

Darters, or snakebirds, are aquatic birds that feed on fish and small invertebrates, which they catch by diving. For diving, they have dense bones (not pneumatic), wettable plumage, and smaller air sacs that help to reduce buoyancy, facilitating the pursuit of prey at different depths (Ryan, 2007). Darters, cormorants, gannets, boobies, and frigatebirds are closely related evolutionarily, being grouped in the clade Suliformes (formerly considered a subset of Pelecaniformes; Smith, 2010). This group includes four families, of which, darters belong to the Anhingidae. The extant darters are all included in a single genus, *Anhinga*, with four species: *Anhinga anhinga*

(South America); *Anhinga rufa* (Africa); *Anhinga melanogaster* (Asia), and *Anhinga novaehollandiae* (Oceania) (Winkler et al., 2020).

The fossil record has revealed that the Anhingidae were more diverse in the past and had a much wider geographic distribution than they do today (Diederle, 2015a; Mayr et al., 2020). Evidence of this fact is found in fossils recovered from different European sites (Diederle, 2015a; Lambrecht, 1916; Mayr et al., 2020) where the genus *Anhinga* does not currently occur (Winkler et al., 2020). Fossil records of darters date back to the upper Oligocene of Australia; however, the most remarkable diversity of the group occurred during the Miocene (Diederle, 2015a). During the upper Miocene of South

America, the Anhingidae reached their greatest diversity of genera and species (Cenizo & Agnolin, 2010; Diederle, 2015a). In addition to the current genus, also found in the fossil record, three other genera of giant anhingids are known from this continent: *Meganhinga*, *Macranhinga*, and *Giganhinga* (Cenizo & Agnolin, 2010).

Most records of South American anhingids come from Huayquerian land mammal age sediments in Argentina and the Solimões Formation in Brazil (Alvarenga & Guilherme, 2003; Cenizo & Agnolin, 2010; Guilherme et al., 2021). The records of known anhingids from the Solimões Formation come from the Acre and Solimões basins in southwestern Amazonia. This formation is well known for its abundant fossil record, mainly of vertebrates (Cozzuol, 2006; Hsiou et al., 2022; Negri et al., 2010; Ribeiro et al., 2013; Riff et al., 2010; Souza-Filho & Guilherme, 2015). In the Acre River, on the triple border between Brazil, Bolivia, and Peru, there is a basal conglomerate from the upper Miocene named by Campbell et al. (1985) as an Acre Conglomerate member. This conglomerate is very rich in vertebrate fossils, including fish, reptiles, mammals, and birds (Frailey, 1986; Kay & Frailey, 1993; Czaplewski, 1996; Campbell, 1996; Bocquentin-Vilanueva & Guilherme, 1997; Gayet et al., 2003; Alvarenga & Guilherme, 2003; Cozzuol et al., 2006;

Kay & Cozzuol, 2006). Among birds, only anhingids were found at this sedimentary level (Alvarenga & Guilherme, 2003; Campbell, 1996). In the 1990s, Campbell (1996) described *Anhinga fraileyi*, a new species from Patos locality (=LACM 4611 or Acre 6), on the Brazil/Peru border, currently treated as a junior synonym of *Macranhinga paransensis* (Diederle, 2017a). Later, Alvarenga and Guilherme (2003) described the smallest known darter, *Anhinga minuta*, from the Cachoeira do Bandeira locality (=LACM 5158) on the Brazil/Bolivia border.

In this study, we present new fossil remains of anhingids found during a recent joint expedition to the upper Acre River on the Brazil/Peru border, by the team from the Federal University of Acre (UFAC), University of São Paulo (USP), and Chico Mendes Institute for Biodiversity Conservation—ICMbio.

2 | MATERIALS AND METHODS

2.1 | Studied species and specimens

The fossil elements described here were all collected from the Patos site (=LACM 4611 or Acre 6) (10°55'59.2"S; 69°55'18.0"W; Figure 1) between July 18 and 26, 2022.

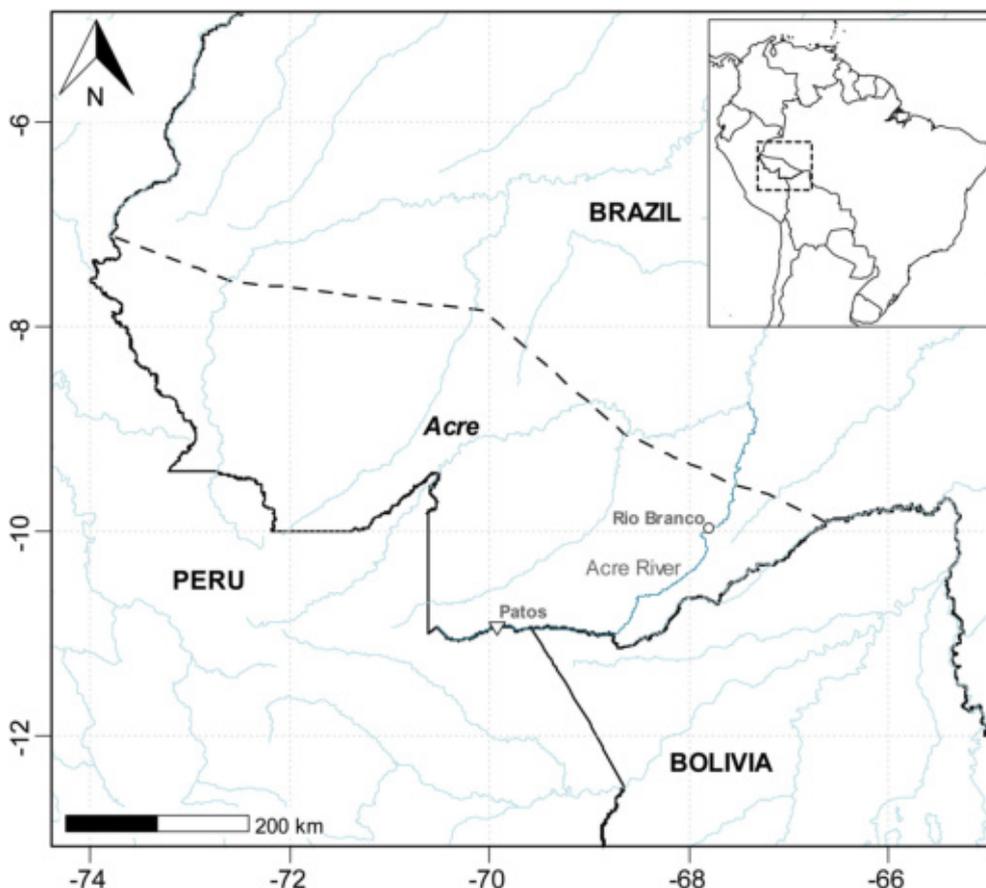


FIGURE 1 Location map showing the state of Acre in southwestern Amazonia and the Patos conglomerate site along the upper Acre River.

TABLE 1 Measurements in millimeters of the four linear dimensions of pelvic girdle + synsacrum of fossil Anhingidae from the Acre conglomerate member in comparison with *Macranhinga ranzii* and those of extant *Anhinga anhinga*.

Pelvic girdle + synsacrum	Maximum width of the vertebral body of the first synsacral vertebra—WVB	Length of the preacetabular region—LPR	Pelvis width between antitrochanters—PW	Dorsoventral diameter of the acetabular cavity—DVD
UFAC 6990	6.88	61.21	37.7 ^a	11.68
UFAC 5086	6.51			
UFAC 6471— <i>Macranhinga ranzii</i>			66.56 ^a	13.47
R-382— <i>Anhinga anhinga</i>	4.81	43.21	31.63	5.74
R-554— <i>Anhinga anhinga</i>	4.99	41.36	29.57	4.79
R-555— <i>Anhinga anhinga</i>	4.59	40.73	28.34	5.39

^aEstimated measurement.

TABLE 2 Measurements in millimeters of the femora of fossil Anhingidae from the Acre conglomerate member in comparison with those of extant *Anhinga anhinga*.

Femora	Total length of the femora—TFL (from trochanter to external condyle)	Least shaft depth—LSD	Least shaft width—LSW	Distal width—DW
UFAC 6991	75.37	9.42	8.92	18.05
UFAC 6993		11.34	10.61	
R-554— <i>Anhinga anhinga</i> (left)	57.19	6	5.47	11.88
R-555— <i>Anhinga anhinga</i> (left)	58.88	5.64	5.87	12.25
R-382— <i>Anhinga anhinga</i> (left)	54.25	5.51	5.9	12.46

The only exception is the fragment of synsacrum UFAC 5086 that was collected 20 years earlier in a curve downstream from Patos in the same locality described by Kay and Cozzuol (2006) and Latrubesse et al. (2010, p. 103). We examined three extant *A. anhinga* specimens (UFAC R-382, R-554, and R-555) as comparative material. To determine the taxonomic affinities of the fossil material, we compared it with extant and fossil specimens (Tables 1–3) based on available information recovered from the published literature (e.g., Boles, 2010; Diederle, 2015b; Diederle & Agnolin, 2017; Mayr et al., 2020; Ono, 1980). The osteological nomenclature follows Baumel and Witmer (1993) and Livezey and Zusi (2006).

2.2 | Body mass estimation

Assuming that proportions are similar between extant *Anhinga* and fossil forms, the body mass estimation was based on the following equation: $M_{Mar}/M_{Aa} = (L_{Mar}/L_{Aa})^3$ (Areta et al., 2007; Guilherme et al., 2021; Martin & Mengel, 1975; Rinderknecht & Noriega, 2002), where M is

the mass and L is the linear dimensions of homologous characters derived from the synsacrum and femora (Tables 1 and 2); Mar is the *Macranhinga* and Aa is the *Anhinga anhinga*. The homologous linear characters between *Macranhinga* and *A. anhinga* used in the body mass estimation equation were: (a) synsacrum, Dvd is the dorsoventral diameter of the acetabular cavity (Table 1) and (b) femora, Tlf is the total length of the femora; Lsd is the least shaft depth; Lsw is the least shaft width, and Dw is the distal width (Table 2). The linear measurements of *A. anhinga* were taken from the average sizes of the homologous bones of the three extant specimens (UFAC R-382, 554, and 555, Tables 1 and 2), while the average mass of *A. anhinga* (1.235 kg) was extracted from Dunning (2008). The dimensions of the fossils described here were measured with digital calipers (0.01 mm precision).

2.3 | Phylogenetic inference

We scored the most complete and informative specimen, UFAC 6990, using an existing morphological data matrix

TABLE 3 Measurements in millimeters of the three cervical vertebrae of fossil Anhingidae from the Acre conglomerate member in comparison with those of extant *Anhinga anhinga*.

Vertebrae	Vertebral body length—VBL (mm)	Width of the facies articularis cranialis—WFAcra (mm)	Maximum width of facies articularis caudalis—WFAcCau (mm)
UFAC—6989 (4)	34.16	8.84	6.74
R-554— <i>Anhinga anhinga</i> (4)	25.67	4.45	3.92
R-555— <i>Anhinga anhinga</i> (4)	25.38	5.9	3.52
UFAC—6992 (15)	21.48	10.92*	7.87
R-554— <i>Anhinga anhinga</i> (15)	16.58	8.02	6.1
R-555— <i>Anhinga anhinga</i> (15)	15.38	6.82	5.08
UFAC 7296 (19)	10.32	9.16	6.79
R-554— <i>Anhinga anhinga</i> (19)	11.75	10.53	6.33
R-555— <i>Anhinga anhinga</i> (19)	11.17	10.15	5.85

*Underestimated measurement (incomplete bone region).

by Diederle (2015b; unpublished thesis) and modified by Guilherme et al. (2021). Coding of character 6 (0 → 1) has been changed for *A. anhinga* and *A. melanogaster*. The scorings of character 6 (0 → ?) and character 12 (1 → 0) of *M. paranensis* were also modified. As the synsacrum of *M. ranzii* does not present the first preacetabular vertebra, we changed the scoring of character 2 (1 → ?). The resulting matrix comprises 27 characters for 14 taxa (Table S1). The parsimony analysis was performed using the implicit enumeration search mode of TNT version 1.5 (Goloboff et al., 2008). Characters were unordered and equally weighted. *Fregata magnificens* was chosen as the outgroup. In an attempt to improve tree resolution, we used the command pcrprune in TNT. *M. chilensis* was identified as an unstable taxon (see Guilherme et al., 2021), so we opted to remove it from the final matrix.

2.4 | Institutional abbreviations

UFAC—Universidade Federal do Acre, Rio Branco, Brazil; LPP/UFAC—collection of vertebrate paleontology of Laboratório de Pesquisas Paleontológicas da Universidade Federal do Acre; UFAC-R—collection of recent vertebrates from the UFAC Paleontology Laboratory; CICYTTP—Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (Diamante, Entre Ríos, Argentina); LACM—Natural Museum Los Angeles (Los Angeles, California, USA).

2.5 | Horizon

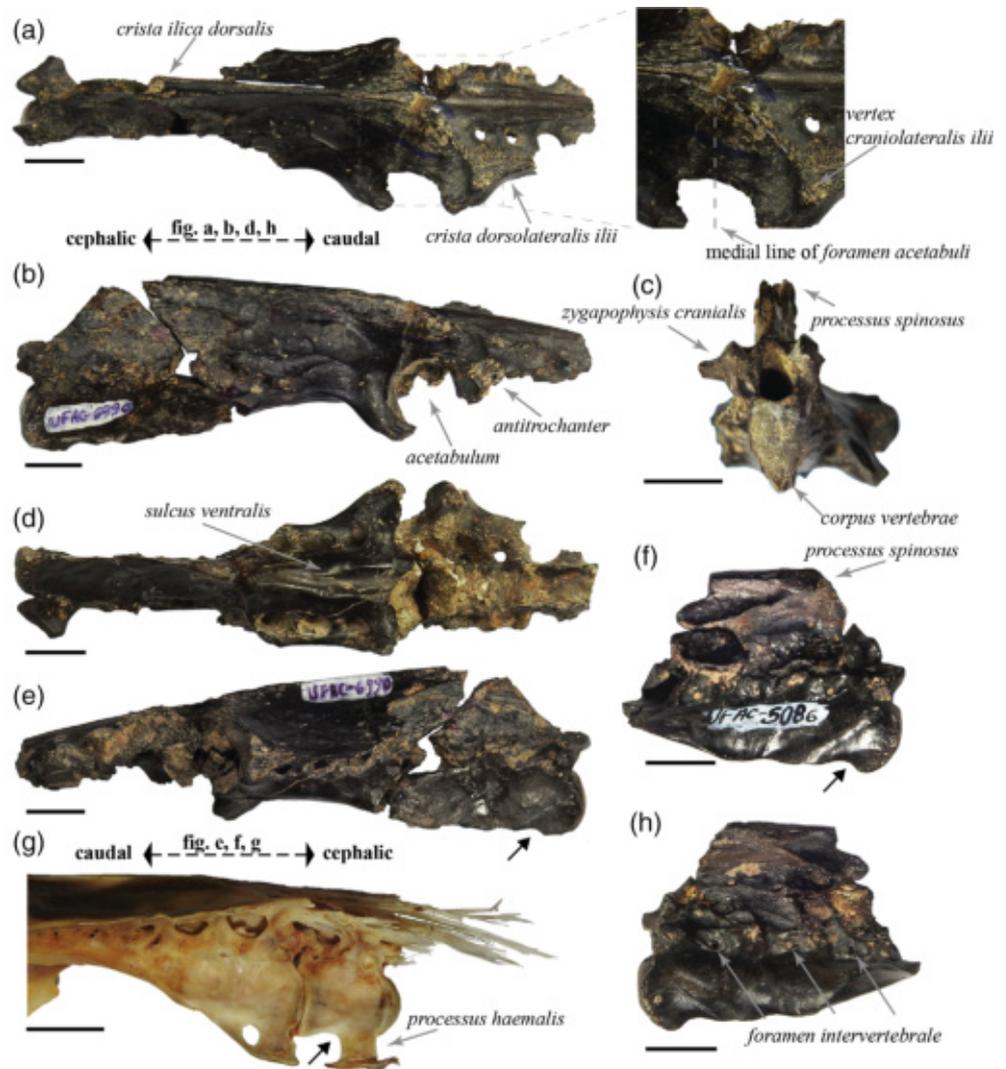
Campbell et al. (1985) proposed the Acre conglomerate member to designate a ferruginous clay-pebble conglomerate

with reworked vertebrate fossils. According to these authors this conglomerate was formed by the reworking and redeposition of “tertiary” sediments at the base of the Iñapari Formation (=Fm. Madre de Dios). This conglomerate would have formed during the Pleistocene (Lujanian) due to heavy rainfall in the Andes, causing catastrophic floods in the lowlands of southwestern Amazonia (Campbell & Frailey, 1984). These floods would have eroded the upper Miocene sediments containing vertebrate fossils and fossilized wood, redepositing them in the form of a rusty conglomerate in what they called the “Pleistocene phase I” (Campbell & Frailey, 1984). Currently, there is a consensus, even among the authors who described the Acre conglomerate member, that this sedimentary package was not formed during the Pleistocene/Holocene but that it belongs to the upper Miocene and is equivalent to the Huayquerian land mammal age (Campbell et al., 2006; Kay & Frailey, 1993; Latrubesse et al., 2010). The formation of the Acre conglomerate member took place in a fluvial-lacustrine system in a megafan system (Hoorn et al., 2022; Hoorn, Wesselingh, Hovikoski, et al., 2010; Hoorn, Wesselingh, Ter Steege, et al., 2010; Latrubesse et al., 2010). The Acre conglomerate member appears discontinuously along the banks of the upper Acre River on the borders of Brazil, Bolivia, and Peru. A succinct description of the locality LACM 4611 (Acre 6), from which most of the current study’s fossils come, can be found in Frailey (1986).

There is still debate about the significance of these fossil-rich conglomerates for the stratigraphy of Neogene deposits in the southwestern Amazon. Some authors have suggested that they are directly overlying the Ucajali Unconformity. This regional feature would separate the younger deposits of the Içá Formation in Brazil (Madre de Dios Fm. in Peru) from the Solimões

FIGURE 2 Pelvic girdle and the synsacrum of *Macranhinga* sp. (UFAC 6990) from Patos locality (=LACM 4611).

(a) Dorsal; (b) lateral; (c) cranial, and (d) ventral views. In (a), detail showing the cranial position of the vertex craniolateralis ilii. (e, f, h) Lateral view of the pelvic girdle and the synsacrum of UFAC 6990 and preacetabular portion of UFAC 5086 compared to the homologous region of *A. anhinga* (R-382) in (g). The black arrows indicate the region where the processus haemalis should be present in the fossils. All scale bars = 1 cm.



Formation (Ipururo Fm. in Peru) (Campbell et al., 2001, 2006). Thus, in this scheme, the fossils reported herein would belong to the Içá/Madre de Dios Formation. However, in an alternative interpretation, the validity of the Ucayali Unconformity as a stratigraphic marker is questioned, and the conglomerates are interpreted as the result of normal fluvial processes (Cozzuol, 2006). This view is followed by the majority of works that studied the fossils from the region, which consider the sediments to belong to the Solimões Formation (e.g., Bergqvist et al., 1998; Cozzuol, 2006; Kay & Cozzuol, 2006; Latrubesse et al., 2010; Souza-Filho & Guilherme, 2015; Kerber et al., 2016).

3 | RESULTS

3.1 | Systematic paleontology

Suliformes Sharpe 1891

Anhingidae Reichenbach 1849

Macranhinga Noriega 1992

Macranhinga sp.

Referred material: UFAC 6990—pelvic girdle fragment and synsacrum (Figure 2a–e; Table 1).

Identification (only for the referred material): The specimen UFAC 6990 is here assigned to the Family Anhingidae, differentiated from the Phalacrocoracidae based on the following characters (sensu Rinderknecht & Noriega, 2002; Diederle, 2015b): facies articularis cranialis of the first synsacral vertebra oval in shape; gradual reduction of the height of the crista iliaca dorsalis preacetabular in the craniocaudal direction. Among the Anhingidae, this pelvic girdle was assigned to the genus *Macranhinga* based on the presence of the following characters (modified from Diederle & Agnolin, 2017). More elongated preacetabular portions of the ilium than in *A. anhinga*; crista iliaca dorsalis preacetabular high; zygapophysis cranialis and corpus vertebrae of the preacetabular vertebrae more robust than in *A. anhinga*; cotyloid cavity ~50% larger than in *A. anhinga*.

3.1.1 | Comparative description

The specimen UFAC 6990 was found on the surface of the conglomerate. This pelvic apparatus is more complete on the left side, where the acetabulum is preserved (Figure 2a,b). In the preacetabular cranial half, there was a fracture at the caudal limit of the third synsacral vertebra (Figure 2b). This region presents thoracic vertebrae fused and laterally compressed in the ventral portion, followed by a high processus spinosus, typical of *Macranhinga* (Figure 2b). The crista iliaca dorsalis is high as in *M. ranzii* (Guilherme et al., 2021). The first synsacral vertebra is opisthocoeleous, in which the convex corpus vertebrae, the foramen vertebrale, and the zygapophysis cranialis can be seen (Figure 2c). The outline of the foramen vertebrale is oval (elliptical) due to the significant compression of the vertebrae in this region (Figure 2c). The dorsal region of the foramen vertebrale appears to be slightly eroded, not forming an apparent figure-eight shape as in *M. paranensis*, *G. kiyuensis*, and *A. melanogaster* (see character 2, pg. 33 in Diederle, 2015b). In the ventral preacetabular region, the corpus synsacri is laterally compressed in the first three vertebrae, becoming more dilated towards the acetabular vertebra (Figure 2d). In *M. paranensis*, this same region is moderately compressed, according to Diederle (2015b; p. 109). In the corpus synsacri, between the first three lumbar vertebrae, there is a conspicuous and well-defined sulcus ventralis (Figure 2d). The margin of the corpus synsacri of the first three vertebrae presents well-marked undulations in the first vertebra in lateral view, becoming discrete in the following ones, suggesting the possible presence of a processus haemalis as observed in extant *A. anhinga* (Figure 2e,g). On both sides of the os coxae, a small part of the ilium was preserved while the ischium and pubis were completely lost (Figure 2a). The synsacrum was relatively well-preserved in the cranial region, while in the caudal (postacetabular) region, there were only remnants of four vertebrae of the corpus synsacri (Figure 2a). The total length of the specimen, from the first synsacral vertebra to the fractured portion of the fourth postacetabular lumbar vertebrae, is 98.48 mm. Comparing the measurement of the preacetabular region (61.21 mm) to the homologous in the extant *A. anhinga* R-554 (41.36 mm), it was possible to estimate the total length of specimen UFAC 6990 at approximately 115.9 mm. Other measurements referring to this pelvic girdle + synsacrum concerning the counterparts of *A. anhinga* and *M. ranzii* are shown in Table 1.

3.1.2 | Os coxae

Ilium—is the only bone partially preserved from the pelvis UFAC 6990. From the ala preacetabularis ilii, only a

small portion between the fracture and the cranial margin of the foramen acetabuli was kept on both sides. On the preacetabular surface of the ilium, the muscle insertion lines are conspicuous (Figure 2b). The most caudal part of the cristae iliaca lateralis is preserved on the left side and broken off on the right side (Figure 2a,b). The cristae iliaca dorsalis preacetabular extends caudally and diverges anterior to the medial line of the foramen acetabuli, the same condition observed in *Meganhinga chilensis*, *Macranhinga ranzii*, *Giganhinga kiyuensis* and extant *Anhinga* but different from *Macranhinga paranensis* (Alvarenga, 1995; Noriega & Alvarenga, 2002; Rinderknecht & Noriega, 2002; Diederle, 2015b; Guilherme et al., 2021; Figure 2a). The cristae iliaca dorsalis in *G. kiyuensis* diverges anteriorly to the medial line of the foramen acetabuli (see Figures 2 and 3 in Rinderknecht & Noriega, 2002) and is not the same as *M. paranensis* as postulated by Diederle (2015b, p. 180). The vertex cranio-lateralis ilii starts caudal to the anterior margin of the foramen acetabuli and ends at the level of the antitrochanter (Figure 2a,b), the same condition observed in *A. anhinga* and *M. ranzii*, and different from *Meganhinga chilensis* and *Macranhinga paranensis* where this same vertex is dislocated from antitrochanter (Guilherme et al., 2021; Noriega & Alvarenga, 2002). A small portion of the crista dorsolateralis ilii was preserved on the left side (13.4 mm in length) from the caudal margin of the sulcus antitrochantericus, between the first and second postacetabular lumbar vertebrae (Figure 2a). This crest runs almost parallel, caudally, to the crista spinosa synsacri, indicating the postacetabular region is narrower (see character 19 in Noriega & Alvarenga, 2002; Figure 2a), the similar condition is observed in *Meganhinga chilensis*, *Macranhinga paranensis*, *M. ranzii* and different from *A. anhinga* (Guilherme et al., 2021; Noriega & Alvarenga, 2002). Although a little worn, the preserved portion of the crista dorsolateralis ilii is at the same level or more elevated than the crista spinosa synsacri. The distance between the preserved crista dorsolateralis ilii, at the level of the second postacetabular synsacral vertebra, and the median part of the crista spinosa synsacri is 12.98 mm, indicating that the estimated width of the pelvis in this region would be 25.96 mm.

Acetabulum—Only the left acetabulum is fully preserved (Figure 2a,b), while on the right side, only a tiny joint region along the ala preacetabularis ilii remained intact (Figure 2a). The outline of the cotyloid cavity on the left side is almost complete except for the missing portion relating to the ischium and pubis. The left foramen acetabuli has a rounded shape with a possibly hollow center. The diameter of the acetabular cavity (11.68 mm) is ~50% larger than *A. anhinga*, ~16% larger than *M. paranensis*, and ~24% smaller than the

FIGURE 3 Left femur UFAC 6991 (a), (c) and UFAC 6993 (e), (g) attributed to *Macranhinga* compared to the *A. anhinga* counterpart (R 554 (b), (d) and R 382 (f), (h)). (a), (b), (e), and (f) Dorsal views; (c), (d), (g), and (h) ventral views. (i) and (j) Muscular insertions in the femora of *Macranhinga* sp. indet. 1 and 2 (UFAC 6991 and 6993) and *M. ranzii* (UFAC 3640) compared to *A. anhinga* (R-554). (i) Insertion of *m. flexor ischiofemorialis* in *A. anhinga* (left) and in UFAC 6993 (right); (j) insertion of *m. psoas* in (left to right): *M. ranzii* UFAC 3640, UFAC 6991, UFAC 6993, and R-554. All scale bars = 1 cm.



counterpart in *M. ranzii* (Diederle, 2015b; Guilherme et al., 2021; Table 1). The antitrochanter was broken, leaving only the inferior joint face next to the surface of the acetabulum (Figure 2b). In the dorsal region, the sulcus antitrochantericus is well marked by the margin of the vertex craniolateralis ilii. Despite being incomplete, the length between the antitrochanter and the midline of the crista dorsolateralis ilii is 18.85 mm, allowing us to estimate the width of the pelvis between the two antitrochanters to be a minimum of 37.7 mm (Table 1). The estimated mass of the individual to whom this pelvis belonged, calculated from the Dvd (Table 1), was 6.0 kg. This value is close to the average mass estimated for *M. paranensis* (Noriega, 2001; Areta et al., 2007, Figure 8).

3.1.3 | *Macranhinga* sp.

Referred material: UFAC 5086—Anterior portion of synsacrum (Figure 2f,h).

Identification (only for the referred material): This small anterior portion of synsacrum is assigned to

Macranhinga based on the presence of the following characters (sensu Diederle & Agnolin, 2017): zygapophysis cranialis and corpus vertebrae of the preacetabular vertebrae more robust than in *A. anhinga*; processus spinosus high.

3.2 | Comparative description

Preacetabular synsacral fragment measuring 39.57 mm (Figure 2f,h). The preacetabular shows the first three synsacral vertebrae fused. The ventral region is well preserved, while in the dorsal region, only a small portion of the processus spinosus remains (Figure 2f). Like the homologous region of specimen UFAC 6990 (Figure 2c), the first synsacral vertebra is opisthocelous with the corpus vertebrae convex. The zygapophysis cranialis was lost on the right side and partially preserved on the left side. The outline of the vertebral foramen is oval (elliptical), compressed laterally, and not forming an apparent figure-eight shape as in the specimen UFAC 6990. At the limit of the zygapophysis cranialis, in the caudal direction, the origin of three processus transversus can be observed, and

among them, three foramen intervertebrale (Figure 2h). On the ventral margin of the corpus synsacri, the undulations are even more conspicuous, mainly on the first vertebra (Figure 2f), reinforcing the hypothesis of the presence of a processus haemalis (Figure 2g), as observed in UFAC 6990 (Figure 2e). The processus haemalis, if they existed, were possibly eroded/broken at some point in the taphonomic process.

3.2.1 | *Macranhinga* sp. indet. 1 (gracile)

Referred material: UFAC 6991—Left femur (Figure 3a,c,j; Table 2).

Identification (only for the referred material): It differs from the femur of *Phalacrocorax* by having (a) a less robustly developed trochlea fibularis and (b) the region of the attachment for m. flexor hallucis longus is shallow and not a deep depression lateral and proximal to the condylus lateralis (see fig. 10 in Boles, 2010). This femur is assigned to *Macranhinga* by the following characters (modified from Diederle & Agnolin, 2017): total length 20% greater than that of extant and fossil *Anhinga* spp. with a known femur, and 13% smaller than that of the smallest *Macranhinga* with a known femur (e.g., *M. paranensis*) (for comparison see tab. 1 in Mayr et al., 2020); minimum shaft width of diaphysis with intermediate robustness between that of *Anhinga* spp. and *Macranhinga* spp. (Diederle, 2015b); distal end wide and caudally pronounced; proximal surface of the fossa poplitea between the distal portions of the linea intermuscularis caudalis and the tuberculum m. gastrocnemialis lateralis wide and shallow; insertion for m. psoas well defined, narrow, and elongated in an anteroposterior direction (Figure 3j).

3.3 | Comparative description

The left femur is almost complete, with moderately eroded joint ends (Figure 3a,c). The eroded regions indicate transport, post fossilization, followed by redeposition. On the outer side of the condylus medialis, the conspicuous and low crista supracondylaris medialis is present (Figure 3c). The tuberculum m. gastrocnemialis lateralis is low as in *Macranhinga paranensis* and extant *A. anhinga* (see character 11 in Diederle, 2015b; Figure 3c,d) and not robust and conspicuous as in *Macranhinga ranzii* and Cf. *Giganhinga kiyuensis* (Alvarenga & Guilherme, 2003; Areta et al., 2007). The sulcus intercondylaris shows strong signs of wear. The fossa poplitea, although relatively eroded, is shallower and well delimited as in *A. anhinga* (Figure 3c,d).

The proximal end is worn, completely missing the region of the trochanter femoris and the crista trochanteris (Figure 3a,c). However, the facies articularis antitrochanterica is preserved, with evident signs of bone erosion. The same can be said of the caput femorale, which is slightly smaller than it should have been originally. Comparing the homologous linear measurements TFL, LSW, and DW between the specimen UFAC 6991 and the mean values of these measurements in *A. anhinga* (Table 2) with the average mass of extant *A. anhinga* (1.235 kg), it was possible to calculate three different estimates of body mass for the fossil specimen. The values obtained were 2.8, 4.8, and 4.0 kg, respectively, with an estimated average of 3.9 kg (Figure 8).

3.3.1 | *Macranhinga* sp. indet. 2 (robust)

Referred material: UFAC 6993—Left femur (Figure 3e,g,i,j; Table 2).

Identification (only for the referred material): differs from the homologous femur of *Phalacrocorax* by presenting (a) a slight expansion of crista trochantericus and (b) facies articularis antitrochantericus slightly bordered on its cranial side (sensu Boles, 2010). This femur is assigned to *Macranhinga* based on the presence of the following characters (modified from Diederle & Agnolin, 2017): femur length longer than extant *Anhinga* (see tab. 1 in Mayr et al., 2020; Figure 3e,f); robust diaphysis; deep insertion of m. obturatorius medialis; remarkably wide insertion of m. ilirotrochantericus caudalis; insertions of m. flexor ischiofemoralis proximodistally elongated (Figure 3i); insertion for m. psoas well defined, broad, and elongated in an anteroposterior direction (Figure 3j).

3.4 | Comparative description

The incomplete left femur is missing the distal end (Figure 3e,g). The specimen was found in the same location as the previous femur (UFAC 6991). The length between the facies articularis antitrochanterica, and the fractured end of the fossil is 70.29 mm. At the proximal end, the trochanter femoris, the crista trochanteris, and the facies articularis antitrochanterica were retained while the caput femoris was mostly eroded. Unlike the condition in UFAC 6991, the linea intermuscularis cranialis is conspicuous and crosses the entire corpus femoris (Figure 3e). The crista trochanteris is conspicuous and poorly developed (Figure 3e), unlike *M. ranzii* (Alvarenga & Guilherme, 2003). The insertions of m. flexor ischiofemoralis are proximodistally elongated as

in *M. paranensis* and *M. ranzii* (Noriega, 2001; Alvarenga & Guilherme, 2003; Diederle, 2015b; Diederle & Agnolin, 2017; Figure 3i). The insertion for m. psoas forms a prominent elongated area in the antero-posterior direction, similar to that observed in UFAC 6991 and *M. ranzii* (UFAC 3640), and differing from extant *A. anhinga* where the insertion area of this muscle is inconspicuous and almost round in mesial view (Figure 3j; Owre, 1967). In the caudal portion, only a part of the condylus medialis and lateralis has been preserved, and between them, the beginning of the sulcus patellaris can be seen. The tuberculum m. gastrocnemialis lateralis is low and slightly more conspicuous than in UFAC 6991. As in UFAC 6991, the proximal and distal ends were not preserved for taking precise measurements, so it was only possible to estimate the mass of this individual based on the minimum shaft depth (LSD) and minimum shaft width (LSW) measurements. The estimated masses were 9.7, and 8.2 kg, respectively, with an average of 8.9 kg (Figure 8).

3.4.1 | *Macranhinga* sp.

Referred material: UFAC 6989—4th cervical vertebra (Figure 4a,c; Table 3).

Identification: Considering the genetic proximity between darters (Anhingidae) and cormorants (Phalacrocoracidae) (Smith, 2010), this vertebra is attributed to the Anhingidae due to the following differences compared to its closest relatives (sensu Diederle et al., 2012): corpus vertebrae longer than wide; sulcus caroticus more concave and with more marked lateral crests. We assign the vertebra UFAC 6989 to the genus *Macranhinga* by the presence of the following diagnostic

characters (modified from Diederle, 2015b): deep and well-defined sulcus caroticus; foramen of the sulcus caroticus oriented more laterally than in *A. anhinga* (Figure 4a,b); facies articularis cranialis wider than in *A. anhinga* (Figure 4a,b); vertebral body length about 25.3% larger than *A. anhinga* and 14.8% smaller than that of *M. paranensis*.

3.5 | Comparative description

Fourth complete cervical vertebra. It is a typical anhingid neck vertebra, quite elongated and thin. The cranial and caudal facies are well preserved, as are the dorsal region and the sulcus caroticus (Figure 4a,c). The sulcus caroticus is deep in the caudal portion and shallow in the middle-caudal part with lateral projections (Figure 4a). The projections extend laterally from each foramen on the ventrolateral margin of the vertebral body, similar to that observed in *A. anhinga* (Figure 4c,d). The foramina are more lateralized in UFAC 6989, while in the *A. anhinga*, they are more horizontal in relation to the margin of the vertebral body (Figure 4a,b). In a homologous vertebra (CICYTTP-PV-A-2-243) attributed to *M. paranensis*, that was first described as the seventh cervical vertebra by Diederle et al. (2012) and reidentified a few years later as the fourth cervical vertebra (Diederle, 2015b, p. 79), these projections are not present and the foramina are similar to UFAC 6989. The vertebral body length is about 25.3% larger than its counterpart, *A. anhinga* (Table 3), and 14.8% smaller than *M. paranensis* (see tab. 22 in Diederle, 2015b, p. 129). Although it presents a morphology quite similar to the fourth cervical vertebra attributed to *M. paranensis* (Diederle, 2015b; Diederle et al., 2012), the differences pointed out here and the smaller size do not allow us to

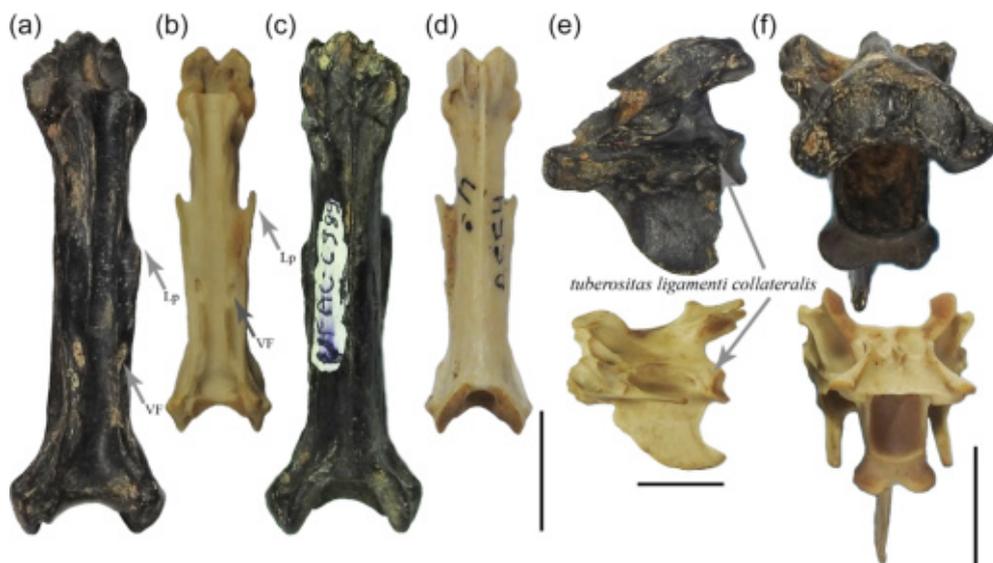


FIGURE 4 Fourth cervical vertebra of *Macranhinga* sp.—UFAC 6989 compared to the *A. anhinga* homologue (R-554). (a) and (b) Ventral view; (c) and (d) dorsal view; (e) and (f) fifteenth cervical vertebra of *Macranhinga* sp. (UFAC 6992) in comparison with the *A. anhinga* homologue (R-554, below). (e) Lateral view; (f) caudal view. Lp, lateral projections; VF, ventral foramina. All scale bars = 1 cm.

assign it to this species. This vertebra may belong to *Macranhinga fraileyi* (sensu Cenizo & Agnolin, 2010) or to a species of the genus not yet described.

3.5.1 | *Macranhinga* sp.

Referred material: UFAC 6992—Fifteenth cervical vertebra (Figure 4e,f; Table 3).

Identification: Differs from Phalacrocoracidae by the following characteristics (modified from Diederle et al., 2012): processus ventralis occupies the entire corpus vertebrae and projects caudally; tuberositas ligamenti collateralis proportionally less concave. We assign UFAC 6992 to the genus *Macranhinga* by the following diagnostic characters (modified from Diederle & Agnolin, 2017): corpus vertebrae robust; tuberositas ligamenti collateralis deeper and broader.

3.6 | Comparative description

The vertebrae are well preserved, with only a small portion of the arcus vertebrae and the entire zygapophysis cranialis missing (Figure 4e). In the cranial region, the facies articularis remained partially complete, lacking a small portion of the right lateral side (Figure 4e). In the caudal region, all elements were preserved (Figure 4f). The well-developed processus ventralis extends from the ventral limit of the facies articularis cranialis to the limit of the facies articularis caudalis, as in *A. anhinga* and *M. ranzii* (Alvarenga & Guilherme, 2003; Figure 4e). This feature is not present in CICYTTP-PV-A-2-242 (see fig. 3G in Diederle et al., 2012). In this vertebra, identified as the fifteenth cervical and attributed to *M. paranensis*, the processus ventralis is restricted to the caudal region and acquires a pronounced backward angulation, very similar to the sixteenth cervical vertebra of *A. anhinga* (Shufeldt, 1902, p. 156). The processus spinosus is low as in *M. paranensis* and *A. anhinga* (Diederle et al., 2012). The area of the elastic ligaments in the dorsocaudal region does not show a conspicuous tuberosity, as in *A. anhinga* and *M. ranzii*. The ridges of zygapophysis caudalis are inconspicuous and lean down, making the region between the two zygapophyses almost flat, unlike *A. anhinga* (Figure 4f) and *M. ranzii* (Alvarenga & Guilherme, 2003) where the high, conspicuous margins make this same region proportionally deeper (Figure 4f). There is no evident torus dorsalis as in modern anhingas and *M. ranzii*. The crista transverso-obliqua is dorsoventrally less conspicuous than in *A. anhinga*. In the caudolateral portion, the tuberositas ligamenti collateralis are deep and rounded, while in *A. anhinga*, they are almost imperceptible (Figure 4e). This vertebra has practically

the same morphometric dimensions as the *M. paranensis* counterpart (see tab. 22 in Diederle, 2015b, p. 129) but is 26.2% smaller than that of *M. ranzii* (see tab. 3 in Alvarenga & Guilherme, 2003) and 22.8% larger than its *A. anhinga* homologue (Figure 4e,f; Table 3). Although this vertebra presents diagnostic characters that allow us to assign it to the genus *Macranhinga*, the previously mentioned differences do not allow us to assign it to either of the two species of this genus for which the fifteenth cervical vertebra is known (e.g., *M. paranensis* and *M. ranzii*). Similarly, to the fourth cervical vertebra discussed above, this vertebra may belong to *M. fraileyi* (sensu Cenizo & Agnolin, 2010) or to another species of a genus not yet described.

3.6.1 | *Anhinga* Brisson 1760

A. minuta Alvarenga & Guilherme, 2003.

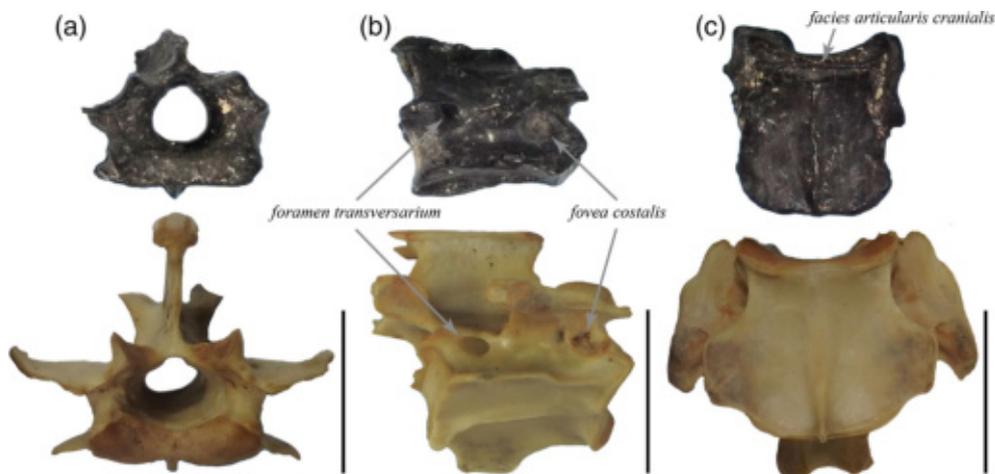
Referred material: UFAC 7296—19th cervical vertebra (Figure 5).

Identification (only for the referred material): 12.1% lower than that of the homologues in *A. anhinga*; the vertebral foramen is narrower and more rounded than in *A. anhinga* (Figure 5a); the ventral edge of the facies articularis cranialis is conspicuous in all its extensions (Figure 5c).

3.7 | Comparative description

Relatively well-preserved vertebra missing the processus transversus and costalis and part of the processus spinosus. The fovea costalis (articular facet for rib) is visible on the right side, and the two foramen transversarium are precisely as in *A. anhinga* (Figure 5b). On the ventral surface, the caudolateral projections observed in the vertebra were eroded (Figure 5c). This region has a prominent central ridge (Figure 5c), similar to that observed in *A. anhinga*. In the homologous vertebra (LACM 135359) attributed by Campbell (1996) to *A. fraileyi*, also from the locality Patos (=LACM 4611), the ventral surface presents two lateral ridges instead of a central ridge as in UFAC 7296 (Figure 5c). The ventral edge of the facies articularis cranialis is conspicuous in all its extensions, contrary to what is observed in *A. anhinga*. The vertebra UFAC 7296 is 12.1% smaller than its homologous in *A. anhinga* (Table 3) and 31.8% smaller than the 19th cervical vertebra (LACM 135359) attributed to *A. fraileyi* (Campbell, 1996). The vertebral foramen is narrower and more rounded than in *A. anhinga* (4.95 mm vs. 5.84 mm in diameter, respectively; Figure 5a). The lack of lateral projections prevents us from comparing more accurately

FIGURE 5 Nineteenth cervical vertebrae of *Anhinga minuta* compared to the homologue of *A. anhinga* (R-554, below). (a) Cranial view; (b) lateral view and (c) ventral view. All scale bars = 1 cm.



with the extant anhinga and specimen LACM 135359 (Campbell, 1996).

4 | PHYLOGENETIC INFERENCE

Our first assessment of the phylogenetic position of UFAC 6990 in the context of the major relationships within Suliformes, including most fossil anhingids from South America, resulted in nine most parsimonious trees (MPTs). The strict consensus tree (CI = 0.720; RI = 0.803) is less resolved than that of Diederle (2015b) and Guilherme et al. (2021). In contrast, the phylogenetic analysis removing *M. chilensis* is much more resolved, and results in only one MPT (CI = 0.739; RI = 0.818; Figure 6). The living representatives of Phalacrocoracidae (*Nannopterum brasilianum*, *Phalacrocorax gaimardi*, *Ph. magellanicus*, *Leucocarbo bougainvilli*) are recovered as a monophyletic group sharing several synapomorphies (Characters 1:1, 3:2, 4:1, 9:0, 13:1, 14:1, 15:1, 18:1, and 27:2), although interrelationships are unresolved. *Morus* is found to be more closely related to the Phalacrocoracidae, which is supported by one synapomorphy: laterally displaced trochlea metatarsi II (25:1). Together, they form a sister group relationship to the Anhingidae. This is at odds with previous morphological and molecular datasets, which recover Phalacrocoracidae as a sister group to the Anhingidae (see Smith, 2010). UFAC 6990 is recovered as a stem Anhingidae outside the monophyletic groups formed by *Anhinga* and the giant anhingids (*Macranhinga* + *Giganhinga*). The total group Anhingidae is supported by only one synapomorphy: well-developed cristae iliaca dorsalis postacetabular (7:0). Our results also support a paraphyletic *Macranhinga*, as *Giganhinga kiyuensis* is recovered as a sister taxon to *Macranhinga ranzii* (Guilherme et al., 2021).

5 | DISCUSSION

The fossils presented here are disarticulated bones that show clear signs of wear and erosion caused by transport under fluvial–lacustrine sedimentation conditions. The fossiliferous conglomerate was formed in a high-energy zone environment of channel deposits (Campbell et al., 1985, 2006; Kay & Frailey, 1993). This explains the disarticulated condition of the bones and the high degree of erosion presented by the fossils found throughout the Patos paleontological site on the upper Acre River. In other sites of the Solimões Formation, formed in a low-energy environment, such as Niterói and Talismã, the degree of wear and erosion of the fossils is relatively lower than that observed in Patos (Muniz et al., 2021). At the Talismã site, an almost complete and articulated alligator (*Caiman brevisrostris*) has already been removed (Fortier et al., 2014), while in Niterói, we found an articulated skull and jaws of *Acresuchus pachytemporalis* (Souza-Filho et al., 2019), situations unlikely to occur in Patos or on any other conglomeratic deposit.

The two pelvic girdle fragments presented here, primarily the more complete specimen UFAC 6990, share many characteristics with *M. paranensis*, including being compatible in body mass. In contrast, the vertex craniolateralis ilii end at the level of the antitrochanter and are not posteriorly displaced as in *M. paranensis* and *Meganhinga chilensis* (Noriega & Alvarenga, 2002); the cristae iliaca dorsalis diverging anterior to the medial line of the foramen acetabuli and the possible presence of a processus haemalis, among other previously reported characters, differentiate them from *Macranhinga paranensis* (Noriega & Alvarenga, 2002; Diederle, 2015b; Figure 6).

The two femora described here are larger and more robust than any femur attributed to the genus *Anhinga*, whether extant or fossil (Mayr et al., 2020). Although both are similar in total length, they are very different in

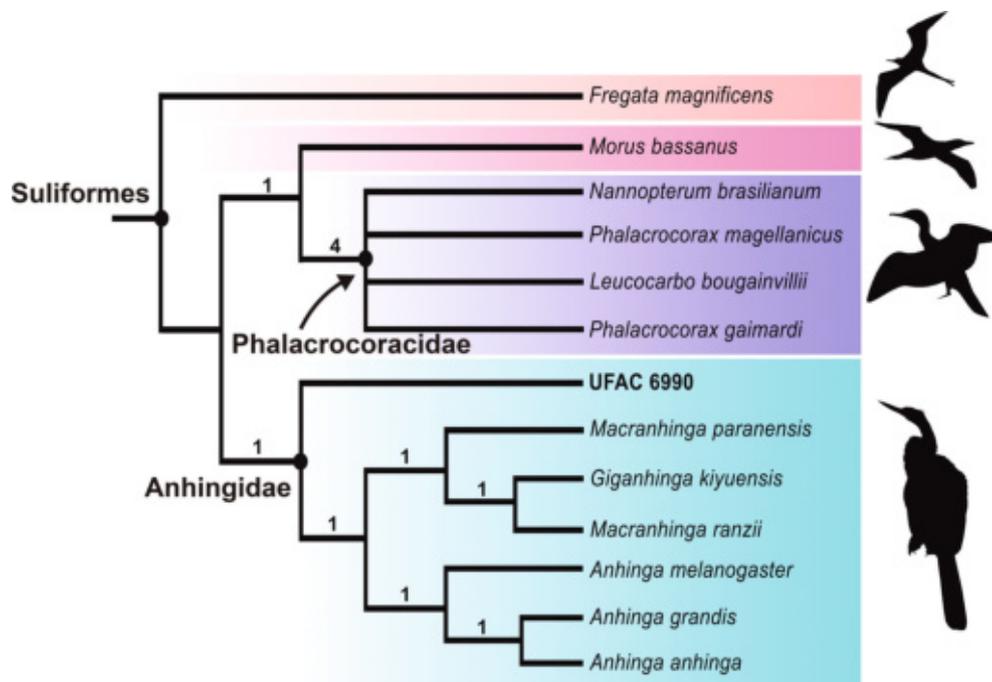


FIGURE 6 Single MPT after pruning *Meganinga chilensis*, showing the relationships of UFAC 6990 within representative Suliformes. Bremer support values are shown above branches. All silhouettes are from PhyloPic (www.phylopic.org).

general morphology, one being a more gracile morphotype (UFAC 6991) and the other a more robust one (UFAC 6993). Although larger in size and robustness, the UFAC 6991 femur is morphologically similar to the genus *Anhinga*. The same cannot be said of the more robust femur (UFAC 6993), whose general morphology and muscle insertion scars are more easily distinguished from its smaller relatives (Figure 3e,i). Although found in situ and in the same location as the UFAC 6990 pelvic girdle, neither eroded caput femoris fits perfectly with the corresponding acetabulum. However, the caput femoris and the facies articularis antitrochanterica of the robust femur (UFAC 6993) fit better with the acetabulum than its homologues in UFAC 6991. The estimated mass indicated that the more robust femur supported an individual of twice the mass estimated for the UFAC 6991 femur (8.9 kg vs. 3.9 kg). As the masses estimated from measurements of the femurs are considered reliable and close to reality for flying birds (Field et al., 2013), it is unlikely that they are two individuals with a mass difference of 100% within the same population. Owre (1967) took the mass of 16 *A. anhinga* specimens (nine males and seven females), and the maximum variation between the lowest and highest mass was 363 g, a variation of 25.3% to the highest mass of the sample. These observations reinforce the idea that the gracile femur (UFAC 6991) belongs to a smaller specimen whose mass is compatible with that calculated for *Anhinga fraileyi* (Noriega, 2001). Although the femur of *Anhinga grandis* is not known (Becker, 1987; Martin & Mengel, 1975; Rasmussen & Kay, 1992) for comparison purposes, it is

unlikely that the femur UFAC 6991 belongs to this taxon since the mass calculated from the humerus of the holotype was ~50% less than the mass of the individual to whom the UFAC 6991 femur belonged (4.2 kg vs. 2.4 kg respectively) (Martin & Mengel, 1975; Noriega, 2001). The robust femur (UFAC 6993) is referred to *Macranhinga*. It is possible to state that this femur and the pelvic girdle (UFAC 6990) belong to the same taxon. Still, the disproportion between the corpus femoris and the more graceful morphology of the pelvic girdle indicates that they do not belong to the same individual.

The fourth and fifteenth cervical vertebrae belong to *Macranhinga*. Both have larger dimensions than the *Anhinga* vertebrae used here for comparison (Table 3; Figure 4). They have morphometric and anatomical similarities with other homologous vertebrae attributed to *Macranhinga* (Alvarenga & Guilherme, 2003; Diederle, 2015b; Diederle et al., 2012). In addition to the similarities between these two vertebrae and those attributed to *M. paranensis*, we also noticed important differences. These differences, as well as those found in the pelvic girdle (UFAC 6990), are elements that indicate the valid taxon for the Acre conglomerate member may be the combination suggested by Cenizo and Agnolin (2010), that is, *Macranhinga fraileyi* instead of *Anhinga fraileyi* (Campbell, 1996). The nineteenth cervical vertebra described here is almost identical to its homologue in *A. anhinga* except for its small size and two other characters previously reported. The attribution of this vertebra to *A. minuta* is plausible, considering that this species was described from bone elements belonging to the Acre

conglomerate member of the Cachoeira do Bandeira site, which is downstream from the Patos locality (Alvarenga & Guilherme, 2003; Figure 7). This is only the third bone element assigned to this species from the Solimões Formation, although this taxon may also occur in Argentina (Noriega & Agnolin, 2008). *A. minuta* competed with larger anhingas in the region where the Acre conglomerate member was formed. According to Diederle (2017b), *A. minuta* was probably a good flyer and could swim, climb and move through the vegetation. Most likely, this little anhinga could not eat large fish or dive into deep waters like macranhingas. For this reason, it could forage in a river-type or delta environment (Latrubesse et al., 2010), with shallower waters (sensu Ryan, 2007), where it could feed on small fish and invertebrates. This is yet another indication that the region where the Acre conglomerate member was formed was more peripheral to the great lake (Hoorn et al., 2022), where the largest of the anhingas of the Solimões Formation lived (Alvarenga & Guilherme, 2003; Guilherme et al., 2021; Figure 7).

Fossils of birds found in Patos (=LACM 4611 or Acre 6) during the 2022 UFAC/USP/ICMBio expedition revealed the undisputed presence of at least three taxa of anhingids in the same locality. This finding has important implications for understanding the fossils described as *A. fraileyi* by Campbell (1996). This author associated a series of fossils from the locality LACM 4611 as belonging to a new taxon (*A. fraileyi*) but also included in this

association a shaft and proximal end of a left humerus (LACM 135362) and a shaft of a right humerus (LACM 135363) from the Cachoeira do Bandeira site (=LACM 5158). This choice was revealed to be an underestimation of anhingid diversity, as these new findings corroborate the idea previously defended by Diederle (2017a) that some of the fossils attributed to *A. fraileyi* in the species description, such as a left ulna (LACM 135361), belong to another taxon of anhingid. Diederle (2017a) presents a series of arguments to defend that *A. fraileyi* is synonymous with *M. paranensis*. However, the author admits that some characteristics of the tarsometatarsus designated to be *A. fraileyi*, such as the smaller measures of the trochlea metatarsi III and the crista plantaris lateralis, which is slightly less developed in "*A. frailey*" are different compared to the holotype of *M. paranensis*. There is growing evidence that the right tarsometatarsus (LACM 135356) holotype of *A. fraileyi* was of an individual of intermediate size between the extant anhingas and the macranhingas, similar to the pattern we observed in relation to the pelvic girdle UFAC 6990 attributed *Macranhinga* sp. indet in this work. Considering the differences mentioned above between the holotype LACM 135356 and UFAC 6990 from homologues of *M. paranensis* (MACN-PV 13507, Diederle, 2017a; MLP-88-IX-20-5, Noriega & Alvarenga, 2002), there is a possibility that *M. fraileyi* as a valid taxon (sensu Cenizo & Agnolin, 2010). As for the other fossils attributed to *A. fraileyi* by Campbell (1996) and reexamined by

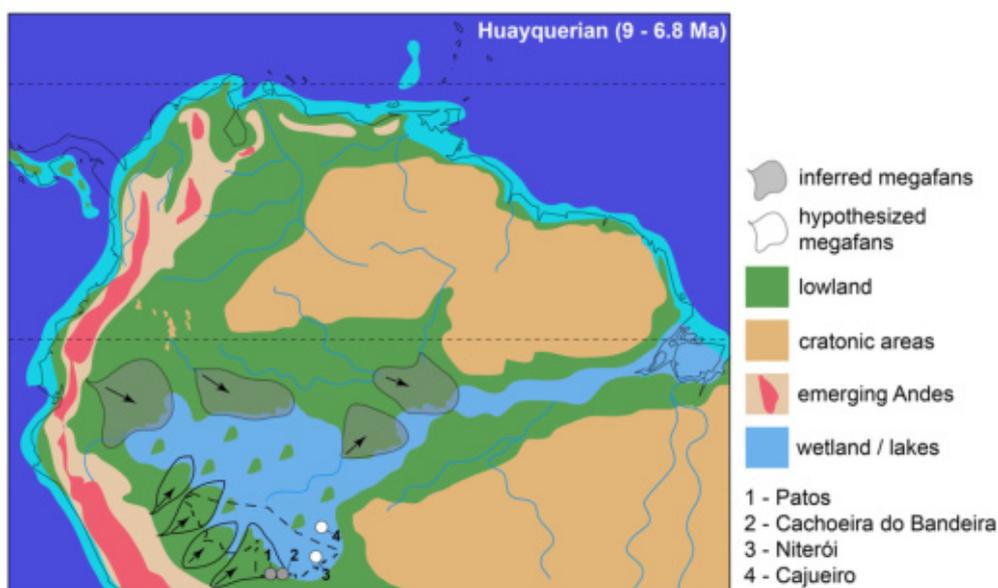


FIGURE 7 Map of northwestern South America and paleogeographic reconstruction of western Amazonia based on Hoorn, Wesselingh, Hovikoski, et al. (2010), Hoorn, Wesselingh, Ter Steege, et al. (2010) and Wilkinson et al. (2010). Continental outline, Acre, and site locations are based on modern geography. The reconstruction is focused on the Late Miocene Huayquerian South American Land Mammal Age, the age of Acre and other southwestern Amazonia fossil sites. Please note that Patos and Cachoeira do Bandeira localities are more affected by hypothesized megafans (after Wilkinson et al., 2010) than Niterói and Cajueiro.

Diederle (2017a), there is a possibility that they belong to *Macranhinga* sp. indet 1 and are associated with our femur UFAC 6991. We believe that these questions can only be fully resolved when new specimens are found and more detailed anatomical and morphometric comparisons become possible.

6 | PHYLOGENETIC INFERENCE

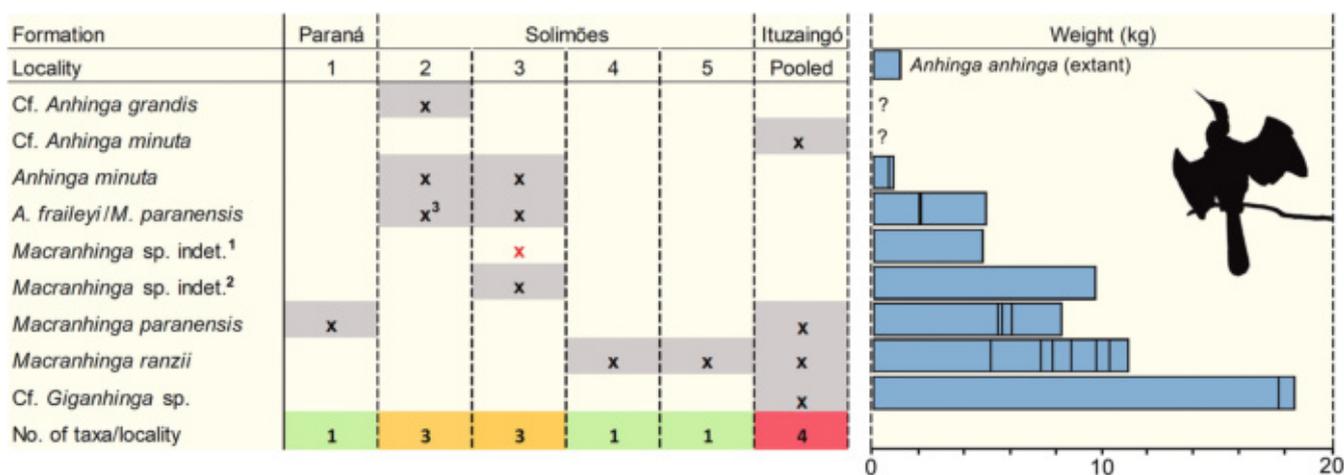
Based on our phylogenetic analysis (Figure 6), UFAC 6990 shares only one synapomorphy with living and fossil anhingids: the presence of well-developed cristae iliaca dorsalis postacetabular (7:0). UFAC 6990 lacks the poorly developed arcus vertebrae at the first preacetabular vertebra and the large postacetabular area of the pelvis as seen in *Anhinga*. It also differs from *Macranhinga paranensis* and *Giganhinga kiyuensis* in not having the vertex cranio-lateralis ilii significantly displaced from the antitrochanters. UFAC 6990 can be further differentiated from *Macranhinga paranensis* in having a divergence of the cristae iliaca dorsalis anterior to the medial line of the foramen acetabuli; in the latter, the divergence is notably posterior in relation to the medial line of the foramen acetabuli. Although the position of UFAC 6990 among the fossil anhingids must be considered with caution due to limited osteological information and statistical support, the phylogenetic results currently favor the hypothesis that the studied specimen is an anhingid

distinct to *Macranhinga paranensis*. As more complete materials are found, we believe this taxon's precise identification will be clarified.

7 | PALEOECOLOGICAL DISCUSSION

At least three different anhingid species lived in the region where the conglomerate deposits were formed (*A. minuta*; *Macranhinga* sp. indet. 1 and *Macranhinga* sp. indet. 2; Figure 8). These three morphs are not new to this sedimentary package (Alvarenga & Guilherme, 2003; Campbell, 1996). Campbell (1996) described *Anhinga fraileyi* from Patos, the same location from which the fossils studied here were recovered, while Alvarenga and Guilherme (2003) described the smallest anhinga (*Anhinga minuta*) and indicated the possible occurrence of a third taxon of darter (cf. *Anhinga grandis*) at the Cachoeira do Bandeira site (Alvarenga & Guilherme, 2003). This suggests that the environment where the conglomerate deposit was formed was quite ecologically complex. Most likely, these three species coexisted in the same ecosystem but did not fully exploit their fundamental niche, avoiding direct competition for food and reproductive sites.

The largest anhingid from the Solimões Formation, *M. ranzii*, has never been found in the sediments of the conglomerate level. To date, there are no records of



¹UFAC 6991; refers to a gracile *Macranhinga* femur. Specimen was not counted because it could belong to previous recorded taxa.

²UFAC 6993; refers to a robust *Macranhinga* femur, that probably belonged to a larger species.

³Cf. *A. fraileyi*/*M. paranensis* for Cachoeira do Bandeira locality (2).

FIGURE 8 Anhingid occurrences for the late Miocene of South America. Locality number (1) corresponds to the La Ensenada locality from the Paraná Formation (Diederle et al., 2012). Localities (2), (3), (4), and (5) correspond, respectively, to Cachoeira do Bandeira, Patos, Niterói, and Cajueiro localities from the Solimões Formation (Alvarenga & Guilherme, 2003; Campbell, 1996; Guilherme et al., 2021). Due to the lack of more precise provenance of the Ituzaingó fossils, they were pooled in a single column (Areta et al., 2007; Noriega & Agnolin, 2008; Diederle & Noriega, 2013; Schmidt et al., 2020). Superscript references are listed after the table. Inferred masses of the fossil representatives are shown in the table; original references are in Table S2.

fossils of this species in any site on the upper Acre River, such as in the Cachoeira do Bandeira, Cavalcante, or Patos (Campbell, 1996; Alvarenga & Guilherme, 2003; Figures 1 and 7). In the original description of *M. ranzii* (Alvarenga & Guilherme, 2003), the Niterói site, from where the holotype was derived, was reported as belonging to the conglomerate level. This attribution was an incorrect generalization, as correctly observed by Campbell et al. (2006). Niterói was formed in a low-energy environment, probably in a lacustrine environment, in contrast to the high-energy environments of the sites located along the upper course of the Acre River (Campbell et al., 2006; Muniz et al., 2021). This suggests that an aninga as heavy as *M. ranzii* and with a high diving capacity (Areta et al., 2007; Guilherme et al., 2021) would have preferred the central region of the great lake (Hoorn et al., 2022; Figure 7) as its favored environment. The aningas from the conglomerate level likely would have explored the periphery of the lake in a more fluvial deltaic environment with running water interspersing shallow and deep ecosystems, including swamps (Latrubesse et al., 2010; Figure 7). The indication that the conglomerate deposit had deeper water environments is also supported by the presence of gigantic fish (e.g., *Acregoliath*), snakes (Madtsoiidae indet.), and *Purussaurus brasiliensis*, the largest crocodylian that ever existed (Aureliano et al., 2015). Shallow environments were probably related to the highly dynamic megafan systems in the region (Latrubesse et al., 2010; Wilkinson et al., 2010; Figure 7). In the conglomerate level, pollen studies have reported between 53% and 69% dominance of grasses (Latrubesse et al., 2010; Leite et al., 2021), which contrasts with only 15% in Niterói. High grass pollen in sedimentary records of the Solimões Formation has been attributed to high energy environments of the Late Miocene (Jorge et al., 2019), explained by grasses being successful pioneers on Andean slopes, megafans and newly formed floodplains (Kirschner & Hoorn, 2020). This setting could have partitioned niches for aningids and other animals, thus explaining the differences in size estimates discussed above.

The recovery of different species of Anhingidae in the same fossiliferous horizon in the Patos locality is evidence that some fossil aningids lived contemporaneously (Figure 8) and may have established distinct strategies to exploit resources. The remarkable differences in size between some species (e.g., *A. minuta* vs. *Macranhinga*) are probably, to some extent, explained by diet-related niche partitioning. The higher levels of diversity, size disparity, and sympatry of Miocene aningids in South America are mirrored and surpassed by the fossil record of crocodylians (Paiva et al., 2022; Salas-Gismondi et al., 2015; Scheyer et al., 2013). Interestingly, the impoverishment of both group's diversity is

coincidental to post-Miocene climatic deterioration in the south (e.g., Cenizo & Agnolin, 2010; Diederle & Agnolin, 2017) and significant landscape modifications in the north triggered by the Andean orogeny, which culminated in the predominance of fluvial environments (e.g., Cidade et al., 2019; Riff et al., 2010; Salas-Gismondi et al., 2015).

AUTHOR CONTRIBUTIONS

Edson Guilherme: Conceptualization; investigation; methodology; writing – original draft; data curation; supervision. **Carlos D'Apolito:** Writing – review and editing; formal analysis; supervision; methodology. **Fellipe Muniz:** Investigation; writing – review and editing; methodology; formal analysis. **Silvia Oliveira Lomba:** Investigation. **Leonardo Aldrin:** Writing – review and editing; investigation. **Annie Schmaltz Hsiou:** Investigation; writing – review and editing; funding acquisition.

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ORCID

Edson Guilherme  <https://orcid.org/0000-0001-8322-1770>

Carlos D'Apolito  <https://orcid.org/0000-0003-1602-0201>

Annie Schmaltz Hsiou  <https://orcid.org/0000-0003-2392-6191>

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