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New anhingid (Aves, Suliformes) from the middle Miocene of Río Negro province, Patagonia, Argentina

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ABSTRACT

During the Miocene in South America, the family Anhingidae constitutes one of the most conspicuous faunal elements. However, the anhingid record from Patagonia is still sparse. The aim of the present contribution is to describe a new species of *Macranhinga* coming from Colloncuran levels (early middle Miocene) in Río Negro province, north-central Patagonia (Argentina). The new species is represented by an incomplete proximal end of a tarsometatarsus, distal end of a tibiotarsus, and distal end of a humerus. The phylogenetic relationships of the new species within *Macranhinga* remains unresolved. South American Neogene anhingids share a number of features that suggest they may belong to a monophyletic clade within this family. Anhingid records from the Miocene of Patagonia indicate that the diversity of this family was far more diverse (at least 4 different species) than currently understood, and was possible comparable to that shown by Miocene beds of Mesopotamian in Argentina and Acre in Brazil.

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Introduction

Darters or snake birds are diving birds of the family Anhingidae that live in tropical and subtropical climate, especially in freshwater environments (Johnsgard 1993). The family is represented by the living species *Anhinga anhinga*, restricted to America, *A. rufa* to Africa, *A. novaehollandiae* to Australasia, and *A. melanogaster* to Asia (Gill & Donsker 2016). Anhingids are the sister group of Phalacrocoracidae, a grouping strongly supported by morphological and molecular evidence (e.g. Pycraft 1898; Owre 1967; Ericson et al. 2006; Livezey & Zusi 2006; Hackett et al. 2008; Smith 2010).

The oldest record for the entire clade is *Anhinga walterbolesi* Worthy 2012 from the late Oligocene of Australia (Worthy 2012). Post-Oligocene records come from Miocene to Pleistocene of Europe, Africa, Australasia, and North America (e.g. Olson 1985; Worthy 2012). However, the largest radiation of anhingids occurred in South America through a Miocene proliferation of genera (see Noriega & Alvarenga 2002; Areta et al. 2007; Cenizo & Agnolin 2010). The oldest record of this family in Australasia, together with its widespread geographical distribution during the Neogene on the Southern Hemisphere, supports to the hypothesis of a southern origin for the group (Worthy 2012).

In South America, extinct giant diving anhingids with body masses between 3.2 and 17.7 kg (Noriega 2001; Areta et al. 2007) are one of the most conspicuous elements of the Neogene avifaunas (Cenizo & Agnolin 2010). Their abundant record extends from the Santacrucian (South American Land Mammal Age, SALMA; late early Miocene) to Marplatan (SALMA; latest Pliocene-early Pleistocene) beds of Colombia, Chile, Argentina, Brazil, Uruguay and Peru (Noriega 1992, 2002; Rasmussen & Kay 1992; Alvarenga 1995; Campbell 1996; Noriega & Alvarenga 2002; Rinderknecht & Noriega 2002; Alvarenga & Guilherme 2003; Noriega & Piña 2004; Areta et al. 2007; Noriega & Agnolin 2008; Cenizo & Agnolin 2010; Diederle et al. 2012). However, the anhingid record from Patagonia is still sparse, being represented by *Anhinga hesterna* (Ameghino 1895) and isolated materials referred to an indeterminate species of the genus *Macranhinga*, both coming from the early Miocene of Santa Cruz province, Argentina (Cenizo & Agnolin 2010; Diederle 2015a). Moreover, from the Chilean Patagonia was described *Meganhinga chilensis* Alvarenga 1995 from early Miocene sediments of Malleco province (Alvarenga 1995). Due to this still incomplete record, the description of fossil material from Patagonia is of special value in order to understand the evolution of darters is the southern tip of the continent.

The aim of the present paper is to describe a new species of *Macranhinga* coming from the early middle Miocene of north-central Patagonia, to discuss its phylogenetic relationships, and the diversity of anhingids during the Miocene in Patagonia.

Material and methods

The fossil samples were compared with the specimens listed in Appendix 1.

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Comparisons were carried out with eleven anhingid species: *Macranhinga ameghinoi* sp. nov., *M. paranensis*, *M. ranzii*, *Meganhinga chilensis*, *Giganhinga kiyuensis*, *A. grandis*, *A. walterbolesi*, *A. subvolans*, *A. beckeri*, *A. anhinga* and *A. novaehollandiae*. Data was taken from the descriptions as follows: Becker (1986) and photographs taken from the official website of the Florida Museum of Natural History for *Anhinga subvolans*, Martin and Mengel (1975), Becker (1987) and photographs from the website of the Florida Museum of Natural History for *Anhinga grandis*, Emslie (1998) and photographs provided by staff of the Florida Museum of Natural History for *Anhinga beckeri*, and Worthy (2012) and photographs provided for this author for *A. walterbolesi*. The femur MACN-PV 12179, originally referred as cf. *Giganhinga* by Areta et al. (2007), was later assigned to *Giganhinga kiyuensis* by Diederle (2015b). *Anhinga fraileyi* (or *M. fraileyi* sensu Cenizo & Agnolin 2010) is excluded of the comparison because it was recently considered synonym of *M. paranensis* (Diederle forthcoming). Two representatives of Phalacrocoracidae (*Phalacrocorax brasilianus* and *Leucocarbo bougainvillii*), a Sulidae (*Morus bassanus*), and a Fregatidae (*Fregata magnificens*) were also used as comparative material. We follow the anatomical terminology of Baumel and Witmer (1993), with modifications in the hypotarsal nomenclature as employed by Mayr (2015). The arthrological nomenclature follows Owre (1967).

Abbreviations of repository institutions

LACM, Natural History Museum Los Angeles (Los Angeles, California, USA); MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (Ciudad Autónoma de Buenos Aires, Buenos Aires, Argentina); MHNT, Museu de História Natural de Taubaté (Taubaté, São Pablo, Brazil); MLP-PV, Museo de La Plata, colección División Paleontología de Vertebrados (La Plata, Buenos Aires, Argentina); MNHN, Museo Nacional de Historia Natural de Montevideo (Montevideo, Montevideo, Uruguay); SGO, Museo Nacional de Historia Natural de Santiago de Chile (Santiago de Chile, Región Metropolitana de Santiago, Chile); UF, University of Florida (Ganeisville, Florida, USA); UFAC, Universidad Federal de Acre (Rio Branco, Acre, Brazil); UNSM, University of Nebraska State Museum (Lincoln, Nebraska, USA).

Systematic paleontology

Suliformes Sharpe 1891
Anhingidae Reichenbach 1849
Macranhinga Noriega 1992

    Type species. *Macranhinga paranensis*
    Included species. *Macranhinga ranzii*; *Macranhinga ameghinoi* sp. nov.

    Emended diagnosis [modified from Noriega (1992), characters taken from Noriega (2002), Noriega & Alvarenga (2002), Diederle (2015c, forthcoming), and new characters]. Species of *Macranhinga* are distinguished from those of *Anhinga* by the following characters. Ninth cervical vertebra: *processus spinosus* high and robust; *incisura arcus caudalis* open; *zygapophysis caudalis* with *facies articularis* notably wide. Fourteenth cervical vertebra: *processus transversus* and *tuberculum ansae* laterally

prominent, and with the caudal edge notably deep; *corpus vertebrae* more robust; *tuberositas ligamenti collateralis* dorsoventrally deeper than in *Anhinga*; *zygapophysis caudalis* with *torus dorsalis* very high and robust. Fifteenth cervical vertebra: *zygapophysis cranialis* transversely wide and strongly caudally oriented; *processus transversus* and *tuberculum ansae* very prominent; lateral muscle impressions more developed than in *Anhinga*; *corpus vertebrae* robust; *tuberositas ligamenti collateralis* deeper and wider than in *Anhinga*; *area ligamentum elastici* very deep and strongly vertically aligned; *crista transverso-obliqua* dorsoventrally higher than in *Anhinga*. Sixteenth cervical vertebra: impression of *m. intercristalis* dorsoventrally deeper than in *Anhinga*; *zygapophysis cranialis* with *facies articularis* very caudally positioned; *zygapophysis caudalis* strongly dorsally positioned with respect to the *corpus vertebrae*, with *facies articularis* wide, and with *torus dorsalis* higher and more caudally directed than in *Anhinga*. Twentieth cervical vertebra: *corpus vertebrae* with lateral sides deeply excavated; *zygapophysis caudalis* with *facies articularis* transversely wide. Coracoids: *cotyla scapularis* wider than in *Anhinga*; origin of *m. subcoracoideus* deep; *impressio m. sternocoracoidei* deep and transversely wide; origin of *m. coracobrachialis caudalis* with more excavated lateroventral portion; origin of *m. supracoracoideus* with dorsoventrally deep lateral edge; *angulus medialis* strongly caudally positioned with respect to *processus lateralis*. Humerus: *tuberculum dorsale* strongly separated from *caput humeri* in proximal view; insertion of *m. subscapularis* notably transversely wide; insertion of *m. scapulohumeralis cranialis* greater and more prominent than in *Anhinga*; insertions of *m. deltoideus pars major* and *pars minor* wider and more excavated than in *Anhinga*; *margo caudalis* very well defined; *condylus dorsalis* with a shallow lateral groove; origin of *m. extensor carpi radialis* notably deep; origin of the posterior division of *m. flexor carpi ulnaris* wide and subcircular in contour; origin of *m. pronator longus* greater and separated from the anterior division of *m. flexor carpi ulnaris* by a notably high edge when compared with *Anhinga*; *sulcus humerotricipitalis* and *sulcus scapulotricipitalis* relatively broad, and separated by a very high prominence; *processus flexorius* prominent and very extended distally; *fossa olecrani* deeper than in *Anhinga*. Carpometacarpus: *fossa infratrochlearis* greater and deeper than in *Anhinga*; *processus pisiformis* notably low; very elongated *processus extensorius*; groove between origin of *m. abductor alulae* and *m. extensor brevis alulae* shallower and narrower than in *Anhinga*; *fovea carpalis cranialis* more reduced and shallower than in *Anhinga*; *fovea carpalis caudalis* wide and deep; *trochlea carpalis* with very prominent distodorsal rim; origin of *m. flexor alulae* shallow and with edge that limit with the *os metacarpale alulare* poorly defined; insertions of *m. ulnometacarpale dorsalis* deeper than in *Anhinga*; *os metacarpale major* more robust and with caudal groove more marked than in *Anhinga*; *symphysis metacarpalis distalis* strongly excavated when viewed caudally. Pelvic girdle: very elongated preacetabular portions of the ilium; first preacetabular vertebra with high *processus spinosus*, *zygapophysis cranialis* very robust and the *facies articularis* transversely wide, *processus transversus* notably wide, and the *arcus vertebrae* laterally expanded and proximally concave; preacetabular vertebrae with *corpus vertebrae* very robust; *ala preacetabularis ilii* more vertically oriented than in *Anhinga*; *fossa iliaca dorsalis* deeply excavated and with dorsal edge prominent; *cristae iliaca dorsalis* poorly laterally

divergent; *antitrochanter* very dorsally oriented; *fossa renalis* at level of the *foramen acetabuli* ovate and with conspicuos distal *processus costalis*. Femur: *crista trochanteris* more prominent than in *Anhinga*; deep insertion of *m. obturatorius medialis*; notably wide insertion of *m. iliotrochantericus caudalis*; insertions of *m. ischiofemoralis* proximodistally elongated; reduced insertions of *m. caudofemoralis*; origin of *m. gastrocnemius pars lateralis* very well excavated; diaphysis more robust than in *Anhinga*; distal end wide and caudally pronounced; proximal surface to the *fossa poplitea*, between the distal portions of the *linea intermuscularis caudalis* and the *tuberculum m. gastrocnemialis lateralis*, wide and deep. Tibiotarsus: *crista cnemialis cranialis* with triangular outline in proximal view, and strongly distally extended; origin of *m. tibialis cranialis* shallow and poorly defined; distal end of *sulcus intercnemialis* strongly excavated; *crista cnemialis lateralis* transversely thin and strongly laterally oriented; shaft of the tibiotarsus with thick cortex and strongly transversally expanded distal end; *depressio epicondylaris medialis* proximally deep and transversely wide. Tarsometatarsus: *cotyla medialis* without a small distal prominence in dorsal view; *eminentia intercotylaris* more proximally extended than in *Anhinga*; edge between the *cotyla medialis* and the *fossa parahypotarsalis medialis* wide; *crista medialis flexoris digitorum longus* very extended distally respect to distal end of the *crista lateralis flexoris hallucis longus* in plantar view; *fossa parahypotarsalis medialis* wider than in *Anhinga*; origin of *m. extensor hallucis longus* transversely wide and more medially located than in *Anhinga*; diaphysis with *facies dorsalis* with gentle transition between proximal and distal ends in lateral view; *sulcus extensorius* deepe and with well-defined medial and lateral edges; *sulcus flexorius* very well defined, proportionally wider and more proximally excavated than in *Anhinga*; *crista plantaris lateralis* very convex and prominent; origin of *m. extensor brevis digiti* IV distally shallow; *foramen vasculare distale* with proximal groove more distally located than in *Anhinga*; very wide *fossa metatarsi* I; *trochlea metatarsi* II with medial edge notably marked in plantar view; *trochlea metatarsi* III shorter and wider than in *Anhinga*.

Macranhinga is distinguished from *Meganhinga* by having the following characters. Pelvic girdle: *cristae iliaca dorsalis* caudally divergent with respect to the *foramen acetabuli*. Tarsometatarsus: *eminentia intercotylaris* proximally prominent and relatively narrower than in *Meganhinga*; *crista medialis flexoris digitorum longus* poorly plantarly projected and oriented perpendicular with the main transverse axis of the proximal end of the bone; *crista lateralis flexoris hallucis longus* very excavated laterally in proximal view; origin of *m. flexor hallucis brevis* less dorsally displaced.

Species of *Macranhinga* are distinguished from *Giganhinga* by having the following characters. Pelvic girdle: *corpus vertebrae* transversely narrower; *foramen acetabuli* medially opened. Femur: proximal surface to the *fossa poplitea*, between the distal portions of the *linea intermuscularis caudalis* and the *tuberculum m. gastrocnemialis lateralis*, proportionally shallower; groove between *condylus lateralis* and *crista tibiofibularis* poorly defined proximally.

Macranhinga ameghinoi sp. nov. (Figure 1(a)–(l))

Diagnosis. Anhingid of the genus *Macranhinga* distinguishable from other species of the genus on the basis of the following autopomorphies: 1-smaller size than other species of the genus; 2-tarsometatarsus with *area intercotylaris* notably deep and well

delimited; 3-tibiotarsus with oval-shaped *canalis extensorius*; 4-tibiotarsus with subtriangular-shaped *condylus medialis*, in cranial view; 5-humerus with shallow and poorly proximally extended *fossa olecrani*.

Holotype. MLP 10-X-15-1, proximal end of right tarsometatarsus with abraded hypotarsus.

Derivation of the name. Ameghinoi, honours the great Argentinian paleontologist Florentino Ameghino (1857–1911), who discovered the first fossil anhingid remains from Patagonia (Diederle 2015a).

Referred material. MLP 10-X-15-2, distal end of left tibiotarsus; MLP 10-X-15-2, distal end of left humerus. The specimens are referred to *M. ameghinoi* sp. nov., because of their size congruence, and because they were found in the same locality and horizon.

Provenance. All specimens were collected by Rodolfo Casamiquela at 2000 meters Southwestern to Puesto Marileo, near Ingeniero Jacobacci city, Río Negro Province, Argentina (Figure 2). They were found at the Level 13 of the stratigraphical profile of Ganduglia (1983), corresponding to the Colloncuran SALMA (early middle Miocene).

Measurements. Tarsometatarsus: proximal width 16.5 mm, shaft width in middle of groove for *m. extensor hallucis longus* 10.8 mm. Tibiotarsus: shaft width 10.6 mm. Humerus: distal width 17.7 mm.

Comparative description

Tarsometatarsus. The holotype tarsometatarsus (MLP 10-X-15-1) is represented by its proximal end and most of the diaphysis. The hypotarsus is heavily abraded (Figure 1(a)–(d)). The tarsometatarsus, based on the proximal width (Table 1), is about 22% larger than living species of *Anhinga*, but is smaller than *Macranhinga paranensis* (19%), and *Meganhinga chilensis* (10%).

The *cotyla medialis* is larger and more excavated than the *cotyla lateralis*, and in proximal view, is subquadrangular in contour as in other Anhingidae. In dorsal view, it is subhorizontally oriented as occurs in other anhingids; also, in this view, it lacks a distal prominence as in *Macranhinga paranensis*. In plantar view, the edge between the *cotyla medialis* and the *fossa parahypotarsalis medialis* is wider with respect to extant species of *Anhinga* and *A. grandis*, resembling in this aspect species of *Meganhinga* and *Macranhinga*. The *fossa parahypotarsalis medialis* is wide, as in *Macranhinga paranensis*, and *Meganhinga chilensis*. The *cotyla lateralis* is transversely compressed and subovoidal in contour in proximal view; its articular surface is dorsodistally inclined, and thus, it is slightly exposed in dorsal view, as in other anhingids. The *cotylae* are separated by a higher and relatively narrower *eminentia intercotylaris* as in the paratype of *M. paranensis* (MACN-PV 12293), unlike *Anhinga anhinga*, *A. novaehollandiae*, *A. grandis* and *Meganhinga chilensis*, and by an *area intercotylaris* that is deeper and more clearly delimited than in all known anhingids.

Based on the preserved portion of the hypotarsus, the *crista medialis flexoris digitorum longus* was robust and longitudinally excavated, and was separated at its base from the *crista lateralis flexoris digitorum longus* by a narrow and concave groove (*sulcus hypotarsi* for the tendon of *m. flexor digitorum longus*), as in anhingids. The *crista medialis flexoris digitorum longus* is more
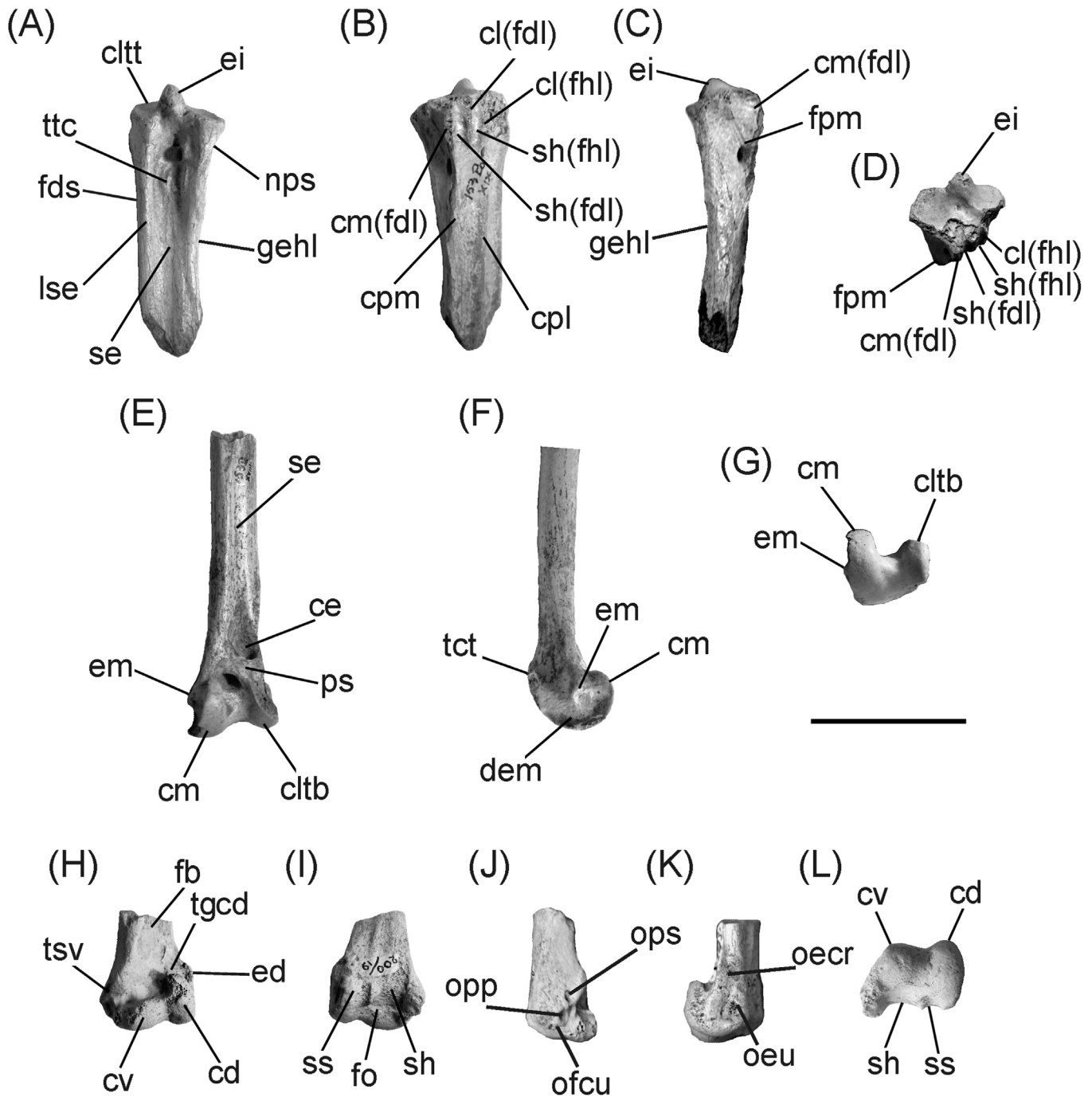
Figure 1. Tarsometatarsus (holotype) and material referred of *Macranhinga ameghinoi* sp. nov. Tarsometatarsus (MLP 10-X-15-1): A, anterior view; B, posterior view; C, medial view; D, proximal view. Tibiotarsus (MLP 10-X-15-2): E, anterior view; F, medial view; G, distal view. Humerus (MLP 10-X-15-2): H, anterior view; I, posterior view; J, ventral view; K, dorsal view; L, distal view.

Note: Scale bars equal 3 cm. Abbreviations: cd, condylus dorsalis; ce, canalis extensorius; cltb, condylus lateralis tibiotarsus; cltt, cotyla lateralis tarsometatarsus; cl(fdl), crista lateralis flexoris digitorum longus; cl(fhl), crista lateralis flexoris hallucis longus; cm, condylus medialis; cm(fdl), crista medialis flexoris digitorum longus; cv, condylus ventralis; cpl, crista plantaris lateralis; cpm, crista plantaris medialis; dem, depressio epicondylaris medialis; ed, epicondylus dorsalis; ei, eminentia intercotylaris; em, epicondylus medialis; fb, fossa m. brachialis; fds, facies dorsalis of the shaft; fo, fossa olecrani; fpm, fossa parahypotarsalis medialis; gehl, groove for the passage of the m. extensor hallucis longus; lse, lateral edge of sulcus extensorius; nps, narrowing of the proximal shaft; oecr, origin m. extensor carpi radialis; oeu, origin m. ectepicondylo-ulnaris; ofcu, origin m. flexor carpi ulnaris; opp, origin m. pronator profundus; ops, origin m. pronator superficialis; ps, pons supratendineus; se, sulcus extensorius; sh, sulcus humerotricipitalis; sh(fdl), sulcus hypotarsi flexoris digitorum longus; sh(fhl), sulcus hypotarsi flexoris hallucis longus; ss, sulcus scapulotricipitalis; tct, throclea cartilaginis tibialis; tgcd, transverse groove that undercuts the condylus dorsalis; tsv, tuberculum supracondylare ventrale; ttc, tuberositas m. tibialis cranialis.

extended distally with respect to the distal end of the *crista lateralis flexoris hallucis longus* in plantar view, as in *Macranhinga paranensis*. The *crista lateralis flexoris digitorum longus* and *crista lateralis flexoris hallucis longus* appear to be proximodistally shorter and thinner than the *crista medialis flexoris digitorum longus*, as commonly occurs in darters and shags. The groove located between the *crista lateralis flexoris digitorum longus* and the *crista lateralis flexoris hallucis longus* (*sulcus hypotarsi* for the tendon of *m. flexor hallucis longus*) is very narrow and shallow. The *crista lateralis flexoris hallucis longus* is very incompletely preserved, but appears to be as proximodistally extended as the *crista lateralis flexoris digitorum longus*.

Figure 2. Fossiliferous localities that yielded fossil anhingids in the southern cone. 1, 'Conglomerado osífero', Ituzaingó Formation, eastern cliffs of the Río Paraná, Entre Ríos Province, Argentina; 2, Paraná Formation, cliffs of the La Ensenada stream, Entre Ríos Province, Argentina; 3, San José Formation, beach of the Balneario Kiyú, San José Department, Uruguay; 4, southwestern to Puesto Marileo, near Ingeniero Jacobacci city, Río Negro Province, Argentina; 5, Cura-Mallin Formation, Cerro Rucananco, Malleco Province, Chile; 6, Santa Cruz Formation, Santa Cruz Province, Argentina; 7, Santa Cruz Formation, Río Bandurrias, Santa Cruz Province, Argentina.

The diaphysis is transversely wide, dorsoplantarly narrow, and with strong muscular impressions, as occurs in other anhingids. The medial margin of the shaft shows a wide groove for the passage of the *m. extensor hallucis longus* on the mid-height of the diaphysis as most anhingids, with the exception of *Anhinga anhinga* and *A. grandis*, in which it is more proximally located. In medial view, the proximal portion of the shaft has a wide and medial origin of *m. extensor hallucis longus* as in *Macranhinga* and *Meganhinga*, whereas in extant snake birds and *A. grandis* this muscle scar is more reduced and dorsaly located; the origin

Table 1. Measurements of *Macranhinga ameghinoi* nov. sp. and other Anhingidae.

	Humerus	Tibiotarsus	Tarsometatarsus
	Distal width	Shaft width	Proximal width
Ma. ameghinoi	17.7	10.6	16.5
Ma. paranensis	20.9–22.0	12.5–12.7	19.1–21.0
	(*n* = 4; 21.5)	(*n* = 2; 12.6)	(*n* = 3; 20.4)
Me. chilensis	14.0	–	18.4
An. minuta	11.5	5.0	–
An. grandis	15.0–17.2	5.9–6.5	12.8[1]
	(*n* = 5; 16.0)[1]	(*n* = 2; 6.2)[1]	
An. anhinga	13.7–15.8	5.6–6.2	11.1–12.4
	(*n* = 6; 14.7)	(*n* = 6; 5.9)	(*n* = 6; 12.0)
An. novaehollan-diae	15.8–16.0	6.5–7.1	13.4–13.5
	(*n* = 2; 15.9)	(*n* = 2; 6.8)	(*n* = 2; 13.45)

[1]Taken from Becker (1987).

of *m. flexor hallucis brevis* is slightly dorsally oriented with respect the longitudinal axis of the bone, as in most known Anhingidae with the exception of *Meganhinga chilensis*. In lateral view, the *facies dorsalis* of the diaphysis has a gentle transition between proximal and distal end as in *Meganhinga* and *Macranhinga*, whereas in *Anhinga anhinga*, *A. novaehollandiae* and *A. grandis* the proximal end is notably wider.

The *sulcus extensorius* is very wide and well-defined as in other anhingids, especially on its medial margin; the proximal end is not transversely delimited by a sharp ridge. This *sulcus* is deeper and more well defined when compared with extant snake birds and *A. grandis*, being similar in this aspect to *Macranhinga paranensis*, and *Meganhinga chilensis*. The *tuberositas m. tibialis cranialis* is represented by a small and rounded mound. In plantar view, the *sulcus flexorius* is deep and delimited by sharp and acute *cristae plantares medialis* and *lateralis* as occurs in other anhingids. This *sulcus* is proximally deeper, more well-delimited (specially, on the *crista plantaris lateralis*) and transversely wider with respect to extant *Anhinga* and *A. grandis*, a morphology shared with *M. paranensis*, and *Meganhinga chilensis*. The origin of the *m. abductor digiti* IV is well defined as in Anhingidae and Phalacrocoracidae, but relative to the latter, it has a more flattened lateral wall at mid-length.

Remarks. The tarsometatarsus MLP 10-X-15-1 is referred to Anhingidae, and differentiated from Phalacrocoracidae by having a shallower *cotyla medialis* that is subquadrangular in contour, and is subhorizontally oriented, a *cotyla lateralis* with a poorly pronounced dorsal slope, a transversely wide and dorso-plantarly narrow shaft, a deep and well-defined medial margin delimiting the *sulcus extensorius*, a wide groove for the passage of the *m. extensor hallucis longus*, a deeply excavated origin of the *m. flexor hallucis brevis*, a deep and well delimited *sulcus flexorius*, a origin of the *m. abductor digiti* IV wide and with flattened lateral wall at mid-length (Alvarenga 1995; Noriega & Alvarenga 2002). MLP 10-X-15-1 is assigned to genus *Macranhinga* and differentiated from species in *Anhinga* and, *Meganhinga* by the characters exposed in the generic diagnosis. Further, differs from *Giganhinga* (in which the tarsometatarsus is still unknown) on its much smaller size.

Tibiotarsus. The tibiotarsus MLP 10-X-15-2 is represented by the distal half of the bone with a strongly abraded *condylus lateralis* (Figure 1(e)–(g)). The tibiotarsus, based on the shaft width (Table 1), is larger than living species (about 43%) and *A. minuta* (53%), but is smaller than *Macranhinga paranensis*

(19%). The shaft is very robust and shows a very thick periosteum, as in *Macranhinga* and *Meganhinga*. In cranial view, the shaft is strongly transversely expanded distally, as occurs in *Macranhinga*. The *sulcus extensorius* is relatively shallow and centrally placed, as in other Anhingidae. This *sulcus* ends on an oval-shaped *canalis extensorius* as in *Anhinga anhinga*, *A. grandis* and *A. beckeri*, whereas is more transversely expanded in *M. paranensis* and *A. novaehollandiae*. The *pons supratendineus* is obliquely oriented and wide, as in Anhingidae and Phalacrocoracidae. The *condylus medialis* is less distally extended with respect to the *condylus lateralis* as occurs in Anhingidae; this condyle in proximal view is subtriangular in contour, a condition different from that known in other Anhingidae, in which this condyle shows subparallel medial and lateral margins. The preserved portion of the *condylus lateralis* indicates that it was smaller than the medial one and has a well-defined proximal pit, as occurs in Anhingidae. In medial view, the *epicondylus medialis* is conical in shape, very well developed, and it is surrounded distally by a well deep and wide *depressio epicondylaris medialis*, as occurs in *Macranhinga paranensis*. In caudal view, the *trochlea cartilaginis tibialis* is wide and shallow, as in Anhingidae and Phalacrocoracidae.

Remarks. The distal end of tibiotarsus MLP 10-X-15-2 is referred to Anhingidae by having a *sulcus extensorius* shallow and centrally placed, a well-defined pit on the proximal margin of the *condylus lateralis*, and *condylus lateralis* smaller and transversally narrower (Noriega 2002; Alvarenga & Guilherme 2003). The tibiotarsus shows a unique combination of characters that allows its inclusion within *Macranhinga* (see generic diagnosis).

Humerus. The distal end of humerus MLP 10-X-15-2 shows slightly abraded distal condyles (Figure 1(h)–(l)). The humerus, based on the distal width (Table 1), is larger than in living species (about 14%), *Meganhinga chilensis* (21%), and *A. minuta* (35%), but is smaller than in *Macranhinga paranensis* (21%; Table 1). The preserved portion of the shaft is rather massive as in *Macranhinga* and *Meganhinga*, with a notably thicker cortex than *Anhinga*. In cranial view, the *fossa m. brachialis* is poorly excavated, do not extends distally to the *tuberculum supracondylare ventrale* and its medial and distal margins are delimited by well-defined ridges of bone as in Anhingidae; this *fossa* is subdivided (proximally shallow and distally deep) as in *Macranhinga*, being homogeneous in depth in *Anhinga*. Distal to this *fossa*, the *tuberculum supracondylare ventrale* is very well defined, obliquely oriented, and laterally extended, being separated from the *condylus ventralis* by a relatively narrow and deep concave surface. In medial view, it is slightly rounded and poorly cranially extended, a combination of characters that occurs in other Anhingidae. The *condylus ventralis* is subhorizontally oriented, ovoidal in contour and separated from the *condylus dorsalis* by a shallow *incisura intercondylaris*. The *condylus dorsalis* is strongly proximally undercut by a deep transverse groove, as in other Anhingidae, but this groove is shallower as in *Macranhinga paranensis* respect to *Anhinga*. The *epicondylus dorsalis* is laterally extended and low, as in *M. paranensis* and *Meganhinga chilensis*.

In medial view, the attachment surface for the anterior division of the *m. flexor carpi ulnaris* is large, as in remaining anhingids. The origin of the *m. pronator profundus* is large, flat, subcircular in contour, and, as occurs in *M. paranensis* and *Meganhinga chilensis* is separated from the attachment of the anterior division of the *m. flexor carpi ulnaris* by a conspicuous

craniocaudal ridge. The origin of the *m. pronator superficialis* is large and deep, as in other Anhingidae. In lateral view, the attachment of the *m. ectepicondylo-ulnaris* is represented by a shallow and subcircular-shaped concavity. The attachment of the *m. extensor carpi radialis* is a very deep, wide and subcircular concavity, as in *Macranhinga paranensis* and *Meganhinga chilensis*. It is strongly proximodorsally located with respect to *epicondylus dorsalis* and is subdivided in two parts.

In caudal view, the *sulcus humerotricipitalis* is proportionally wider and is separated from the *sulcus scapulotricipitalis* by a prominence that is relatively higher than in *Anhinga*. The *fossa olecrani* is relatively shallow and poorly proximally extended, as in *A. anhinga*, *A. novaehollandiae*, *A. grandis* and, *A. beckeri* whereas in *Macranhinga paranensis*, and *Meganhinga chilensis* is more deeply excavated and proximally extended.

Remarks. The distal end of the humerus MLP 10-X-15-2 is referred to Anhingidae because it shares the dorsal margin of *condylus dorsalis* deeply and extensively undercut by a groove, the *tuberculum supracondylare ventrale* is prominent and ovate in outline, a very expanded *epicondylus dorsalis*, and large attachment of the anterior division of the *m. flexor carpi ulnaris* (Miller 1966; Owre 1967; Martin & Mengel 1975; Walsh & Hume 2001; Noriega & Alvarenga 2002).

Discussion

The phylogenetic position of Macranhinga ameghinoi *sp. nov.* and other fossil anhingids

As indicated along the text, *Macranhinga ameghinoi* sp. nov. is clearly nested within *Macranhinga* based on a large number of features. However, because of the still incomplete knowledge of *Macranhinga* species, the relationships of the new taxon to other species of the genus are uncertain. *Macranhinga ameghinoi* sp. nov. is clearly nested within Anhingidae, based on a combination of features present in the distal end of tibiotarsus, proximal end of the tarsometatarsus, and the distal end of the humerus.

Regrettably, the only phylogenetic analysis performed with the aim to resolve the phylogenetic relationships within anhingids is that of Noriega & Alvarenga (2002), based on 21 characters coded for six taxa. In that analysis, Noriega & Alvarenga (2002) found that the South American giant anhingas are stem group representatives of the genus *Anhinga*. However, it is curious to note that together with very large size (Noriega 1992; Alvarenga 1995; Alvarenga & Guilherme 2003) and greater robustness, South American Neogene anhingids, including *M. ameghinoi* sp. nov., share a number of features absent in *Anhinga* species (e.g. *A. anhinga*, *A. novaehollandiae*). These features include: tarsometatarsus with a high and conspicuous internal margin delimiting the *sulcus extensorius*, very well defined *sulcus flexorius* on both sides, especially on the lateral one, proximal *cotyla lateralis* slightly sloping dorsally, insertion of *m. hallucis longus* dorsoventrally expanded and well-developed on medial aspect, notably wide *fossa metatarsi* I, and very prominent *cristae plantares*, specially the lateral one, femur with the distal end of the bone having very wide *tuberculum m. gastrocnemialis lateralis*, and external facet for insertion of the *m. gastrocnemialis* proximally located, and a large number of pelvic traits, including strongly transversely compressed, narrow, and compact

preacetabular pelvis, strongly transversely compressed postacetabular pelvis, and caudodorsally located *foramen acetabuli* (Alvarenga 1995; Noriega & Alvarenga 2002; Rinderknecht & Noriega 2002; Alvarenga & Guilherme 2003; Areta et al. 2007). It is possible to infer that these features, exhibited by the genera *Giganhinga*, *Macranhinga*, and *Meganhinga*, support a close relationship between these taxa, suggesting that they conform a monophyletic clade within Anhingidae.

The fossil record of Anhingidae in Patagonia

As explained above, the fossil record of Anhingidae in South America is relatively abundant and composed by numerous taxa, a fact that contrasts with the single living species inhabiting the entire continent. Indeterminate species of *Macranhinga* (Cenizo & Agnolin 2010) and *Anhinga hesterna* were reported from different localities of the Santa Cruz Formation in Patagonia, whereas *Meganhinga chilensis* comes from the nearly coeval Cura Mallin Formation (Alvarenga 1995; Soto-Acuña et al. 2013). In addition to these species, Ameghino (1891, 1895, 1899) described several other avian taxa that still await detailed reconsideration. One of these is *Pseudolarus eocaenus* Ameghino 1891, type species of the genus *Pseudolarus*, which was considered as a Psilopteridae (Phororhacoidea) by the great majority of modern contributions (Brodkorb 1967; Tonni 1980; Agnolin 2006; Tambussi & Degrange 2013), but recently regarded as a possible anhingid by Agnolin (2016).

Anhinga hesterna, *Meganhinga chilensis* and *Macranhinga ameghinoi* sp. nov., and possibly *Pseudolarus eocaenus*, indicate that the anhingid diversity during the Miocene of Patagonia was far more diverse than currently understood. This diversity is comparable to that exhibited in northern localities, as the Mio-Pliocene beds of Acre State (Brazil), where four different coetaneous anhingids were reported (Alvarenga & Guilherme 2003), and in the late Miocene beds of Entre Ríos Province of Argentina, that yielded at least four different taxa (Noriega & Agnolin 2008; Diederle & Noriega 2013).

The new species *Macranhinga ameghinoi*, as the extinct anhingids *Giganhinga kiyuensis*, *Meganhinga chilensis*, and *Macranhinga paranensis* clearly shows osteological details correlated with diving capabilities, much more developed than in *Anhinga* (Alvarenga 1995; Noriega 2001; Rinderknecht & Noriega 2002). This suggests that probably one important factor that driven the evolutionary history and extinction of these South American extinct anhingas was their extreme diving capabilities.

The progressive climatic deterioration that occurred at the end of the Miocene in Patagonia, before retraction of epicontinental seas and development of more arid conditions (Pascual & Bondesio 1982; Pascual et al. 1996; Ortiz-Jaureguizar 1998; Ortiz-Jaureguizar & Cladera 2006), may explain the absence of anhingid birds from post-Miocene beds in Patagonia (Cenizo & Agnolin 2010). During this period, savannas and rainforests retracted to northern South America, and very probably the large freshwater lakes and ponds that were once abundant in the southern cone became smaller, shallower, and possessed more turbid waters, a harmful environment for anhingids (Alvarenga & Guilherme 2003). The same may have occurred to diving Patagonian anhingids, such as *Macranhinga ameghinoi* sp. nov. and *Meganhinga chilensis*, which may have not survived this

climatic depauperation, and thus, disappeared from the fossil record in these southern beds by Mid-Miocene times.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix 1. Comparative material

Macranhinga paranensis: MACN-PV 12281, MACN-PV 12293, MACN-PV 12736, MACN-PV 12747, MACN-PV 12748, MACN-PV 13507, MACN-PV 14365, MLP-PV 88-IX-20-1, MLP-PV 88-IX-20-2, MLP-PV 88-IX-20-10, MLP-PV 88-IX-20-11, MACN-PV 12292, MACN-PV 13299, MACN-PV 14363, MACN-PV 14366, MLP-PV 41-XII-13-929, MLP-PV 88-IX-20-5, MLP-PV 88-IX-20-12, MLP-PV 88-IX-20-15. *Macranhinga ranzii*: UFAC 3640, UFAC 4860, UFAC 4034, UFAC 3523. *Giganhinga kiyuensis:* MNHN 1632, MACN-PV 12179. *Meganhinga chilensis*: SGO-PV 4001-A, SGO-PV 22212b, SGO-PV 4001-B, SGO-PV 4002. *An. minuta*: UFAC-4719, UFAC-4720. *Anhinga anhinga*: MACN-A 54807, MNHNP s/nº 1, MHNT 25, 882, 924, 1039, 2856. *Anhinga novaehollandiae*: MNHT 1210, 1195. Photographs (P) and descriptions (D) of *Anhinga grandis* (see main text): UNSM 20070 (P,D), UF 61399 (P), UF 114587 (P), UF 114600 (P), UF 114631 (P), UF 114646 (P). Photographs and descriptions of *Anhinga subvolans* (see main text): UF 4500 (P, D). Photographs and descriptions of *Anhinga beckeri* (see main text): UF 102203 (P), UF 159432 (P), UF 95948 (P).