AN EVALUATION OF THE FOSSIL ANHINGAS OF AUSTRALIA

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Anhingas were early recorded among the remains of other water birds from Pleistocene deposits in Australia. Until the present such records have consisted solely of three bones described by De Vis in 1888 and 1906. This paper evaluates these early reports and records additional Pleistocene material.

This study has been made possible through the loan of De Vis' type material from the Queensland Museum through the kindness of the late George Mack and of Alan Bartholomai. Modern skeletons of *Anhinga novaehollandiae* have been loaned by H. J. de S. Disney and H. O. Fletcher of the Australian Museum, Sydney, and by A. R. McEvey of the National Museum of Victoria, Melbourne, to whom I am much indebted. The collecting of skeletons of modern and fossil birds in Australia was supported by grants G15957 and GB 1990 of the National Science Foundation and by the aid and interest of the South Australian Museum, Adelaide.

"ANHINGA PARVA"

De Vis (1888:1286) gave the name *Plotus* (= *Anhinga*) *parvus* to a complete humerus obtained from the River Condamine beds, three miles from Chinchilla, Darling Downs, southeast Queensland. These sand deposits cut by the river contained remains of a (? early) Pleistocene fauna. The humerus shown in De Vis' figures (plate 35, 10a, b) is a right humerus, not a left as he states, and this is now further verified with the holotype (no. F 1130 Queensland Museum) in hand. The figure matches the type almost exactly in size and is a fairly good representation of its shape.

Originally in studying the figure and some parts of De Vis' description, I became concerned with the resemblance of the fossil to the cormorants rather than to the anhingas or darters. Curiously, De Vis made all his analysis in comparison with *Pelecanus* and mentioned no cormorant of any species. With the type before me, it is now clear that it does not represent the family Anhingidae but is a bone from a small cormorant. Indeed it is inseparable from a comparable bone of the present-day small Pied Cormorant *Haliëtor melanoleucos* of Australia.

The important characters in distinguishing the humeri of anhingas from those of cormorants are as follows: (1) In cormorants the median crest overhangs the pneumatic fossa and fully covers its upper end, but in anhingas it leaves the less-extensive fossa well exposed; (2) The ligamental furrow of the palmar surface is longer and deeper and extends transversely to, but is narrowly separated from, the bicipital furrow in cormorants whereas the ligamental furrow is shorter and deep only medially in anhingas; (3) The attachment for the anterior articular ligament (terminology of Howard, 1929:318) on the distal end is elongate and narrow in cormorants but is ovoid in anhingas; (4) The distal end of the bone is less expanded

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TABLE 1

MEASUREMENTS IN MILLIMETERS OF HUMERI OF CORMORANTS

No. (M.V.Z.)	Sex	Length	Width of head	Diameter of pneumatic fossa
P. sulcirostris				
113256	♂	116.2	17.9	6.1
143252	♀	112.3	17.3	6.0
143254	♀	111.3	16.4	5.9
143250	♀	109.8	16.5	5.6
143255	♀	109.3	16.7	5.6
143255	♀	108.1	16.1	5.9
143251	♀	107.3	17.4	6.1
H. melanoleucos				
143272	♀	108.5	15.4	5.0
143273	♀	105.1	15.6	4.5
143274	♂	104.9	15.9	5.2
141908	♀	104.2	15.9	5.0
143276	♀	104.1	16.9	5.3
143277	♀	104.0	16.8	5.3
143759	?	98.4	14.8	4.5
143275	♀	98.3	15.8	4.7
Fossil	—	106.5	15.4	4.9

and the ectepicondyle more produced distally in cormorants than in anhingas. In all these particulars the type of *parvus* accords with cormorants.

There remain to be developed means for the separation of the humeri of the small cormorants of the Australasian region of today, namely *Phalacrocorax sulcirostris* and *Haliëtor melanoleucos*, and to see whether or not the fossil *parvus* clearly relates to one of them. Table 1 shows the measurements useful in this connection. The series of modern skeletons available represents chiefly females. In *melanoleucos*, at least, it appears that males are not consistently larger than females. Measurements of total length and of greatest width of the proximal end of the humerus show some overlap between the species. The fossil in both respects falls below the zone of overlap and also below the minimum of the sample for females of the somewhat larger *sulcirostris*. Nevertheless, it seems likely from inspection that this indication of affinity based on size would not stand a rigorous statistical test.

However, a further character useful in separation is the relatively smaller size in *melanoleucos* of the pneumatic fossa in which the triceps muscle inserts. The larger fossa in *sulcirostris* results in a straighter anconal shaft ridge, one that does not bow medially so distinctly as it does in *melanoleucos*. These aspects of configuration can be partly reflected by taking the approximately transverse diameter of the fossa, although precise points of reference make the measurement somewhat subjective. Nevertheless, a fair approximation of size, taken as consistently as possible, is given in table 1. There it may be seen that the species do not overlap in this respect. The average of *sulcirostris* is 5.86 mm, and that of *melanoleucos* is 4.91 mm. The fossil with a value of 4.9 mm is more than four times the standard deviation (0.21) below the mean for *sulcirostris* and thus falls far outside the probable range of that species.

TABLE 2

MEASUREMENTS IN MILLIMETERS OF CRANIA OF ANHINGAS

Specimen	Width of frontonasal hinge	Least interorbital width of frontals	Length upper rim of foramen magnum to frontal hinge	Length opisthotic process to postorbital process	Length postorbital process to posttemporal process	Greatest breadth of brain case	Greatest depth of cranium over presphenoid
Type of *A. laticeps*	11.0	8.2	49.7	32.0	20.8	24.1	17.7
A. novaehollandiae							
♂ 143017 M.V.Z.	—	—	—	—	—	—	17.0
♂ W4795 N.M.V.	9.5	6.4	46.2	29.2	17.2	22.7	17.1
♀ 154314 M.V.Z.	9.4	6.4	49.0	31.1	18.5	23.1	17.1
♀ 149268 M.V.Z.	9.2	5.5	46.0	30.1	17.6	22.3	—
♀ W5907 N.M.V.	9.7	7.0	48.1	30.7	18.6	23.6	17.5
? S291 A.M.	9.7	6.2	46.7	30.6	18.5	23.3	17.9
? S1258 A.M.	8.5	5.0	44.7	29.1	16.8	21.2	16.3
A. anhinga							
♂ 85509 M.V.Z.	9.0	5.8	45.8	29.0	16.9	21.9	16.4
♂ 93701 M.V.Z.	—	—	—	29.9	17.1	23.0	16.8

As a consequence of the small dimensions of the fossil and the concordant characters of small fossa size, which is statistically significant, and the related aspects of shape, *parvus* may be identified as *Haliëtor melanoleucos* rather than *Phalacrocorax sulcirostris*. *Plotus parvus* De Vis (= *Anhinga parva*) therefore becomes a synonym of *H. melanoleucos*.

ANHINGA LATICEPS

De Vis (1906:17) based this species on a cranium from Cooper Creek in the Lake Eyre region, which is a horizon of late Pleistocene age. He also mentioned a fragment of a pelvis but did not clearly assign it to *laticeps*. To avoid any possible later confusion, since De Vis did not formally specify a type, I now designate the cranium (no. F 3747 Queensland Museum) as the lectotype.

The cranium is large, as De Vis indicates. But the most important features that distinguish it from those of modern anhingas (*A. novaehollandiae* and *A. anhinga* have been compared) are the broad frontonasal and interorbital areas (table 2).

The difference suggests that the base of the bill was also broader and the orbits set farther apart. One may assume therefore that the needlelike aspect of the anterior head and bill was less developed or specialized in this species. Also, the head of *laticeps* shows greater length, especially in the brain case, as measured between the postorbital process and the process that borders the temporal groove posteriorly. The cranium is not significantly deeper or broader, however.

Statistical tests for the width feature of the nasal hinge and interorbital area and for the length of brain case show that the differences are clearly significant when compared with the grouped measurements of modern material of the genus (two species). The measurements of *laticeps* exceed the mean of the modern material by more than three times the standard deviations (0.47, 0.70, and 0.72, respectively) and are therefore outside the range of the latter.

In view of the distinctive features of the cranium, *laticeps* must be regarded as a valid and well-marked species. We are left, however, with the problem of evaluating other skeletal material of anhingas from the Pleistocene of Australia. There is insufficient evidence for the general large size of *laticeps* to allow us to infer that its limb bones and body skeleton would depart much if at all from those of the modern species. In the absence of such evidence it seems best to assign these other late Pleistocene bones of anhingas to the modern *A. novaehollandiae*, which at such a recent period in time most probably occupied the continent, and since, as proves true, no departures whatsoever in size or configuration can be detected. The alternate assignment to *laticeps*, which we know was present, makes even greater assumptions about features of its unknown skeletal parts. To do so would, of course, avoid the assumption that two Pleistocene anhingas coexisted, which is not impossible but still is not a very likely situation in terms of modern experience. Nevertheless, we must recall that three species of cormorants coexist today in such an area and did in the Pleistocene and that two species of pelicans (Miller, 1965) coexisted there in the Pleistocene. Other highly specialized birds (for example, flamingos) also have two or three species present in the same area.

Other Pleistocene anhingas that have been reported are the very small *Anhinga nana* from Mauritius and Madagascar and the bones of the modern *Anhinga anhinga* from Florida (see Brodkorb, 1963:257). *A. nana* is too small to raise any question of identity of *laticeps* with it.

From the Tertiary Lambrecht (1916:9) described *Plotus* (= *Anhinga*) *pannonicus* from the Lower Pliocene of Hungary. It is represented by a carpometacarpus and a neck vertebra that are fairly large. According to Lambrecht, the separation of the hyperapophyses of the sixth vertebra as against their coalescence seems to be the principal difference distinguishing *pannonicus* from modern anhingas. The size difference may or may not prove significant. As regards the carpometacarpus, I have a modern skeleton (no. 154314) of *A. novaehollandiae* that nearly equals the length (72.3 versus 73.0 mm) reported for *pannonicus*. Lambrecht made his comparison by using figures and descriptions of the vertebrae provided by Mivart (1878). Thus there is some chance that a direct comparison of the fossil with modern material would reveal no real differences. On the other hand, I am similarly handicapped by not having the fossil at hand and being forced to rely on Lambrecht's figures only. A reassessment of the type material of *pannonicus* should be undertaken when opportunity affords.

From the early Tertiary, possibly the Eocene, of Sumatra, Lambrecht described (1931:17) *Protoplotus beauforti*. This is a skeletal impression of what is undoubtedly an anhinga but in which the rami of the lower jaw are more arched laterally and posteriorly than in *Anhinga* and in which several aspects of proportions and configuration of the limb bones depart from those of the later darters.

ANHINGA NOVAEHOLLANDIAE

In accord with previously described policy, the following Pleistocene remains of anhingas are allocated to *Anhinga novaehollandiae* from which they differ in no aspects of size or shape.

Early Pleistocene, Katipiri Sands, Lake Kanunka, South Australia, Kanunka Fauna. Locality V 5772 Univ. Calif. Mus. Paleo., no. 60570 (site 1, *in situ*), distal end of right tarsometatarsus with trochleae II and III complete; 60572 (float, may

be locality V 5773), proximal half of left tarsometatarsus; no. 56886, proximal end of left ulna; 56885, proximal end of right humerus, complete. Locality V 5773, no. 60545, proximal end of right humerus, complete.

Late Pleistocene, lower Cooper Creek, South Australia, Malkuni Fauna. Locality V 5380, site 4, Univ. Calif. Mus. Paleo., no. 56319, proximal end of left ulna. Locality V 5862, site 10, no. 56414, proximal end of right humerus, complete. Locality V 5866, site 14, no. 56358, distal end of right coracoid. Locality of "Lower Cooper," no. F 5748 Queensland Mus., fragment of pelvis consisting of vertebrae extending from near acetabulum to anterior end (De Vis, 1906, pl. 6, figs. 2A, 2B).

The separation of anhinga bones from those of cormorants has proved to be readily achieved for the elements listed above. The characters used in connection with the humerus have already been mentioned. The tarsometatarsus of *Anhinga* is shorter and broader through the shaft than in cormorants with an unbroken medio-frontal ridge and a greater extension of trochlea II beyond trochlea III. On the proximal end of the ulna, cormorants show a distinct groove between the edge of the internal cotyla and the prominence for the anterior ligament (see Howard, 1929: 319), whereas these merge in *Anhinga*. On the distal end of the coracoid the brachial tuberosity overhangs the triosseal canal and pneumatic foramina to a greater degree in cormorants than in anhingas. On the dorsal surface of the pelvis a crest runs from near the acetabulum on each side to join in a lyrate pattern in the midline. This crest is lacking in cormorants.

In describing the pelvic fragment from Cooper Creek in conjunction with *Anhinga laticeps*, De Vis stated that he could not relate it with certainty to *laticeps*, "*Plotus*" *parvus* (= *Haliëtor melanoleucos*), or *novaehollandiae*, but added that "the only thing that can be said . . . is that it is not from . . . *novaehollandiae*." He gives no reasons for this latter assertion. I find I can match this pelvis completely with some modern specimens of *novaehollandiae*.

SUMMARY

A review of the type material of darters or anhingas previously described from the Pleistocene of Australia shows that *Anhinga parva* (De Vis) is a small cormorant identifiable as *Haliëtor melanoleucos*. *Anhinga laticeps* (De Vis) proves to be a distinct species of darter in which the base of the rostrum and the interorbital area are significantly broader and less specialized than in modern anhingas. *Anhinga* bones inseparable from those of the modern *Anhinga novaehollandiae* of Australia are recorded from the early Pleistocene (5 specimens) of the Lake Eyre region of Australia and from the late Pleistocene (4 specimens) of this same area. The distinctive *Anhinga laticeps* also occurred there in the late Pleistocene.

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