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A NEW SPECIES OF OLIGO-MIOCENE DARTER (AVES: ANHINGIDAE) FROM AUSTRALIA

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ABSTRACT.—A single fossil tarsometatarsus from the Etadunna Formation, of Late Oligocene–Early Miocene age, at the Snake Dam Locality in South Australia reveals the first pre-Pliocene record of anHINGIDS in Australia. *Anhinga walterbolesi* sp. nov. provides the oldest record globally for the AnHINGIDAE and, with the contemporary presence of stem-group phalacrocoracids in the same formation, indicates a probable Early Oligocene to Eocene age for the common ancestor of anHINGIDS and phalacrocoracids. Received 15 September 2011, accepted 16 December 2011.

Key words: *Anhinga*, bird fossil, Oligo-Miocene, South Australia.

Una Nueva Especie de AnHINGIDAE del Oligo-Mioceno de Australia

RESUMEN.—Un único tarsometatarso fósil de la formación Etadunna, que data del Oligoceno tardío o Mioceno temprano de la localidad de Snake Dam en el sur de Australia revela el primer registro australiano de AnHINGIDAE anterior al Plioceno. *Anhinga walterbolesi* sp. nov. representa el registro más antiguo para toda la familia AnHINGIDAE. Aunado a la presencia contemporánea de el grupo basal (“stem group”) de los Phalacrocoracidae en la misma formación, este registro indica que el origen probable para el ancestro común de los AnHINGIDAE y los Phalacrocoracidae data de entre el Oligoceno temprano y el Eoceno.

DARTERS (ANHINGIDAE) ARE specialist diving piscivores that live mainly in tropical freshwater habitats (Johnsgard 1993). These highly distinctive birds, also known as “snakebirds” for their elongate sinuous necks, have a narrow skull with an elongate pointed bill used for spearing fish. AnHINGIDS and cormorants (Phalacrocoracidae), also specialist fish-eaters, are sister taxa (Pycraft 1898, Owre 1967, Siegel-Causey 1988, Ericson et al. 2006, Livezey and Zusi 2007, Hackett et al. 2008, Smith 2010) and together comprise Phalacrocoracoidea.

Two species of living darters are generally recognized (del Hoyo et al. 1992, Johnsgard 1993, Dickinson 2003): *Anhinga anhinga* from the New World and *A. melanogaster* in Africa, India–Southeast Asia, and Australia. *Anhinga melanogaster* comprises three or four subspecies: *A. m. melanogaster* (India to Southeast Asia, Sumatra, Java, Borneo, Philippines, and Sulawesi), *A. m. rufa* (Africa and Middle East), *A. m. novaehollandiae* (New Guinea and Australia), and sometimes *A. m. vulsini* (Madagascar) (e.g., Marchant and Higgins 1990, del Hoyo et al. 1992, Christidis and Boles 1994, Dickinson 2003). More recently, Christidis and Boles (2008), on the basis of genetic divergence, advocated that *A. m. melanogaster*, *A. m. rufa*, and *A. m. novaehollandiae* should all be ranked as full species. However, from an osteological perspective, Harrison (1978) noted that all subspecies of *A. melanogaster* had a similar tarsometatarsus morphology, which differed from that of *A. anhinga* in key features of the hypotarsus and proximal

cotylae. Harrison’s observations suggest that just two species can be recognized on tarsometatarsus morphology alone—*A. anhinga* and *A. melanogaster*—and because the fossil studied herein is a tarsometatarsus, this taxonomic arrangement is used here.

The global fossil history of darters was reviewed most recently by Mackness (1995) and Alvarenga (1995). More recent additions to the anHINGID fossil record include several fossils from the Old World that have been referred to *A. pannonica* (Lambrecht 1916), a Miocene–Pliocene species slightly larger than *A. melanogaster*, for example from Africa (Dyke and Walker 2008, Louchart et al. 2008) and Germany (Dalsätt et al. 2006); a third fossil taxon from the Pleistocene of North America (Emslie 1998); and a diverse fauna of minimally seven species in four genera from Oligocene and Miocene deposits of South America (Noriega 1992, 1995, 2002; Rasmussen and Kay 1992; Alvarenga 1995; Campbell 1996; Noriega and Alvarenga 2002; Rinderknecht and Noriega 2002; Alvarenga and Guilherme 2003; Noriega and Piña 2004; Noriega and Agnolín 2008; Cenizo and Agnolín 2010).

The fossil history of darters in Australia is confined to the Pliocene and Quaternary. Miller (1966) and Mackness and van Tets (1995) reviewed previous records of Australian fossil darters and found that most Pleistocene specimens were the extant *A. melanogaster novaehollandiae*. Miller (1966) accepted as valid a second larger species, *A. laticeps* (De Vis 1905), that is represented

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by a unique cranium from Pleistocene deposits in Cooper Creek, South Australia. This taxon was described as *Plotus laticeps* by De Vis (1905), a paper published on 30 September 1905 (fidé images of the cards in the Richmond Index, Bird Division, National Museum of Natural History, Washington, D.C., accessed 15 August 2011 via www.zoonomen.net and confirmed by the accession date on the Australian Museum library copy), not 1906 as has been frequently cited (Miller 1966, Mackness 1995, Mackness and van Tets 1995). However, the holotype cranium of *Plotus laticeps* was noted to differ insufficiently from those in a larger sample of *A. novaehollandiae* than that used by Miller (1966), and *P. laticeps* was synonymized with *A. novaehollandiae* by Mackness and van Tets (1995). The third and smallest fossil species from Australia, *A. malagurala*, was described from a carpometacarpus by Mackness (1995) from the Early Pliocene Bluff Downs Local Fauna of Queensland.

A Late Oligocene–Early Miocene record for Phalacrocoracidae has recently been reported from Australia with the description of *Nambashag* and two included species (Worthy 2011). Until now, there has been no indication of anHINGIDS having been contemporary with these phalacrocoracids in the early Neogene of Australia. The identification of an anHINGID of this age from Australia is significant not only because it considerably extends the record of AnHINGIDAE in Australia, but because it is the oldest record for the family globally. The fossil, a single tarsometatarsus, derives from Etadunna deposits at the Snake Dam locality on Muloorina Station, southeast of Lake Eyre, South Australia (Fig. 1). This site is known for a very thick fragment of eggshell referred to Dromornithidae (Williams and Vickers-Rich 1992) and an anatid tarsometatarsus referred to *Pinpanetta tedfordi* by Worthy (2009).

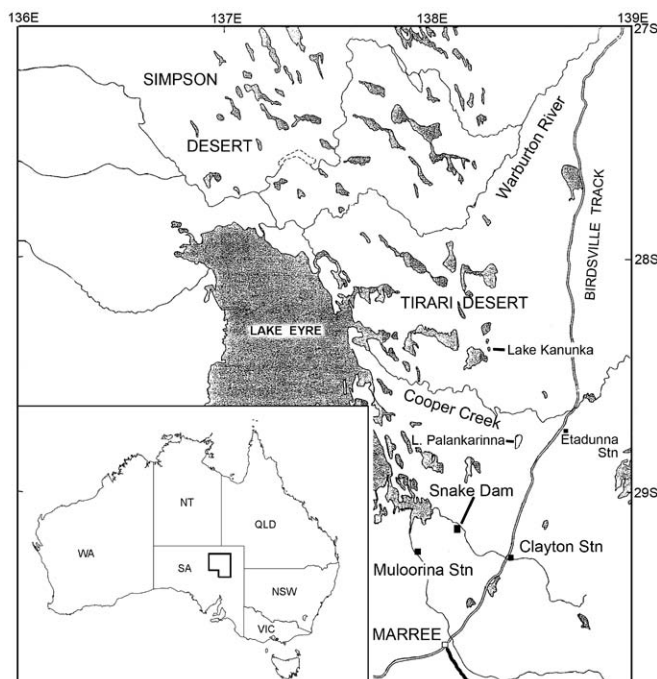


FIG. 1. Location of the Snake Dam fossil site in South Australia.

METHODS

Abbreviations.—Institutions: AM = Australian Museum, Sydney, New South Wales, Australia; MV = Museum Victoria, Melbourne, Victoria, Australia; and KUNHM = University of Kansas Natural History Museum and Biodiversity Research Center, Lawrence.

Anatomical nomenclature.—Names for specific bone landmarks generally follow Baumel and Witmer (1993). Some common terms are abbreviated: char. = character; m. = musculus.

Comparative material.—The following modern specimens were examined: *A. melanogaster novaehollandiae*, AM S.291, S.1258, O.62367, O.65075, O.65076, O.65077, O.65078; *A. anHINGA*, KUNHM 30244, 37543; *Microcarbo melanoleucos*, AM O.4704; *Pelecanus conspicillatus*, AM O.57540, 71383; *Fregata minor*, MV B.24450; *Morus serrator*, AM O.65332, O.56723; *Sula leucogaster*, AM O.57509.

SYSTEMATIC PALEONTOLOGY

Pelecaniformes Sharpe, 1891

AnHINGIDAE Lesson, 1831

AnHINGA Brisson, 1760

The fossil is referred to AnHINGIDAE and *AnHINGA* in particular, rather than other “pelecaniform” families (Pelecanidae, Fregatidae, Sulidae, and Phalacrocoracidae), by the following unique combination of characters: (1) short, broad tarsometatarsus (interpreted here as an apomorphy of anHINGIDS within Phalacrocoracoidea, but convergent in sulids and *Fregata*); (2) the crista medialis hypotarsi is the largest hypotarsal ridge (plesiomorphic for pelecaniforms); (3) the tendinal canals for m. flexor digitorum longus (fdl) and m. flexor hallucis longus (fhl) have subequal diameter with fdl only slightly plantar of fhl (autapomorphy of anHINGIDS); (4) the sulcus for the tendon of m. fibularis [peronei] longus, seen in proximal aspect, opens laterally (plesiomorphic for pelecaniforms); (5) the dorsoplantar depth of the proximal end is subequal to its width (plesiomorphic for pelecaniforms); (6) the crista medialis hypotarsi has a flattened plantar facet that is not hooked distally relative to the crista medianoplantaris (plesiomorphic for pelecaniforms); (7) the groove for the tendon of m. extensor hallucis longus is broader than shaft width and creates a distinct broad notch in the medial profile defined by ridges along its proximal and distal margins where it crosses the dorsomedial shaft margin (apomorphy of Phalacrocoracoidea); (8) a deep, elongate sulcus for m. abductor digiti IV extends down length of shaft bordered dorsally by a crista plantaris lateralis that is narrowly separated from the dorsal facies and parallel to that facies over its length (apomorphy of Phalacrocoracoidea); (9) the dorsal surface of trochlea metatarsi IV adjacent to the most proximal extent of the incisura intertrochlearis lateralis is wider than the length of this trochlea distal to the notch (plesiomorphic for pelecaniforms); (10) trochlea metatarsi IV is in line with the shaft axis, not splayed laterally (plesiomorphic for pelecaniforms); and (11) the foramen vasculare distale is very small or closed plantarily with the major exit in the incisura intertrochlearis lateralis (apomorphy of anHINGIDS within Phalacrocoracoidea).

Compared to those of anHINGIDS, the tarsometatarsus of *Pelecanus* is more elongate; the shaft is deeper than wide; there is

no sulcus for m. abductor digiti IV; the trace for m. extensor hallucis longus is shallow and does not create a notch in the medial profile; and the foramen distale is large. Sulids differ from anHINGIDS in having a very shallow sulcus for m. abductor digiti IV, a shallow trace for m. extensor hallucis longus that does not create a notch in the medial profile, and the canal for fdl has a much larger diameter than that for fhl. In *Sula*, but not *Morus*, the trochlea metatarsi IV is longer than it is wide at the most proximal extent of the incisura intertrochlearis lateralis. *Fregata* differ from anHINGIDS with very reduced tarsometatarsi with trochlea metatarsi IV splayed laterally, no trace for m. extensor hallucis longus, no sulcus for m. abductor digiti IV, and a single canal carries the tendons of fhl, fdl, musculi flexores perforati digitorum III et IV (pIII–IV) and m. flexor perforans et perforatus digiti III (ppIII).

Two tarsometatarsal characters have been identified as apomorphies of Phalacrocoracoidea (anHINGIDS and phalacrocoracids) by Mayr (2009). First is the presence of a marked sulcus for m. abductor digiti IV (char. 8 above). Second is a well-marked trace for m. extensor hallucis longus where it crosses the dorsomedial margin to the medial facies, which is better defined in anHINGIDS and phalacrocoracids than in *Pelecanus* and sulids, being marked by a shallow notch that is bound by ridges proximally and distally (this overlaps with 7 above). The apomorphy in each case is the well-marked nature of the groove or sulcus, rather than its presence or absence. The relative width of the trace for m. extensor hallucis longus is plesiomorphically broad in pelecenids, sulids, anHINGIDS, and the stem-phalacrocoracid *Nambashag*, whereas crown-group phalacrocoracids have a relatively narrow groove (Worthy 2011), but only in anHINGIDS and phalacrocoracids is it well marked. Although apomorphies of Phalacrocoracoidea would not be expected to distinguish anHINGIDS from phalacrocoracids, there is variation in the extent and shape of the sulcus for m. abductor digiti IV among cormorants: it is similarly deep and broad in *Microcarbo* and *Anhinga*, but phalacrocoracids that are sister to *Microcarbo* have the sulcus markedly shallower at midlength than at either end.

Tarsometatarsi of anHINGIDS are distinguished from those of phalacrocoracids apart from being relatively shorter and broader by several features: (1) the proximal end has a dorsoplantar depth less than or subequal to proximal width (char. 99, Worthy 2011); (2) the sulcus for the tendon of m. fibularis [peronei] longus (see Mitchell 1913) opens laterally in anHINGIDS, but in phalacrocoracids it opens plantarly and is bound laterally by a larger tuberculum m. fibularis [peronei] brevis that forms a plantar projection from the cotyla lateralis. The relatively small tuberculum and lateral opening of the sulcus in *Fregata*, *Pelecanus*, and sulids (e.g., *Morus* and *Sula*) suggest that this is the plesiomorphic condition and that a plantar opening thus is an apomorphy for phalacrocoracids; (3) a short trochlea metatarsi IV such that its dorsal surface adjacent to the most proximal extent of the incisura intertrochlearis lateralis is wider than its length distal to the notch, whereas in phalacrocoracids its width is less than or equal to its length (char. 110, Worthy 2011); and (4) the foramen vasculare distale is very small or closed plantarly with the major exit in the incisura intertrochlearis lateralis, whereas the plantar opening is large in phalacrocoracids (char. 111, Worthy 2011). This last character is homoplasious, occurring in the highly reduced tarsometatarsi of *Fregata*.

Anhinga walterbolesi, sp. nov.

Holotype.—MV P166373, left tarsometatarsus (Fig. 2A–E, H).

Diagnosis.—An *Anhinga* species distinguished by the following combination of features: the tendinal canal for m. flexor digitorum longus (fdl) is open to the canal for the tendons for m. flexor perforatus digiti II and m. flexor perforans et perforatus digiti II (pII–ppII), with the conjoined canal broadly open laterally (autapomorphy); the crista medialis hypotarsi is very robust, being lateromedially wider than fdl adjacent to that canal; the plane of the plantar facet on the crista medialis hypotarsi diverges distally from the shaft at about 30 degrees; the fossa parahypotarsalis medialis is shallow; the tuberositas m. tibialis cranialis comprises a larger elongate medial scar distinctly separated from a conical lateral tuberosity; and the impressio ligamentum collateralis lateralis, which lies distad of and slightly dorsad of the tuberculum m. fibularis brevis, protrudes farther laterally than the cotyla lateralis and the tuberculum m. fibularis brevis and so is visible in proximal aspect.

Etymology.—After Walter Boles, Australian Museum, Sydney, for his many contributions to the paleo-ornithology of Australia.

Type locality.—Snake Dam, Clayton River, southeast of Lake Eyre, Muloorina Station, South Australia, Australia (Fig. 1); MARREE Sheet (1:250,000), 138°06'E, 29°7.5'S, collected by T. Rich 23.6.1982; field code THR 1982-301. The specimen was collected from the base of a slope on the west side of the north end of a low ridge formed of Etadunna Formation, at a point ~1 km from Snake Dam on a bearing of 15 degrees (true north) (Tom Rich field notes for 23 June 1982; Museum Victoria files).

Stratigraphy-age.—Etadunna Formation, Late Oligocene 24–26 Ma (million years), (Woodburne et al. 1994). The presence of *Pinpanetta tedfordi* in the Snake Dam fauna supports the referral of the deposits at Snake Dam to the Etadunna Formation, because this duck is a common element in faunas from the Etadunna at Lake Palankarina, Lake Eyre Basin, and its lateral equivalent Namba Formation at Lake Pinpa in the Frome Basin (Worthy 2009).

Measurements of holotype.—Maximum length 52.2 mm, proximal width 14.6 mm, proximal depth from the dorsal margin of the cotylae (not eminentia intercotylaris) to the plantar surface of the hypotarsus 15.9 mm, shaft width at the distal margin of the groove for m. extensor hallucis longus 9.5 mm, least shaft width (SW1) in middle of groove for m. extensor hallucis longus 8.9 mm, shaft depth at SW1 6.0 mm, maximum distal width 18.1 mm, width trochlea metatarsi III 6.3 mm, depth trochlea metatarsi III 7.8 mm.

Description and comparison with extant anHINGIDS.—The fossil MV P.166373 is a complete left tarsometatarsus, light tan in color, with some small patches of dendritic black manganese oxide deposits (Fig. 2A–E, H). Its surface is slightly weathered and cracked but is unworn, with only minor breakage restricted to a part of the distal margin of the crista medianoplantaris and a small part of the medial margin of the facet on the crista medialis hypotarsi. Importantly, the cristae hypotarsi that define the hypotarsal canals are undamaged.

In addition to the generic characters and those used to diagnose the species, the fossil exhibits the following features. The

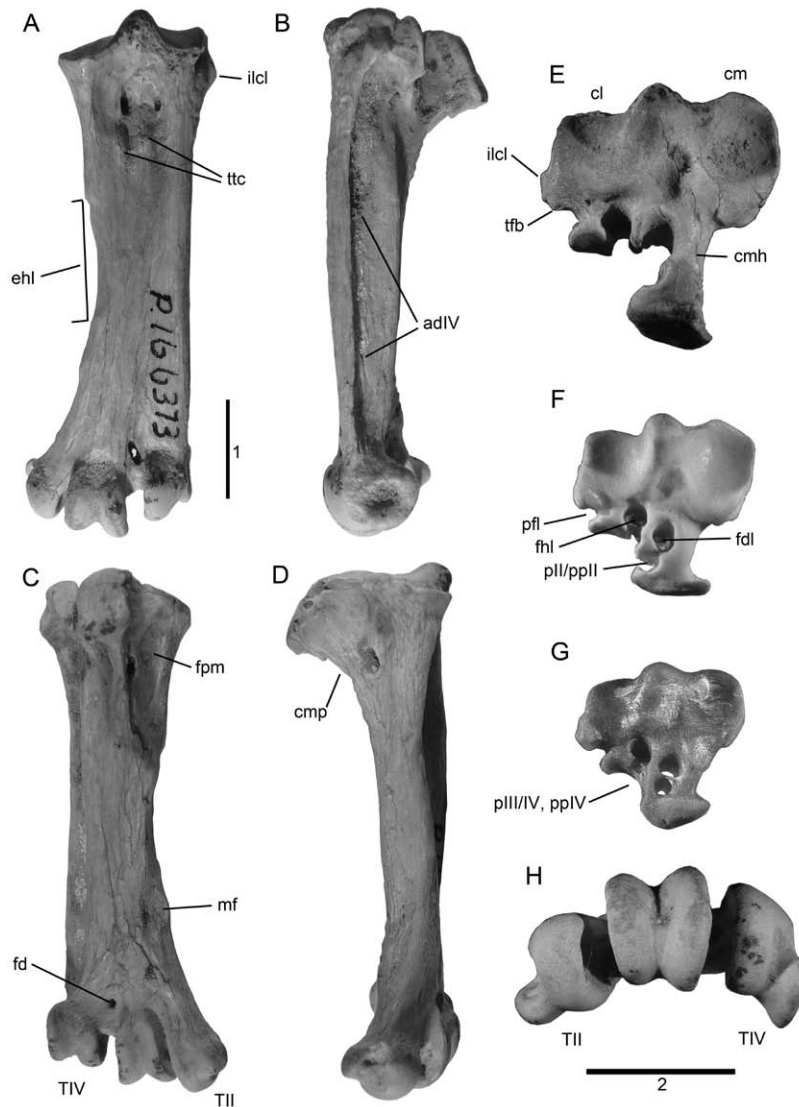


FIG. 2. *Anhinga* tarsometatarsi: (A–E, H) *A. waltherbolesi* and *A. melanogaster novaehollandiae*; (F) AM S.291; *A. anhinga* (G) KUNHM 37543, in (A) dorsal, (B) lateral, (C) plantar, (D) medial, (E–G) proximal, and (H) distal views. The appearance of plantar closure of fhl in G is due to the presence of dried ligament. Abbreviations: adIV = sulcus for m. abductor digiti IV; cl = cotyla lateralis; cm = cotyla medialis; cmh = crista medialis hypotarsi; cmp = crista medianoplantaris; ehl = groove for the tendon of m. extensor hallucis longus; fd = foramen vasculare distale; fdl = tendinal canal for m. flexor digitorum longus; fhl = tendinal canal for m. flexor hallucis longus; fpm = fossa parahypotarsalis medialis; ilcl = impressio ligamentum collateralis lateralis; mf = fossa metatarsi I; pfl = sulcus for the tendon of m. fibularis longus; pII–ppII = canal for tendons for m. flexor perforatus digiti II and m. flexor perforans et perforatus digiti II; pIII–IV, ppIII = sulcus for tendons of m. flexores perforati digitorum III and IV and m. flexor perforans et perforatus digiti III; tfb = tuberculum m. fibularis brevis; ttc = tuberositas m. tibialis cranialis; TIV = trochlea metatarsi IV; TII = trochlea metatarsi II. Scale bars = 10 mm: bar 1 for A–D, bar 2 for E–H.

canal for fhl is only slightly offset dorsally to that for fdl (Fig. 2E), which is associated with the dorsoplantar depth of the cotyla lateralis being more similar to that of the cotyla medialis, rather than markedly less, as in *A. melanogaster*. The fossa parahypotarsalis medialis is shallow (Fig. 2C), more so than in the compared extant anHINGIDS, yet is better defined by a ridge both proximally and dorsally. The sulcus for m. abductor digiti IV is deeply excavated dorsally adjacent to the crista plantaris lateralis over its entire length with a pronounced plantar border over most of its

length (Fig. 2B). It is more deeply excavated in its proximal half than in extant anHINGIDS. The fossa infracotyloidea dorsalis contains small pneumatic foramina, fewer and smaller than in *A. melanogaster*, but in contrast to *A. anhinga*, in which there are none. The foramina vascularia proximalia are well separated from one another but centrally located in the sulcus extensorius level with each other. The foramen vasculare proximale laterale is about half the size of the medial foramen (Fig. 2A), as in *A. melanogaster*: in *A. anhinga*, the lateral foramen is considerably smaller than the

medial one (KUNHM 30244) or absent (KUNHM 37543). On the dorsal facies, the trace of the tendon of *m. extensor hallucis longus* passes over the medial margin distinctly distad of the *tuberositas m. tibialis cranialis* (Fig. 2A), as in *A. melanogaster*, but unlike *A. anHINGA*, in which the tendon passes over the medial margin adjacent to the *tuberositas m. tibialis cranialis* and immediately distad of the *impressiones retinaculi extensorii* (Harrison 1978).

The *tuberositas m. tibialis cranialis* comprises two separate tuberosities—a smaller, conical, more lateral one centered on the shaft, and a larger but lower medial rugosity lapping up the medial side of the *sulcus extensorius* (Fig. 2A). Both *A. melanogaster* and *A. anHINGA* have only a single tuberosity that lies partly on the floor of the *sulcus extensorius* and partly laps up the medial wall of the *sulcus*. The presence of two tuberosities may be plesiomorphic as this condition is seen in *Pelecanus*, although the lateral tuberosity is not conical, and in *Sula* where the medial tuberosity is smaller than the lateral one. *Morus*, however, has only one large, centrally placed tuberosity. The floor of the *sulcus* between the *impressiones retinaculi extensorii* faces dorsolaterally, as in *A. melanogaster*, but unlike the more dorsally oriented state in *A. anHINGA*.

The *crista lateralis hypotarsi* is ~2.0 mm high (dorsoplantarily), ~1.0 mm thick at minimum, bounds the *fhl* laterally and the *sulcus* for the tendon for *m. fibularis longus* medially, and expands plantarily to a flattened *crista* ~2.8 mm wide (Fig. 2E). Its least width is therefore thinner than the width of the adjacent canal for *fhl* (2.0 mm). The least width of the *crista lateralis hypotarsi* is broader than the width of *fhl* in phalacrocoracids and much broader in sulids. Among anHINGIDS, the width of this *crista* is similar to that of *fhl* in *A. melanogaster*, but it varies in *A. anHINGA*, being either narrower (KUNHM 30244) or wider (KUNHM 37543) and thus perhaps of no phylogenetic significance. The *fossa metatarsi I* spans most of the dorsoplantar depth of the shaft and is ~7.5 mm long (Fig. 2C). The proximomedial corner of *trochlea metatarsi IV*, adjacent to the *incisura intertrochlearis lateralis* rises dorsally adjacent to the *incisura*, whereas in both *A. melanogaster* and *A. anHINGA* it forms a flange overhanging the *incisura* that is partly undercut proximally by a groove leading to the *incisura*. The extant *A. melanogaster* and *A. anHINGA* are further distinguished from *A. walterbolesi* by their considerably smaller size and their relatively narrower shaft and distal widths (Table 1).

Comparisons with fossil anHINGIDS.—*AnHINGA walterbolesi* is not directly comparable with the Early Pliocene *A. malagurala*, the only valid fossil darter from Australia, because that species is only known from a *carpometacarpus* (Mackness 1995). However, although the holotype is markedly smaller, it is otherwise very similar to *carpometacarpi* of *A. m. novaehollandiae* and differs in several undescribed details from those of *A. anHINGA* (state in parentheses) as follows: *processus extensorius* relatively longer and not so hooked proximally; *fossa* between *processus pisiiformis* and *processus extensorius* deep with steep abrupt cranial edge (cranial margin of *fossa* with gentle slope); *fovea carpalis cranialis* very small or absent (large, intrudes into *trochlea carpalis* between dorsal and ventral rims); *os metacarpale minus* distinctly grooved at proximal *synostosis* (very shallow groove or not grooved), and broader proximally such that the dorsal margin is near level with the dorsal margin of *os metacarpale majus* and partially occludes in caudal view the rugosity for the insertion of *m. extensor carpalis ulnaris* (= for insertion of *m. flexor metacarpi radialis*; Owre 1967) that lies just distad of the *synostosis* on the dorsocaudal edge of *os metacarpale majus* (narrower, such that dorsal margin is distinctly offset ventrally of the edge of the *os metacarpale majus* and the insertion for *m. extensor carpalis ulnaris*); and the cranial facies of the distal end of the *os metacarpale majus* has a distinct *sulcus* that extends proximal of the *synostosis* (*sulcus* lacking). These observations suggest that *A. malagurala* is probably best interpreted as a precursor of *A. m. novaehollandiae* and, given its smaller size, markedly younger age, and multiple differences between *tarsometatarsi* of *A. walterbolesi* and *A. melanogaster*, preclude its conspecificity with *A. walterbolesi*.

AnHINGA walterbolesi is markedly older than the two known Old World fossil darters. *AnHINGA pannonica* (Lambrecht 1916) is a poorly defined species based on a sixth cervical vertebra and a referred *carpometacarpus* 5–20% larger than those of *A. melanogaster* (see Louchart et al. 2008) and derives from the Late Miocene of Romania (= Hungary). Other anHINGID fossils from Germany (Middle Miocene), Austria (Late Miocene), Tunisia (Late Miocene), Kenya (Middle Miocene, 12–10.5 Ma), Chad (Late Miocene, ca. 7 Ma), Pakistan (Late Miocene), Libya (Mio-Pliocene) and Thailand (upper Early Miocene), have been referred to *A. pannonica* mainly on the basis of size (Cheneval et al. 1991, Mlíkovský 1991, Mackness 1995, Dalsätt et al. 2006, Dyke and Walker 2008,

TABLE 1. Measurements (mm) and ratios of *tarsometatarsi* of *AnHINGA* species (PW = proximal width, PD = proximal depth, SW = shaft width, and DW = distal width).

Taxon	Catalogue number	Maximum length	PW	PD	SW	DW	PW/L	SW/L	DW/L	SW/DW
<i>A. melanogaster</i>	AM O.291	47.5	12	12.3	7.4	15.8	25.26	15.58	33.26	46.84
<i>A. melanogaster</i>	AM O.1258	42.6	11.2	11.9	6.3	14.9	26.29	14.79	34.98	42.28
<i>A. melanogaster</i>	AM O.62367	49.5	12.3	12.5	7.8	16.3	24.85	15.76	32.93	47.85
<i>A. melanogaster</i>	AM O.65075	48.7	12.8	13.3	7.7	17.4	26.28	15.81	35.73	44.25
<i>A. melanogaster</i>	AM O.65076	46.7	12.4	12.6	7.4	15.6	26.55	15.85	33.40	47.44
<i>A. melanogaster</i>	AM O.65077	48.5	12.5	12.7	7.4	16.5	25.77	15.26	34.02	44.85
<i>A. melanogaster</i>	AM O.65078	47	12.8	12.7	7.6	15.8	27.23	16.17	33.62	48.10
<i>A. anHINGA</i>	KUNHM.37543	39.2	11.8	10.7	6.9	14.6	30.10	17.60	37.24	47.26
<i>A. anHINGA</i>	KUNHM.30244	39.1	11	10.6	6.7	13.7	28.13	17.14	35.04	48.91
<i>A. walterbolesi</i>	MV P.166373	52.2	14.6	15.9	9.5	18.1	27.97	18.20	34.67	52.49

Louchart et al. 2008). It is improbable that the Late Oligocene Australian fossil could be conspecific with *A. pannonica* because of the age disparity of more than 15 Ma. Also, *A. pannonica* and the specimens referred to it, including a tarsometatarsus, are said to be morphologically very similar to *A. melanogaster* (e.g., Cheneval et al. 1991, Louchart et al. 2008). Significantly, examination of Cheneval et al. (1991: fig. 2) reveals that the Thai fossil tarsometatarsus differs from *A. walterbolesi* in its deeper fossa parahypotarsalis medialis, more rounded medial profile immediately distal to the cotyla medialis (in dorsal view), and less prominent impressio ligamentum collateralis lateralis. Because *A. walterbolesi* varies greatly from *A. melanogaster* in these features of the tarsometatarsus, and also in hypotarsal morphology and the form of the tuberositas m. tibialis cranialis, similar morphological divergence might be expected in other elements as well. This combination of age disparity and morphological differences (where comparable) suggests that *A. walterbolesi* cannot be conspecific with *A. pannonica* nor with most of the specimens referred to this Old World taxon. The only other valid Old World fossil darter is *A. hadarensis* Brodkorb and Mourer-Chauviré, 1982, from the Plio-Pleistocene of East Africa, which is smaller than *A. melanogaster* (fidé Cheneval et al. 1991, Louchart et al. 2008) and, thus, much smaller than *A. walterbolesi*.

Anhinga walterbolesi is likewise older than any of the three described fossil anhingids from the North America. It is 6–8 Ma older than *A. subvolans* (Brodkorb 1956), which is known only from the holotype proximal humerus from Early Miocene (~18 Ma) deposits in Florida (Becker 1986) and is about the size of *A. m. novaehollandiae*, but otherwise is incomparable to the Australian fossil. Conspecificity of *A. walterbolesi* and *A. subvolans* is unlikely, given their distant geographic provenances. *Anhinga grandis* Martin and Mengel, 1975, recorded from several Late Miocene localities in North America, is of similar size to *A. m. novaehollandiae*, with a tarsometatarsus 47.8 mm long, but is similar to *A. anhinga* and differs from *A. walterbolesi*, with enclosed hypotarsal canals for fdl and pII–ppII (Becker 1987). The Early Pleistocene (1.5–1.0 Ma) age of *Anhinga beckeri* Emslie, 1998, from Florida, and its size and proportions—it has a shorter more robust tibiotarsus than *A. anhinga* yet longer, more robust, wing elements (Emslie 1998)—precludes a conspecific relationship with *A. walterbolesi*.

Of the seven species of fossil anhingids described from South America, six are readily distinguished from *A. walterbolesi* by their much larger size and different osteology, as follows: *Macranhinga paranensis* Noriega, 1992, Late Miocene age from Argentina, length of tarsometatarsus 75.5 mm, has the canals for the tendons fdl and pII–ppII conjoined and the crista hypotarsalis lateralis relatively broad (Noriega and Alvarenga 2002); *M. ranzii*, Late Miocene from Brazil, was 20–25% larger than *M. paranensis* (Alvarenga and Guilherme 2003); *Meganhinga chilensis* Alvarenga, 1995, late Early Miocene (17.5–13.0 Ma) age from Chile, length of tarsometatarsus 61.0 mm, has a more projecting crista hypotarsi medialis with the plantar facet aligned subparallel to the shaft, a relatively broad crista hypotarsalis lateralis, and separate wholly enclosed canals for the tendons of fdl and pII–ppII as in *A. anhinga* (Alvarenga 1995, Noriega 1995); *A. fraileyi* Campbell, 1996, Late Miocene from Peru, length of tarsometatarsus 68.5 mm, has a concave lateral profile due to the

trochlea metatarsi IV being slightly divergent from the lateral shaft margin; and *Giganhinga kiyuensis*, known only from a partial pelvis of Pliocene–Pleistocene age from deposits in Uruguay (Rinderknecht and Noriega 2002). A partial femur representing a darter larger than any other known to date and of Late Miocene age (about 11–7 Ma) was tentatively referred to *Giganhinga* by Areta et al. (2007). *Anhinga minuta*, from the Late Miocene of Brazil, is smaller than all known darters (Alvarenga and Guilherme 2003). Finally, *A. walterbolesi* differs markedly from *Protoplotus beauforti* Lambrecht, 1931, of Eocene age from Sumatra, which was described as a darter but is now attributed to its own pelecianiform family Protoplotidae (Lambrecht 1931, van Tets et al. 1989). Specifically, on the tarsometatarsus of *Protoplotus* the eminentia intercotylaris is lower, trochlea metatarsi IV is splayed laterally from the shaft and is elongate, and trochlea metatarsi II lacks a prominent plantar–medial flange.

DISCUSSION

The fossil *A. walterbolesi* and various stem-group phalacrocoracids reveal that several features that characterize extant anhingids and phalacrocoracids do not distinguish stem-group taxa of either lineage and therefore are not of familial significance, but rather pertain only to less inclusive clades. For example, several features of anhingids are also observed in stem-group phalacrocoracids (e.g., *Nambashag* and *Nectornis*), which indicates that only crown-group phalacrocoracids have the derived condition (Worthy 2011): (1) on the hypotarsus, the tendinal canal for fhl is partly enclosed plantarly, whereas it is more broadly open plantarly in phalacrocoracids, with the exceptions of *Nambashag* and *Leucocarbo chalconotus* (char. 97, Worthy 2011); (2) the eminentia intercotylaris in lateral aspect extends distinctly proximad of the lateral margin of the cotyla lateralis, whereas in phalacrocoracids, except *Nectornis*, it does not (char. 100, Worthy 2011); and (3) the width of the groove for the m. extensor hallucis longus where it crosses the dorsomedial shaft margin to the medial facies, as measured proximodistally parallel to the shaft in medial aspect, is greater than the shaft width, whereas in phalacrocoracids except *Nambashag*, its width is less than or equal to shaft width (char. 101, Worthy 2011), although in some *Microcarbo melanoleucos* specimens (e.g., AM O.4704) it is wider. The observed states for these characters in anhingids, including *A. walterbolesi*, are therefore plesiomorphic and the derived conditions do not characterize all phalacrocoracids.

Some other character states are shared by tarsometatarsi of *A. walterbolesi*, extant *Anhinga* species, stem-group phalacrocoracids (*Nectornis* and *Nambashag*), and *Microcarbo* as follows, to the exclusion of remaining crown-group phalacrocoracids: (4) the lateral shaft margin in dorsal view distad of the foramina vascularia proximalia is planar, except in some *Microcarbo melanoleucos* (e.g., AM O.4704) but is concave in other phalacrocoracids (char. 105, Worthy 2011); (5) in lateral view, the crista plantaris lateralis lies close to the dorsal surface bounding a broad sulcus for musculus abductor digiti IV down the length of the shaft, unlike remaining phalacrocoracids, where the crista is widely separated from the dorsal margin at mid length and is plantarly concave, so that the sulcus has dorsoplantarly deeper sections proximally and distally (char. 106, Worthy 2011); and (6) the trochlea metatarsi II

surpasses or is subequal distally with trochlea metatarsi III, rather than being shorter (char. 108, Worthy 2011). The derived state for characters 4–6 defines phalacrocoracids to the exclusion of *Microrocarro*; therefore, as in characters 1–3, the condition in anhingids is plesiomorphic and not restricted to the family.

Extant anhingids are further distinguished from phalacrocoracids by the canal for the tendons of m. flexor perforatus digiti II and m. flexor perforans et perforatus digiti II (pII–ppII) that lies immediately laterad of the large robust crista medialis plantaris being enclosed (*A. anhinga*) or near enclosed (*A. melanogaster*), but broadly open laterally in phalacrocoracids (char. 98, Worthy 2011). The condition in the new species described here appears to be more plesiomorphic than seen in extant anhingids, with both the tendinal canals for fdl and pII–ppII open laterally. A series from *A. waltherbolesi* to *A. melanogaster* to *A. anhinga* demonstrates progressive ossification of these canals, with first that for fdl becoming completely enclosed, then that for pII–ppII entirely enclosed in bone in the New World anhingids. These observations show that no single feature characterizes tarsometatarsi of *Anhinga*, and this justifies the use of a combination of characters in the generic attribution. They further demonstrate that fossil taxa have important roles in inferring relationships of extant taxa.

Anhinga waltherbolesi of Late Oligocene 24–26 Ma age is significant as the oldest fossil anhingid globally. It is minimally 6 Ma older than the next youngest species, *A. subvolans* from the Early Miocene ~18 Ma (Brodkorb 1956). Globally, the largest radiation of fossil anhingids (seven species) is derived from South America, indicating significant Miocene proliferation of the genus in the Americas. However, the earlier presence of *Anhinga* in Australia indicates a broader Southern Hemisphere distribution of the genus in the early Neogene and adds to the likelihood of a southern origin for the group.

The discovery of a fossil darter in the Etadunna Formation adds significantly to the waterbird diversity of the Late Oligocene–Early Miocene faunas of the Eyre Basin, South Australia. A diverse assemblage of waterbirds such as phoenicopteriforms, anseriforms, and pelecyaniforms, including *Pelecanus* and phalacrocoracids, is already known from these deposits (Vickers-Rich 1991; Boles 2006; Worthy 2009, 2011). The addition of *A. waltherbolesi* to this fauna adds another fish predator to this assemblage and attests to the productivity of this former lacustrine system.

The contemporary occurrence of *Anhinga* and the stem phalacrocoracid *Nambashag* (Phalacrocoracidae) in the Late Oligocene Etadunna Formation indicates that the common ancestor of Phalacrocoracoidea must have occurred considerably earlier, minimally in the Late Oligocene, but more likely well before, in the Early Oligocene or Eocene. The single fossil of *Protoplotus beauforti* from the Eocene of Sumatra presents a mosaic of pelecyaniform features (van Tets et al. 1989) and potentially may represent such an ancestor. However, further study of this specimen, but more likely additional fossils, will be needed to resolve this relationship. In the interim, a pre-Oligocene origin for these families appears likely.

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