REIDENTIFICATION OF *"PHALACROCORAX"* *SUBVOLANS* BRODKORB AS THE EARLIEST RECORD OF ANHINGIDAE

JONATHAN J. BECKER[1]

Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

ABSTRACT.—The putative cormorant *Phalacrocorax subvolans* Brodkorb 1956, from the early Miocene of Florida, is moved from the Phalacrocoracidae to the Anhingidae and should be known as *Anhinga subvolans* (Brodkorb 1956). This species is the earliest known anhinga and demonstrates that the family Anhingidae has been present in North America for at least 18 million years. It has been at least 30 million years since the Anhingidae and the Phalacrocoracidae shared a common ancestor. *Received 18 December 1985, accepted 17 March 1986.*

IN a study of fossil birds from the Hawthorn Formation, Brodkorb (1956) described a new species of cormorant, *Phalacrocorax subvolans*, from the Thomas Farm local fauna, Gilchrist Co., Florida. This species, known only from the holotypical proximal end of a humerus (Brodkorb 1956), "agrees with *Phalacrocorax wetmorei* Brodkorb (1955) in conformation of caput humeri and bicipital crest, but differs as follows: proximal width less; width of shaft less; ligamental furrow [sulcus ligamentosus transversus] shorter and less deep; deltoid crest [crista pectoralis] longer; internal tuberosity [tuberculum ventrale] sharper and capital groove [incisura capitis] correspondingly deeper; bicipital furrow [impressio m. coracobrachialis cranialis] wider." Brodkorb noted that the greater width of the bicipital furrow in *P. subvolans* leaves a larger surface for the attachment of M. coracobrachialis anterior (= M. coracobrachialis cranialis) and suggested that this indicates that *P. subvolans* was a better soarer than living or fossil cormorants. Brodkorb also noted that this condition of the humerus in *P. subvolans* approached that of anhingas, birds that customarily soar for long intervals.

Reexamination of the holotype indicates that *Phalacrocorax subvolans* should be moved to the genus *Anhinga* in the family Anhingidae.

MATERIALS AND METHODS

Fossil specimens included in this study are housed in the Vertebrate Paleontology collections of the Florida State Museum (UF). Comparative material of

living species is in the collections of P. Brodkorb; Florida State Museum; National Museum of Natural History, Smithsonian Institution; American Museum of Natural History; University of Michigan; and Royal Ontario Museum. Anatomical terminology follows Baumel et al. (1979). Measurements are described in Table 1.

SYSTEMATICS

Family Anhingidae Ridgway 1887

The proximal ends of humeri of the Anhingidae may be distinguished from those of the Phalacrocoracidae using two characters (Miller 1966). In cormorants the crus dorsale fossae overhangs the fossa pneumotricipitalis (see Fig. 1) and fully covers its proximal end, whereas in anhingas the less extensive fossa is well exposed. The sulcus ligamentosus transversus on the cranial surface is longer, deeper, and extends transversely to, but is narrowly separated from, the impressio M. coracobrachialis cranialis in cormorants; the sulcus is shorter and deep only ventrally in anhingas. In addition, anhingas have a strong sulcus on the cranial face of the humerus paralleling the distal portion of the crista pectoralis. In cormorants this sulcus is absent, causing the crista pectoralis to merge more smoothly with the shaft. Also, anhingas tend to have a proportionally longer crista pectoralis than do cormorants.

Genus *Anhinga* Brisson 1760

Anhinga subvolans (Brodkorb 1956)

Holotype.—UF 4500, proximal half of right humerus. Florida State Museum, Vertebrate Paleontology collection. From the Thomas Farm

TABLE 1. Measurements of humeri of living and fossil *Anhinga* species. Data are means ± SD and observed ranges. Number of specimens for *A. anhinga* and *A. rufa* = 10, all other n = 1. Measurements of the humerus are as follows: W-SHAFT = transverse width of midshaft; D-SHAFT = depth of midshaft; W-PROX = transverse width of proximal end from the external tuberosity (tuberculum dorsale) to the most ventral face of the bicipital crest (crista bicipitalis); D-PROX = depth of proximal end, from the bicipital surface (facies bicipitalis) to the internal tuberosity (tuberculum ventrale), measured at right angles to the long axis of the shaft; D-HEAD = depth of head, measured parallel to the axis of the head; L-DELTOID = length of deltoid crest (crista pectoralis), measured from the external tuberosity to the most distal extension of the deltoid crest.

Measurement	anhinga	rufa	novaehol-landiae	melano-gaster	grandis	subvolans
W-SHAFT	6.66 ± 0.39	6.81 ± 0.55	7.0	6.4	8.7	7.6
	5.7–7.1	6.2–7.9	—	—	—	—
D-SHAFT	5.76 ± 0.38	6.06 ± 0.54	5.8	6.2	7.7	6.7
	5.1–6.2	5.4–7.1	—	—	—	—
W-PROX	18.02 ± 0.80	19.85 ± 1.11	20.0	18.5	23.1	21.4
	17.2–19.8	18.1–21.6	—	—	—	—
D-PROX	8.62 ± 0.35	9.85 ± 0.54	9.8	8.9	—	9.7
	8.0–9.1	8.8–10.5	—	—	—	—
D-HEAD	6.71 ± 0.25	7.22 ± 0.49	7.7	6.8	8.0	7.4
	6.1–7.1	6.5–7.9	—	—	—	—
L-DELTOID	35.19 ± 1.88	37.86 ± 2.61	40.7	38.5	42.3	37.5
	31.7–37.8	35.0–43.3	—	—	—	—

locality, early Miocene (early Hemingfordian; approximately 18 million years before present), Gilchrist Co., Florida. Collected by R. Bader in the spring of 1955. Webb (1981) reviewed this local fauna. The Thomas Farm locality represents a high-sided sinkhole that was at least partially water filled (A. E. Pratt pers. comm.). The fossil birds of Thomas Farm local fauna were studied by Wetmore (1943, 1958), Brodkorb (1954, 1956, 1963a), Cracraft (1971), Olson and Farrand (1974), and Steadman (1980).

Emended diagnosis.—Referable to the family Anhingidae by the characters listed above. The type of *Anhinga subvolans* differs from the proximal ends of the humeri of all species of *Anhinga* examined (*A. grandis*; UF 25739, Love Bone Bed locality, Alachua Co., Florida; *A. rufa*; *A. melanogaster*; *A. anhinga*) in having a deeper fossa pneumotricipitalis and impressio M. coracobrachialis cranialis, a more prominent crus dorsale fossae, and a better-developed and sharper ridge that extends distally down the shaft from the crus dorsale fossae. The proximal end of the humerus of *A. subvolans* is similar in size to that of *A. rufa* (*A. anhinga* smaller, *A. grandis* larger; Table 1).

Discussion

The two implied generic characters (configuration of caput humeri and bicipital crest)

originally used by Brodkorb (1956) are found in both the Anhingidae and the Phalacrocoracidae. Two of the original specific characters of *A. subvolans* (sulcus lig. transversus and length of the crista pectoralis) are actually diagnostic of the family Anhingidae. All other characters in the original description are either size dependent or serve only to distinguish *Anhinga subvolans* from *Phalacrocorax wetmorei*.

Olson (1985) reviewed the fossil history of this family. I can add that *Anhinga grandis* Martin and Mengel (1975) is now known from three additional localities in the late Miocene of Florida (Becker 1985). Ballman (MS) reported a species of *Anhinga* from the Pliocene Sahabi Formation of Libya. It is about the size of *Anhinga grandis* and therefore can be distinguished from *Anhinga subvolans* on the basis of size. There is also a large, indeterminate species of anhinga from the earliest Pliocene (early Hemphillian) Bone Valley Mining District (Becker 1985) and from the early Pleistocene (Irvingtonian) Coleman III locality (Ritchie 1980). Based on only a few ulnae, this species does not appear to be referable either to the living *Anhinga anhinga* or to *Anhinga grandis* (contra Ritchie 1980). Fossils representing the living species, *Anhinga anhinga*, are known from numerous localities in the late Pleistocene (Rancholabrean) of Florida (Brodkorb 1963b).
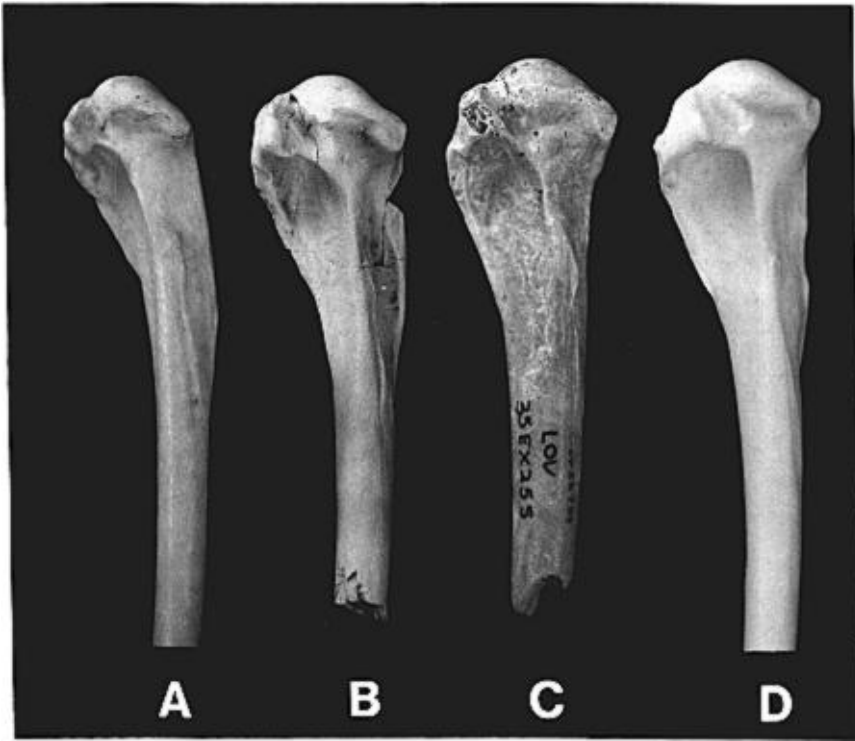
Fig. 1. Caudal view of the proximal end of humeri of anhingas. (A) *Anhinga anhinga*, USNM 500870. (B) *A. subvolans*, UF 4500, holotype. (C) *A. grandis*, UF 25739. (D) *Phalacrocorox auritus*, USNM 500819. All photos are 1×.

Protoplotus beauforti Lambrecht from the middle Eocene of Sumatra is probably not referable to the Anhingidae (Rich in litt., cited in Olson 1985). *Protoplotus beauforti* is smaller and has different limb proportions than any anhinga. Regardless of its familial affinities, little detail can be seen on the humerus of this species (Lambrecht 1931). The humerus is not known in the fossil species *Anhinga pannonica* Lambrecht from the late Miocene of Hungary, *A. hadarensis* Brodkorb and Mourer-Chauviré from the Plio-Pleistocene of Ethiopia and Tanzania, and *A. laticeps* Devis from the Pleistocene of Australia. Considering their geographic and geologic provenances, none of these species is likely to be conspecific with *Anhinga subvolans*.

Olson (1985), citing cranial and tarsometatarsal characters, showed that the New World *Anhinga anhinga* is distinct from the Old World species of *Anhinga* and that all members of this genus should not be viewed as a single superspecies. A number of additional characters support Olson's view. The Old World species share a similar structure of the proventriculus (glandular tissue in two separate patches; proventricular glands collected in a diverticulum in *A. anhinga*; Garrod 1876, 1878; Forbes 1882), pyloric lobe (conical and retractile pyloric plug present; absent in *A. anhinga*; Garrod 1876, 1878; Forbes 1882), structure of temporal fossa (fossae boundaries distinct; indistinct in *A. anhinga*; Beddard 1892), development of the postorbital process (smaller; well developed in *A. anhinga*; Beddard 1892), and structure of the bridge of Dönitz (ossified; not ossified in *A. anhinga*; Garrod 1876; pers. obs., $n = 10+$). Additionally, the sexes are dimorphic in *Anhinga novaehollandiae* and in *A. anhinga* but are similar in *A. rufa* and *A. melanogaster* (Vaurie 1965).

Fossil evidence shows the Anhingidae to be present in the early Miocene and the Phalacrocoracidae to exist in the Eo-Oligocene (Phosphorites du Quercy; Mourer-Chauviré 1982). Therefore, these two groups have not shared a common ancestor for at least 30 million years (see Savage and Russell 1983 for information

and references on the age of the Phosphorites du Quercy), and probably much longer.

Some authors (Dorst and Mougin 1979, Cracraft 1985) have reduced the Anhingidae to a subfamily of the Phalacrocoracidae without comment. Anhingas have a feeding behavior and a straight, laterally compressed rostrum with serrated tomia that is unique in the Pelecaniformes. Other studies have shown that cormorants and anhingas differ significantly in their habitat preference, locomotion, ecology, and arrangement of the carotid arteries (Garrod 1876, 1978; Beddard 1892; Owre 1967). Given that anhingas and cormorants have had a long fossil history, that the magnitude of morphological difference between cormorants and anhingas is comparable to that found among other pelecaniform families, and that the ranking of anhingas at the family level is consistent with the taxonomy of the order as a whole, it seems more reasonable to maintain the Anhingidae and the Phalacrocoracidae at their traditional family ranks, as recently suggested by Brodkorb and Mourer-Chauviré (1982) and Olson (1985).

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