Number 460
25 March 1996

Contributions in Science

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Natural History Museum of Los Angeles County

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Natural History Museum of Los Angeles County
900 Exposition Boulevard
Los Angeles, California 90007

Printed at Allen Press, Inc., Lawrence, Kansas
ISSN 0459-8113

A New Species of Giant Anhinga (Aves: Pelecaniformes: Anhingidae) from the Upper Miocene (Huayquerian) of Amazonian Peru

Kenneth E. Campbell, Jr.[1]

ABSTRACT. A new species of giant anhinga is described from Upper Miocene (Huayquerian) deposits of southeastern Peru, the first species of fossil bird to be described from the Tertiary of lowland Amazonia. In addition to the holotype tarsometatarsus, three partial humeri, the distal end of an ulna, a tibiotarsus, and two cervical vertebrae are referred to the new species. The new species is slightly larger than *Meganhinga chilensis* from Chile, but it is smaller than *Macranhinga paranensis* from Argentina, both recently described Miocene paleospecies of giant anhingas. The hindlimb of the new species is approximately 65 per cent larger than that of modern *A. anhinga*, but the wing appears to be only about 25 per cent larger. The size of the wing relative to that of the hindlimb appears to be a highly variable feature of anhingas of the Americas.

INTRODUCTION

Anhingas are water birds of the suborder Sulae, order Pelecaniformes. Primarily predators on fish, they are excellent underwater swimmers, but they are also good fliers and roost easily in trees. Anhingas are commonly known as darters or snakebirds, the latter in reference to the snake-like manner in which they hold and move their head while swimming partially submerged.

The family Anhingidae is one of four families comprising the suborder Sulae, the other three being the Sulidae, the Phalacrocoracidae, and the extinct, marine family Plotopteridae (Olson, 1980, 1985). Occasionally, the family Anhingidae has been reduced in rank to subfamilial status (e.g., Dorst and Mougin, 1979), but this effort has had little support (Olson, 1985; Becker, 1986). The fossil record of anhingas has been reviewed by Olson (1985), Becker (1986, 1987), Rasmussen and Kay (1992), and Alvarenga (1995). Until recently, most paleospecies of anhingas were known from Europe and North America, but a recent series of finds, including those reported by Wall et al. (1991), Rasmussen and Kay (1992), Noriega (1992), and Alvarenga (1995) and those described in this paper, have expanded our knowledge of Tertiary anhingas of South America considerably. These new discoveries do not yet reveal much about the phylogenetic relationships of anhingas, but they do demonstrate a surprising diversity of large-bodied anhingas during the Miocene in South America.

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MATERIALS AND METHODS

Anatomical terminology is principally that of Baumel et al. (1979). Measurements accurate to 0.01 mm were taken with vernier dial calipers; they were then rounded one decimal point. Measurements from other sources were also rounded to one decimal point if originally given to more than one. Osteological comparisons were made with six modern specimens of *Anhinga anhinga* (Linnaeus 1766), two of *A. novaehollandiae* (Gould 1847), and one of *A. rufa* (Daudin 1802). Comparisons were also made with the holotype of the early Miocene *Meganhinga chilensis* Alvarenga 1995 and a cast of the holotype of the late Miocene *Macranhinga paranensis* Noriega 1992.

SYSTEMATICS

Order Pelecaniformes Sharpe 1891

Suborder Sulae Sharpe 1891

Family Anhingidae Ridgway 1887

Genus *Anhinga* Brisson 1760

DISCUSSION. I have chosen not to erect a new genus for the species described below because I see no characters that justify such action. In fact, I doubt that the recently described genera *Meganhinga* Alvarenga 1995 and *Macranhinga* Noriega 1992 are sufficiently distinct from *Anhinga* to warrant recognition. Alvarenga (1995) based his genus primarily on two features of the tarsometatarsus: a prominent hypotarsis and a wide proximal me-

taphysis. Both of these characters would be expected in a larger version of a foot-propelled diving bird and they do not, in themselves, justify the recognition of a separate genus. Alvarenga (1995) was also influenced in his decision by the fact that the wing was very small relative to the rest of the bird, possibly indicating flightlessness. As noted below, however, such variation between fore- and hindlimbs may be common in anhingas. Perhaps this is a situation analogous to that seen in cormorants, where one species only of *Phalacrocorax* is flightless, whereas the remaining species are volant.

Noriega (1992:220) erected *Macranhinga* primarily on the basis of size, which is not a generic character. The other characters he listed are more readily interpreted as specific, not generic, characters. Unfortunately, other available elements of *Macranhinga paranensis* were not described by Noriega (1992, 1995), so we do not know if their characters would support the establishment of the genus. Until it can be documented that *Meganhinga* and *Macranhinga* are valid genera, I consider them to be junior synonyms of *Anhinga*.

Anhinga fraileyi new species

Figures 1, 2

HOLOTYPE. Right tarsometatarsus; proximal end damaged, lacking hypotarsus; LACM 135356.

TYPE LOCALITY. LACM 4611; Acre VI, southwest bank of Río Acre, about 0.5 km downstream from the confluence of the Río de Los Patos, Departamento de Madre de Dios, Peru; approximately 69°55′41″W, 10°56′15″S.

TYPE HORIZON AND AGE. Acre Conglomerate of Campbell et al. (1985); Upper Miocene (Huayquerian). This unit was originally described as the Acre Conglomerate Member of the upper Pleistocene Iñapari Formation (ONERN, 1977) [= Madre de Dios Formation of Oppenheim (1946) (Campbell and Romero-P., 1989) = Içá Formation of Maia et al. (1977)]. When this horizon was described, the fossils in it were thought to have been redeposited from Tertiary [Upper Miocene (Huayquerian)] deposits in the Pleistocene, as also suggested by Simpson and Paula Couto (1981). Recent advances in our understanding of the geology of the region now lead me to consider this unit and its contained fossils to be *in situ* Upper Miocene (Huayquerian) deposits (see also Kay and Frailey, 1992). Assignment of the fossils from the Acre Conglomerate to the Huayquerian South American Land Mammal Age is based on the presence in the fauna of such characteristic Huayquerian taxa as *Kiyutherium orientalis* Frances and Mones 1965, *Tetrastylus* sp. (Pascual et al., 1966), and possibly *Potamarchus murinus* Burmeister 1885 (Frailey, 1986).

DIAGNOSIS. The holotypical tarsometatarsus can be distinguished from all living species of *Anhinga* by its large size. It differs from that of *Anhinga anhinga* 1) by being approximately 65 per cent larger and by having 2) eminentia intercondylaris more prominent, 3) shaft with medial and lateral sides much less excavated immediately distal to cotylae, 4) shaft with medial side not expanded mediad at the fossa metatarsal I, 5) shaft lacking small, ridge-like projection on anterior face immediately distal to cotyla medialis, and 6) shaft lacking sharp corner or ridge on interno-medial portion leading to base of trochlea metatarsi II.

The holotypical tarsometatarsus differs from that of *Anhinga chilensis* (Alvarenga 1995) by having 1) eminentia intercondylaris more pronounced (not much elevated above hypotarsus, in external view, in *A. chilensis*); 2) cotyla medialis smaller, less pronounced anteriad; 3) cotyla lateralis smaller, sloping more steeply anteriad; 4) shaft wider in anterior view, narrowing less distal to cotylae and widening more as it approaches trochlea metatarsi II; 5) shaft of similar depth, but wider; 6) shaft less excavated between proximal lateral ridge and hypotarsus, in medial view, with proximal lateral ridge meeting distal end of crista plantaris mediana of hypotarsus at low angle (much higher angle in *A. chilensis*) and proximal lateral ridge meeting distal end of crista plantaris mediana about 45 per cent of the shaft length downshaft (about 33 per cent in *A. chilensis*); 7) shaft with area between lateral ridge and postero-external ridge less excavated, in external view, with postero-external ridge less prominent and located more mediad; 8) shaft, in medial view, not curving as far craniad to meet lip of cotyla medialis; 9) trochlea metatarsi III with central canal more pronounced, sides smaller and less rounded, and extending less anteriad, i.e., shorter overall. In addition, in *A. chilensis,* in medial view, the distal lateral ridge is rotated slightly posteriad, suggesting that trochlea metatarsi III, which is missing from the holotype, was positioned more posteriorly.

The holotypical tarsometatarsus differs from that of *Anhinga paranensis* (Noriega 1992) by having 1) eminentia intercondylaris narrower, but more prominent, with external side nearly vertical (does not approach vertical in *A. paranensis*); 2) both cotyla medialis and cotyla lateralis smaller, with latter sloping less steeply anteriad; 3) shaft, in medial view, curves farther anteriad to meet anterior lip of cotyla medialis; 4) hypotarsus missing, but crista hypotarsi medialis a low ridge from level of foramina vascularia proximalia medialis distad (much more prominent ridge in *A. paranensis*); 5) shaft with crista lateralis of plantar side less prominent; 6) trochlea metatarsi tertii turned slightly laterad, in anterior view, but very nearly parallel to axis of shaft (turned mediad in *A. paranensis,* at a slight angle to axis of shaft); 7) trochlea metatarsi II narrower, with medial side at low angle to axis of shaft, and extending distad beyond trochlea metatarsi III (broad, turned much more mediad at greater angle to axis of shaft, and not extending distad beyond trochlea metatarsi III in *A. paranensis*); 8) trochlea metatarsi II with "wing" missing, but proximal portion of trochlea metatarsi II much

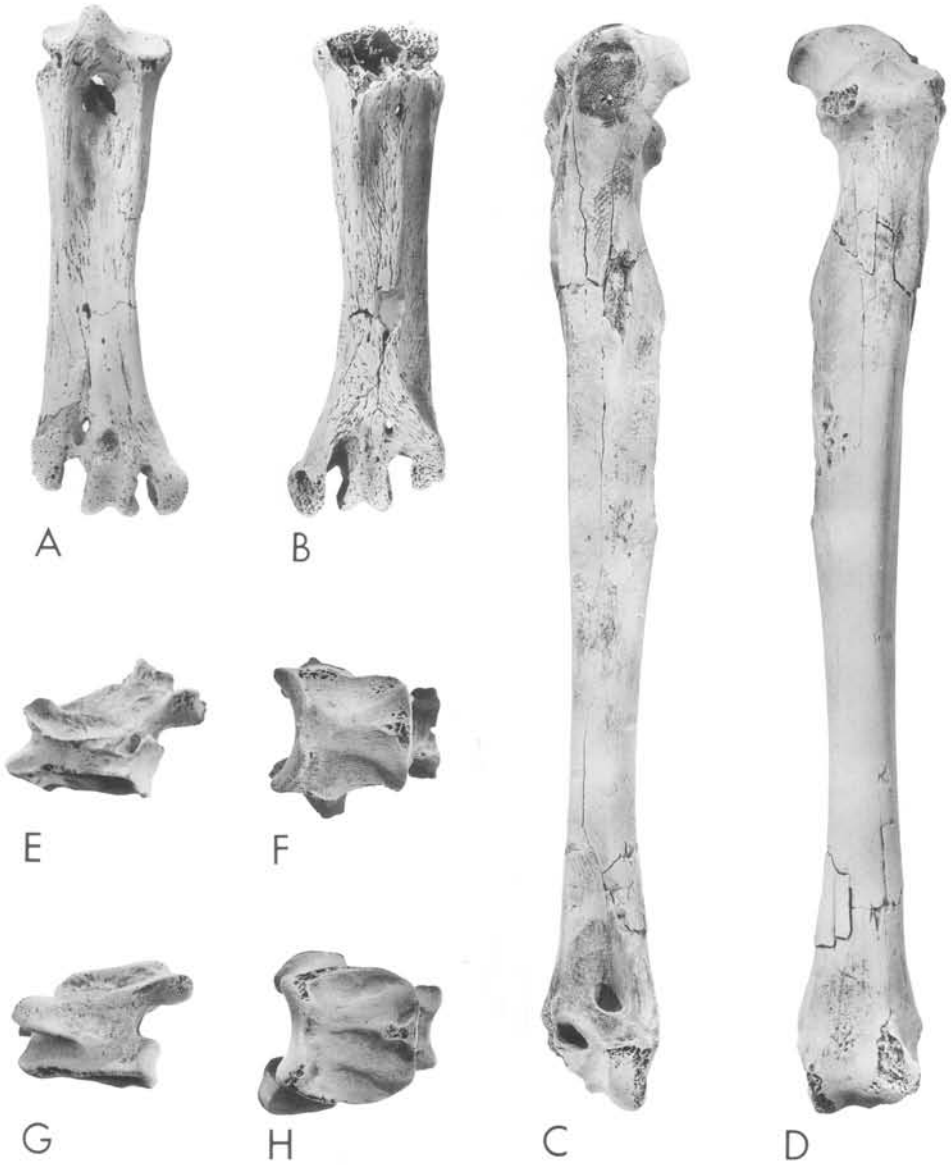

Figure 1. Specimens of *Anhinga fraileyi* new species, including the holotype tarsometatarsus (LACM 135356), in cranial (**A**) and caudal (**B**) views; the referred left tibiotarsus (LACM 135357), in cranial (**C**) and caudal (**D**) views; the referred 19th cervical vertebra (LACM 135359), in left lateral (**E**) and ventral (**F**) views; and the referred 18th vertebra (LACM 135358), in left lateral (**G**) and ventral (**H**) views.

smaller than in *A. paranensis*, suggesting "wing" much smaller than in latter; 9) trochlea metatarsi IV narrower, more rounded distally in lateral view. Although the trochleae of *A. fraileyi* appear to be farther apart than in *A. paranensis*, this effect may be a result of postmortem wear.

The holotypical tarsometatarsus differs from that referred to *Anhinga grandis* by Becker (1987) by its 1) larger size, 2) broader midshaft region, 3) more prominent eminentia intercondylaris, and 4) a distal crista plantaris mediana that extends farther distad.

MEASUREMENTS. See Table 1.

REFERRED MATERIAL. From type locality LACM 4611: distal end and shaft of right humerus (LACM 135360), distal end of left ulna (LACM 135361), complete left tibiotarsus, condylus medialis broken (LACM 135357); cervical vertebra #18 (LACM 135358); cervical vertebra #19 (LACM 135359). From locality LACM 5158: proximal end and shaft of left humerus (LACM 135362), shaft of right humerus (LACM 135363).

ETYMOLOGY. Patronymic, in honor of Dr. Carl

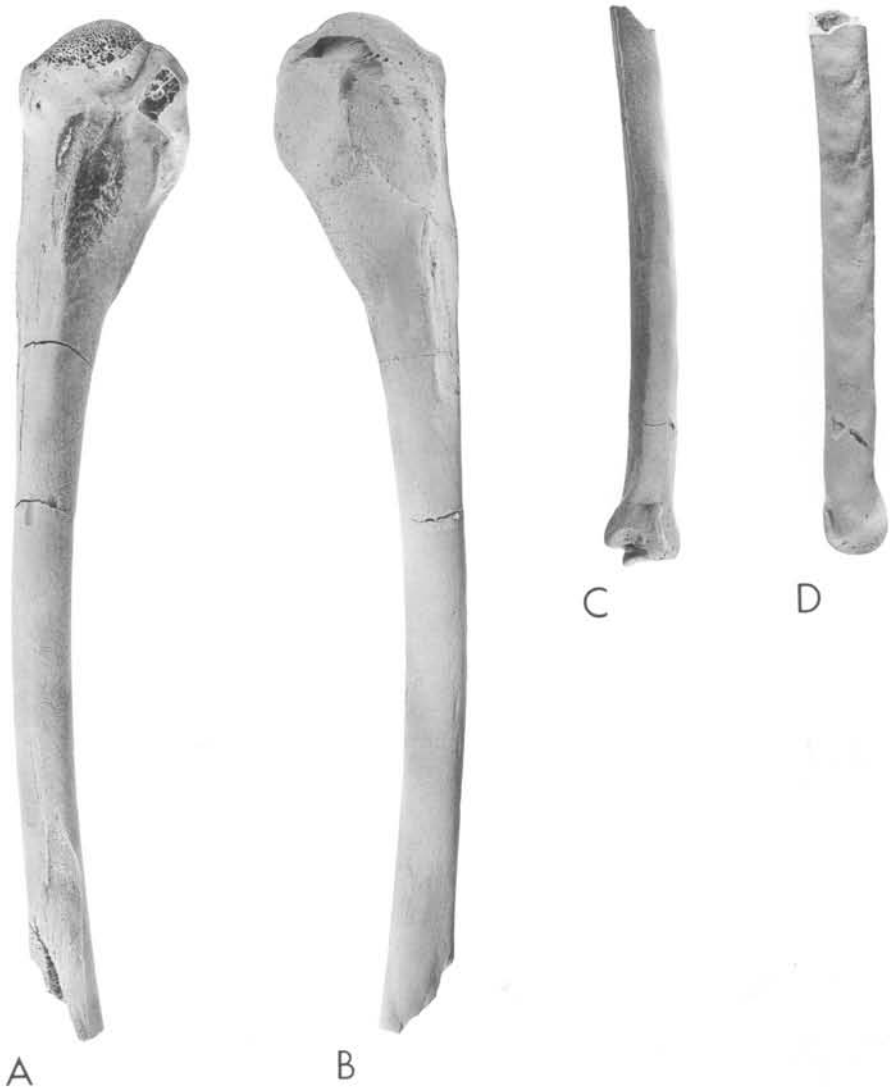

Figure 2. Specimens referred to *Anhinga fraileyi* new species. Proximal end and shaft of left humerus (LACM 135362), in caudal (**A**) and cranial (**B**) views, and the distal end of left ulna (LACM 135361), in dorsal (**C**) and caudal (**D**) views.

David Frailey, in recognition of his contributions to Amazonian paleontology.

DESCRIPTION. Humerus. The humeri are referred to the family Anhingidae on the basis of those characters listed by Becker (1986). These specimens are referred to *Anhinga fraileyi* and differ from *A. anhinga*, by having 1) larger size; 2) tuberculum dorsale projecting less prominently from shaft; 3) margo caudalis a distinct ridge confluent with attachment of coracohumeralis ligamentum (not confluent in *A. anhinga*); 4) fossa pneumotricipitalis and impressio M. coracobrachialis cranialis shallower; 5) attachment of M. pectoralis undivided (divided into proximal and distal portions in *A. anhinga*); 6) sulcus ligamentosus transversus proportionately deeper ventrally, undercutting intumescentia; and 7) distal end with processus flexorius more prominently developed, bordering a more deeply excavated olecranon fossa. The distal humerus (LACM 135360) is too badly worn to reveal any other clear characters. Interestingly, this specimen carries paired tooth marks on both the shaft and distal end. This may be taken as evidence of predation, although it could also represent postmortem gnawing on the bone.

In spite of being badly worn, the distal humerus can be seen to differ from the holotype of *Anhinga grandis* Martin and Mengel 1975 from the Upper Miocene of North America by having the condylus dorsalis as deeply undercut, or more, as in *A. an-*

hinga; the processus flexorius larger and more prominent, projecting farther distad; and the epicondylus dorsalis less developed and extending less proximad. The proximal humerus differs from that referred to *A. grandis* by Becker (1987) by having a more acute angle between the sulcus ligamentosus transversus and the impressio M. coracobrachialis cranialis, a shallower impressio M. coracobrachialis, and a less excavated fossa pneumotricipitalis.

For measurements, see Table 2.

Ulna. The ulna is placed to the family Anhingidae and differs from those of cormorants by having the

Table 1. Measurements (mm) of the holotype tarsometatarsus of *Anhinga fraileyi* in comparison with those of *A. anhinga* (n = 4), *A. grandis*, *A. chilensis*, and *A. paranensis*.

Measurements	*Anhinga anhinga*	*Anhinga anhinga*[1]	*Anhinga fraileyi*	*Anhinga grandis*[2]	*Anhinga chilensis*[1]	*Anhinga paranensis*[3]
Total length	39.5–41.8 x = 41.2	41.5–43.5 x = 42.5	68.5	47.8	61.0	75.3 (75.5)
Distal width, excluding "wing" of trochlea metatarsi II	12.5–14.4 x = 13.5	—	22.0	16.5	—	25.7
Midshaft width	6.1–6.9 x = 6.5	6.7–7.4 x = 7.1	11.9	7.8	10.0	12.5
Midshaft depth	3.6–4.7 x = 4.0	4.5–5.0 x = 4.7	7.3	4.9	7.3	
Proximal width	10.7–12.5 x = 11.2	11.8–12.7 x = 12.3	19.5 ± 0.5	12.8	18.0	21.1 (21.5)
Width trochlea metatarsi III	4.4–4.9 x = 4.6	5.0–5.4 x = 5.2	8.0	—	8.0	9.6

[1] This set of measurements for *Anhinga anhinga* (n = 5) and those for *Anhinga chilensis* from Alvarenga (1995).

[2] Measurements for *Anhinga grandis* from Becker (1987).

[3] Measurements from a cast. Figures in parentheses from Noriega (1992).

Table 2. Measurements (mm) of the humeri of *Anhinga fraileyi*, *A. grandis*, and *A. anhinga*.

	Anhinga fraileyi					
Measurement	LACM 135362	LACM 135360	LACM 135363	*A. grandis*[1]	*A. anhinga*	*A. anhinga*[1]
Proximal width	22.3	—	—	23.1	17.3–19.1 x = 18.2 (n = 4)	17.2–19.8 x = 18.0
Depth of caput humeri	7.5	—	—	8.0	6.2–7.2 x = 6.7 (n = 4)	6.1–7.1 x = 6.7
Length of crista deltopectoralis	44.6	—	—	42.3	32.6–37.6 x = 34.5 (n = 4)	31.7–37.8 x = 35.2
Midshaft width	8.3	9.1	8.7	8.7	5.8–7.1 x = 6.5 (n = 5)	5.7–7.1 x = 6.7
Midshaft depth	7.4	8.3	7.1	7.7	5.3–6.2 x = 5.8 (n = 5)	5.1–6.2 x = 5.8
Distal width	—	15.7 ± 2.0	—	—	13.6–16.2 x = 14.7 n = 5	—

[1] Measurements from Becker (1986); n = 10 for *Anhinga anhinga*.

condylus ventralis less protruding distad, the tuberculum carpale more set off from the shaft proximally, and the condylus dorsalis not elevated above the shaft proximally, in ventral view. The ulna differs from that of *Anhinga anhinga* by having 1) condylus ventralis less prominently protruding distad, 2) tuberculum carpale more massive, and 3) condylus dorsalis extending farther proximad ventrally and by lacking 4) prominent papillae remigiales caudales.

This distal ulna is very close in size to the Middle Miocene specimen from Colombia referred to *Anhinga* sp. cf. *A. grandis* by Rasmussen and Kay (1992). It differs from that specimen by having the tuberculum carpale more set off from the shaft and the ventral edge of the condylus ventralis projecting distad less prominently.

For measurements, see Table 3.

Tibiotarsus. The tibiotarsus is placed to the family Anhingidae and differs from those of cormorants by its less prominent crista cnemialis lateralis and its more centrally placed canalis extensorius. The tibiotarsus differs from that of *A. anhinga* by having 1) crista patellaris less covered medially by area of attachment of Lig. patellae; 2) crista cnemialis cranialis not extending as far proximad as the crista patellaris (the junction of the crista patellaris and crista cnemialis cranialis is a prominent, proximad-pointing projection in *A. anhinga*); 3) crista cnemialis lateralis with cranial end roughly triangular in proximo-lateral view, with apex pointing posteriad (linear in *A. anhinga*); 4) shaft leading to crista cnemialis lateralis much more massive; 5) fossa flexoria less deeply excavated; posterior lip of facies articularis medialis very thick, rounded, and only slightly excavated distad; 6) groove for peroneus profundus not as distinct, especially proximad (not as distinctly set off laterally in *A. anhinga*); and 7) concavity at the antero-proximal end of condylus lateralis linear and moderately deep, appearing as a sharp cleft (a deep, oval pit in *A. anhinga*).

A larger size distinguishes tibiotarsus LACM 135357 from that referred to *Anhinga grandis* by Becker (1987). For measurements, see Table 4.

Cervical Vertebrae. Two water-worn cervical vertebrae were found at the type locality. If it is reasonable to assume that the same general vertebral form would have existed in *Anhinga fraileyi* as in *A. anhinga*, these three vertebrae would fall within numbers 17–19 of the cervical series. In *A. anhinga* these cervical vertebrae (cv) have a broad, relatively flat or slightly concave ventral surface with a small central spine or ridge. In cv #17 the ventral surface is significantly longer than it is wide, but in cv #18 and cv #19 the ventral surface is approximately as wide as it is long, as is the case in the fossil specimens.

In *Anhinga anhinga*, cv #18 is characterized by a fairly sizable incisura in the side of the vertebral wall immediately dorsal to the facies articularis caudalis. The dorsal edge of this incisura leads in a straight line to the base of the facies articularis of the postzygapophysis. LACM 135358 has a comparable notch. Cv #19 also has an incisura in the corresponding position, but it is much reduced in size. This latter condition is observed in LACM 135359.

The ventral surface of cv #18 of *Anhinga anhinga* is slightly concave, but with two small lateral ridges in addition to a central ridge with a caudal spine. The lateral ridges are at an angle to the long axis of the bone, approaching the midline more craniad. The ventral surface is more excavated, or concave, lateral to these ridges. A corresponding condition is seen in LACM 135358.

The ventral surface of cv #19 of *Anhinga anhinga* lacks the two lateral ridges seen in cv #18, and it has a narrower, more prominent central ridge. Instead of the two lateral ridges, the ventral surfaces lateral to the medial ridge have an excavated, or concave, surface. Specimen LACM 135359 differs by lacking a central ridge, but it does have a broad, roughly triangular, elevated platform that narrows craniad.

In *Anhinga anhinga*, cv #19 is the first in a series of vertebrae extending caudad that has a foramen through the vertebral wall into the foramen vertebrale immediately craniad of the dorsal extension

Table 3. Measurements (mm) of ulnae of *Anhinga fraileyi*, *A. anhinga* (n = 4), and *A.* sp. cf. *A. grandis*.

Measurement	*Anhinga fraileyi* LACM 135361	*Anhinga anhinga*	*A. anhinga*[1]	*Anhinga* sp. cf. *A. grandis*[1]
Maximum distal width	11.1	10.1–10.9 x = 10.5	— x = 10.6	12.4
Depth condylus dorsalis ulnaris	8.9	7.8 x = 7.8	— x = 7.7	10.0
Shaft width proximal to condylus dorsalis ulnaris	6.7	6.3–6.8 x = 6.4	— x = 6.2	7.7
Shaft depth proximal to condylus dorsalis	6.7	4.7–5.1 x = 5.0	— x = 4.8	5.3

[1] Measurements from Rasmussen and Kay (1992); n = 8 for *Anhinga anhinga*.

Table 4. Measurements (mm) of the tibiotarsus referred to *Anhinga fraileyi* in comparison to those of *A. anhinga* (n = 4).

Measurements	*Anhinga anhinga*	*Anhinga fraileyi* LACM 135357
Total length	85.1–90.3 x = 87.0	143 ± 1.0
Total length to eminentia intercotylaris	81.7–85.5 x = 83.1	136.2 ± 0.5
Proximal width	9.5–11.2 x = 10.4	17.0 ± 1.0
Proximal depth	11.7–18.9 x = 13.9	20.5 ± 0.5
Midshaft width	4.6–5.8 x = 5.4	9.5
Midshaft depth	4.0–4.6 x = 4.3	7.2

of the facies articularis caudalis. A corresponding foramen is present in LACM 135359, but it is lacking in LACM 135358. Cv #19 also has facets for the articulation of a rib, as does the last cervical vertebra (#20) (Garrod, 1876), but cv #18 does not. Both of the fossil vertebrae lack articular facets for ribs.

In *Anhinga anhinga*, the facies articularis cranialis of cv #19 extends farther dorsad than it does in cv #18, to partially extend around the foramen vertebrale. In the former, there is also a small, but prominent, protuberance immediately dorsal to the tips of the facies articularis cranialis and caudal to the small notch. These features also occur in LACM 135359.

The two fossil vertebrae appear to agree with the 18th and 19th cervical vertebrae (LACM 135358 and LACM 135359, respectively) of *Anhinga anhinga* in the characters that are determinable from these well-worn specimens. One obvious difference, however, is the lack of articular facets for ribs on LACM 135359. Nonetheless, I am inclined to refer to LACM 135359 as a cv #19.

For measurements, see Table 5.

DISCUSSION

The two Old World Tertiary species of anhingas not mentioned in the descriptions above, *Anhinga pannonica* Lambrecht 1916 and *A. hadarensis* Brodkorb and Mourer-Chauviré 1982, may be distinguished from *A. fraileyi* on the basis of their smaller size. The only other purported Tertiary species of anhinga, *Protoplotus beauforti* Lambrecht 1931, is quite small and may not even be an anhinga (van Tets et al., 1989). The Tertiary species of anhingas were reviewed by Alvarenga (1995).

Measurements of the various fossil bones assigned to the several species of anhingas known from the Americas suggest that limb proportions among the fossil and living species were highly variable. For example, the proximal humerus of *Anhinga fraileyi* is approximately the same size as that assigned to *A. grandis* by Becker (1986), whereas the tarsometatarsus of the latter is only 70 per cent the length of the former. Similarly, the distal ulna referred to *A. fraileyi* is slightly smaller than that referred to *Anhinga* sp. cf. *A. grandis* by Rasmussen and Kay (1992) and only slightly larger than that of *A. anhinga*. *Anhinga chilensis* was described as a probably flightless anhinga because its referred ulna and carpometacarpus were smaller than those of *A. anhinga*, but the holotype tarsometatarsus was about 45 per cent larger than that of *A. anhinga* (Alvarenga, 1995).

If the wing : leg proportions of *Anhinga anhinga* are considered to be "normal" for anhingas, then *A. grandis* had larger than normal wings relative to its legs than the former. On the other hand, *A. chilensis* had very small wings relative to its legs, whereas the wings of *A. fraileyi* were smaller than normal relative to the size of its legs. It can be assumed that these differences among the fore- and hindlimbs had some significance in the overall functional attributes of these species, but more material is needed of each species before any conclusions pertaining to that subject can be drawn. It must also be noted that although *A. chilensis* is known from an associated skeleton, the wing elements of *A. grandis* and *A. fraileyi* are only referred to those species; they have yet to be found in association.

ASSOCIATED FAUNA. The paleofauna from the type locality for *Anhinga fraileyi*, LACM 4611, is the most diverse known from the Amazon Basin. It contains both a sizable megafauna (Frailey, 1986) and the first, and most diverse, vertebrate microfauna yet known from Amazonia. The most abundant fossils in terms of numbers of specimens are those of fish, with representatives of at least nine

Table 5. Measurements (mm) of cervical vertebrae of *Anhinga anhinga* (n = 3) and those referred to *A. fraileyi*.

	Anhinga anhinga		*Anhinga fraileyi*	
Measurement	Cervical Vertebra #18	Cervical Vertebra #19	LACM 135358	LACM 135359
Width of facies articularis cranialis	9.7–10.9 x = 10.2	9.3–10.5 x = 9.9	15.2	16.5
Length along midline from facies articularis cranialis to facies articularis caudalus	10.0–11.76 x = 10.6	10.2–11.9 x = 11.1	16.6	15.5

families included. Perhaps the most interesting within this group are sharks, rays, piranhas, and lungfish, the latter reaching sizes several times larger than those of modern lungfish of Amazonia.

The largest vertebrate from the site is the giant crocodylian *Purussaurus brasiliensis* Barbosa Rodrigues 1892 (Campbell and Frailey, 1992), which is represented at this site by several vertebrae and numerous isolated teeth. Other reptiles present include snakes, lizards, turtles, and other species of crocodylians. In addition to the variety of mammals described by Frailey (1986), dolphins, toxodonts, marsupials, primates (Kay and Frailey, 1992), a fish-eating bat (Czaplewski, 1996), and possibly as many as a dozen species of several genera of micro-rodents were found at this site.

The overwhelming majority of the vertebrate species present at LACM 4611 indicates an aquatic habitat, which is in keeping with the habitat of modern anhingas. The only certainly terrestrial vertebrates represented at the site are a few species of mammals. The habitat preferences of the micro-rodents are still unknown.

A similar but less diverse paleofauna is known from Cachuela Bandeira, Bolivia, the second locality (LACM 5158) producing bones of *Anhinga fraileyi.*

SUMMARY

A new species of anhinga, *Anhinga fraileyi,* whose hindlimb was approximately 65 per cent larger than the modern *A. anhinga,* is described from Upper Miocene (Huayquerian) deposits of Amazonian Peru. In addition to the holotype tarsometatarsus, three partial humeri, a distal ulna, a tibiotarsus, and a cv #18 and #19 are referred to the new species. The referred wing elements suggest that *A. fraileyi* had a smaller wing relative to its hindlimb than does *A. anhinga.* Limb proportions of other paleospecies of anhingas from the Americas also appear to be quite different from those of *A. anhinga.*

This is the third large paleospecies of anhinga to be described from the Miocene of South America, and still additional, undescribed species of anhingas are known from the Miocene of Argentina (Noriega, 1995). This is the first avian paleospecies to be described from the Tertiary of Amazonia.

ACKNOWLEDGMENTS

I thank F. Hertel for his critical comments on earlier drafts of this manuscript and for access to comparative materials at the University of California, Los Angeles; H. Alvarenga for access to and photographs of the specimens of *Anhinga chilensis*; N. Johnson for access to collections at the University of California, Berkeley, Museum of Comparative Zoology; and L. Martin and S. Olson for their critical reviews of the manuscript. I am grateful to J. Noriega, Museo de La Plata, Argentina, for providing a cast of the holotype of *A. paranensis.* Fieldwork in Amazonia was funded by NSF DEB 78-05861 and NSF BSR 84-20012 and accomplished, in part, in collaboration with the Universidade Federal do Acre, Brazil.

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Received 9 March 1995; accepted 5 December 1995.