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The Fossil Waterfowl (Aves: Anseriformes) from the Eocene of England

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ABSTRACT

The taxonomy and phylogenetic positions of the fossil waterfowl (Aves: Anseriformes) described from the Eocene of England are reviewed. Although a total of six species within five genera have been described, only the phylogenetic positions of the two taxa *Anatalavis oxfordi* Olson and *Headonornis* (Lydekker) can be hypothesized with confidence within the order Anseriformes. *Anatalavis oxfordi* is considered to be the sistertaxon to a clade comprising another fossil waterfowl, *Presbyornis* Wetmore, and the extant true ducks, Anatidae, whereas *Headonornis* may be congeneric with *Presbyornis*. Fossil material referred to the genera *Palaeopapia* Harrison and Walker and *Paracygnopterus* Harrison and Walker is considered Aves incertae sedis.

INTRODUCTION

The avian order Anseriformes includes the extant waterfowl, the screamers, ducks, and geese. Considered by most systematists to be one of the most basal clades within modern birds (Neornithes sensu Cracraft, 1988; see also reviews in Sibley and Ahlquist, 1990; Ericson, 1997; Livezey, 1997; Groth and Barrowclough, 1999), the fossil record of this group has been considered to extend back into the Mesozoic period, prior to the Cretaceous-Tertiary (KT) boundary (Howard, 1955; Olson and Parris, 1987; Olson, 1999).

From rocks of Eocene age (ca. 55 million years ago), the fossil remains of anseriform birds have been recovered from a number of deposits in both Europe and North America. From the Lower Eocene Green River Formation of Wyoming and Utah comes perhaps the most famous of the fossil anseriforms, the taxon *Presbyornis pervetus* Wetmore. For a number of years, this taxon was considered to be ‘‘intermediate’’ in morphology, provid-

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ing evidence for an evolutionary link between a number of traditional avian orders by the time of the early Eocene (Olson and Feduccia, 1980; Feduccia, 1995, 1996). However, the recent inclusion of *Presbyornis* within cladistic analyses of Recent waterfowl has demonstrated that this taxon can be placed well within the order Anseriformes, closely related to the extant true ducks (Anatidae; Ericson, 1997; Livezey, 1997).

From the Lower Eocene London Clay Formation and contemporary deposits in England, the remains of fossil birds have been known for over 100 years (Koenig, 1825; Owen, 1841; Andrews, 1899). However, much of this material remained unstudied after this time until the various works of Harrison and Walker in the 1970s and 80s (e.g., Harrison, 1982a, 1982b, 1983; Harrison and Walker, 1976, 1979a, 1979b, 1979c). Recent considerations of the fossil bird assemblage from the London Clay Formation include Mayr and Daniels (1998), Dyke and Cooper (2000), and Dyke and Waterhouse (2001). Notably, Harrison and Walker (1976, 1979a) named four species of waterfowl within three genera from the Tertiary of England (*Headonornis hantoniensis, Paracygnopterus scotti, Palaeopapia eous* and *Palaeopapia hampsteadiensis*) and remarked on the possible referral of the taxon *Proherodius oweni* Lydekker to the order. Recently, Olson (1999) described a new species within the genus *Anatalavis* Shufeldt (*Anatalavis oxfordi*) on the basis of material collected from a basal member of the London Clay Formation.

In this paper, the fossil records of waterfowl from the Eocene of England are reviewed in light of recent phylogenetic hypotheses regarding the relationships of extant anseriforms. In cases where material is complete enough (i.e., preserves characters that have been employed in phylogenetic considerations of Recent taxa), fossil birds can be used in the production of minimum age estimates for the divergences of internal nodes within cladograms, and are therefore invaluable for unravelling the pattern of the evolutionary radiation of the modern birds as a group (Dyke, 1998, 2001).

MATERIALS AND METHODS

The material discussed in this paper is held in the Palaeontology Department Collections of The Natural History Museum, London (formerly the British Museum of Natural History; BMNH PAL), the Sedgewick Museum, Cambridge (SMC), and in the United States National Museum, Washington D.C. (USNM). Recent comparative osteological specimens were examined in the collections of The Natural History Museum, Tring. The anatomical nomenclature employed is as outlined by Baumel and Witmer (1993), with some modifications to English following the standard work of Howard (1929). References to Recent avian taxa and higher-level groups follow Sibley and Monroe (1990). Rules governing the synonymy and designation of taxonomic names are used as outlined by the International Commission on Zoological Nomenclature (ICZN, 1999).

DISCUSSION AND SYSTEMATICS OF FOSSIL TAXA

AVES

ANSERIFORMES

Anatalavis Shufeldt, 1915

ANATALAVIS OXFORDI Olson, 1999

The holotype specimen (BMNH PAL 5922; fig. 1A–C) of *Anatalavis oxfordi* Olson is one of the best preserved fossil birds known from the London Clay Formation. Unfortunately, however, it is also one of the most fragile fossil bird specimens known. Although both the partially complete skull, sternum, and pelvis (along with a number of forelimb elements) have been prepared, studying this material is complicated by the delicate preservation of the material. This specimen was collected from bed A of the London Clay at Walton-on-the-Naze, Essex, England (King, 1981) in 1991 (Olson, 1999).

FOSSIL MATERIAL: BMNH PAL 5922 (fig. 1A–C), an incomplete skeleton consisting of skull (fig. 1A), incomplete rostral portion of mandible, pterygoid, atlas, axis, thoracic and caudal vertebrae, complete furcula (fig. 1B), left and right coracoids (fig. 1C), left and right scapulae, incomplete sternum (lacking posterior portions), incomplete anterior por-

Fig. 1. Parts of the holotype specimen of *Anatalavis oxfordi* Olson (BMNH PAL 5922). **A,** skull in lateral views; **B,** furcula; **C,** coracoid in dorsal and medial views. Scale bars are 10 mm. HYP indicates hypocleidium (apophysis furculae); FP, foramen pneumaticum.

tion of pelvis, complete right and incomplete left humeri, distal ends of left radius and ulna, left ulnare, complete left carpometacarpus, complete phalanges, and minor digits of left forearm. For complete description and illustration of this material, see Olson (1999).

TAXONOMIC HISTORY: Olson (1999) considered the holotype specimen of *Anatalavis oxfordi* and referred it to within the extant family Anseranatidae, as the sole member of a new subfamily, the Anatalavinae (fig. 2). The only other member of this family of anseriforms is the extant Australian Magpie Goose, *Anseranas semipalmata.* On the basis of this referral, a number of significant conclusions were proposed by Olson (1999): (1) that the fossil record of this extant family can be traced back to the Lower Eocene of the northern hemisphere, and (2) the origin of this group of waterfowl can be inferred to have occurred in the northern hemisphere (of course, the distribution of the family is currently restricted to the southern continents). Olson (1999) further proposed that the early fossil record of the order Anseriformes in the northern hemisphere may have been dominated by anseranatid-like taxa during this time, to be replaced later by the members of the Anatidae, or true ducks.

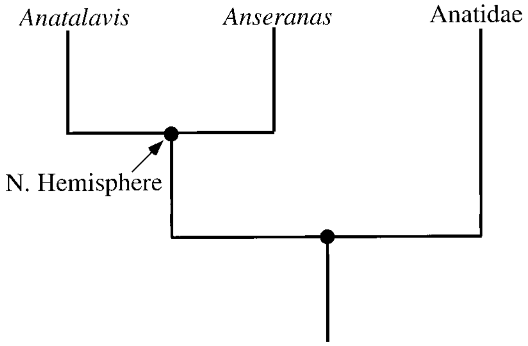

Fig. 2. Phylogenetic position of *Anatalavis oxfordi* proposed by Olson (1999).

Referral of the holotype specimen of *Anatalavis oxfordi* to the Anseranatidae was made by Olson (1999: 232) on the basis of the following osteological characters: the V-shaped conformation of the furcula, the size of the symphysis (fig. 1B), and the presence of a distinct foramen pneumaticum on the dorsal surface of the distal coracoid (fig. 1C). All of these features were considered by Olson (1999) to be uniquely derived within the Anseranatidae. In particular, with regard to the presence of a foramen pneumaticum on the dorsal coracoid, he noted that (p. 232) ‘‘although a similar condition exists in modern Anhimidae [screamers], which have one of the most pneumatized skeletons in any group of birds, this foramen is absent in Eocene Anhimidae, which are evidently completely nonpneumatic''. Although it is true that the this character is present in the extant screamers (Livezey, 1997), the extent of variation of this feature in the known fossil forms is unclear since little material has been described to date. Indeed, examination of material described and illustrated by Alvarenga (1999) as a fossil screamer from the Oligocene of southeastern Brazil shows that this foramen is clearly present (albeit broken distally: Alvarenga, 1999: figs. 3, 4). Although Olson (1999) cited as yet unpublished material of fossils referred informally by some to screamers or similar birds from the Eocene of England and Wyoming (p. 232), clearly the distribution (and primitive absence) of this character requires further investigation. In the absence of a cladistic analysis including all available osteological evidence, as well as the characters cited by Olson (1999), the referral of this specimen to the extant family Anserantidae cannot be considered unequivocal.

PHYLOGENETIC ANALYSIS: The phylogenetic relationships of the exant genera of waterfowl have been considered most recently by Ericson (1997) and Livezey (1997, 1998). Both of these workers included the fossil *Presbyornis pervetus* Wetmore (see above) within osteological character analyses and agreed that it should be placed as the sister taxon to the Recent Anatidae (true ducks: Ericson, 1997; Livezey, 1997).

By use of the osteological matrix presented by Livezey (1998), the holotype specimen of *Anatalavis oxfordi* (BMNH PAL 5922) was coded for inclusion in a parsimony analysis. Of the 96 osteological characters presented by Livezey (1998), only 22 (23 %) are informative for *Anatalavis* because of the incomplete and fragile preservation of the holotype. These character codings are given in appendix 1. Some small changes were made to the character-state definitions provided by Livezey (1997) for the analysis presented here: characters 3 (presence / absence of ventral prominence of processus paraoccipitalis relative to plane of os paraspenoidale) and 20 (presence/absence of processus retroarticularis) were amended as outlined to simple binary states because of uncertainties in the coding of these characters in the skull of *Anatalavis* (these changes do not affect the results of the analysis). Consideration of these features in the holotype skull will represent an area for further work.

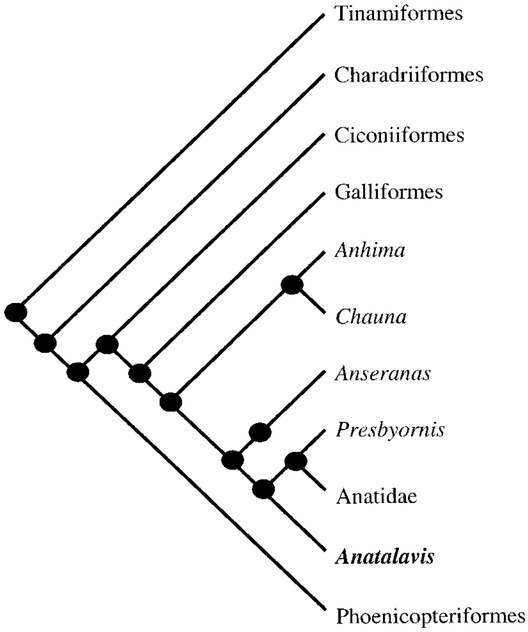

Fig. 3. Single tree (138 steps) resulting from reanalysis of Livezey (1997) and including the London Clay fossil *Anatalavis* (consistency index CI = 0.761; retention index RI = 0.815).

Parsimony analysis of the osteological dataset presented by Livezey (1997) by use of the software package PAUP (version 4.0b; Swofford, 1999: all characters unordered using Tinamiformes as the outgroup), and including the holotype of *Anatalavis oxfordi*, resulted in the production of a single most parsimonious tree (MPT) of length 138 steps (fig. 3). The inclusion of *Anatalavis* within the analysis has no effect on the relationships of the remaining extant taxa and *Presbyornis* (see Livezey, 1997): the London Clay fossil is hypothesized to occur as the sister taxon to the extant Anatidae and *Presbyornis* (fig. 3), in a more derived position with respect to the Anseranatidae (*Anseranas*). The position for this taxon hypothesized by Olson (1999) is not supported by parsimony analysis.

REVISED TAXONOMY OF *ANATALAVIS OXFORDI*: Although consideration of the phylogenetic position of *Anatalavis oxfordi* Olson is complicated by incomplete preservation of the holotype, the position of this taxon within the single MPT (fig. 3) is unequivocal. On the basis of the osteological characters (and analysis) presented by Livezey (1997), monophyly of the waterfowl (order Anseriformes) is supported by 11 unambiguous characters (see Livezey, 1997, for details), one of which, the presence of a long and ventrally terminating lamina basiparasphenoidalis (relative to the plane of the parasphenoidale; character 3, Livezey, 1997), is preserved in *Anatalavis* (appendix 1). Olson (1999: 232) noted that the skull of the holotype has all of the features typical of the order Anseriformes, to which it clearly belongs. These include (according to Olson, 1999) a ‘‘duck-billed’’ upper jaw shape; the configuration of the quadrato-mandibular articulation; an enlarged, deep, curved, retroarticular process; and an enlarged rounded or ovoid ‘‘basipterygoid process’’ on the parasphenoid rostrum, with a correspondingly enlarged facet on the pterygoid.

The position of *Anatalavis* within the clade Anseres (true waterfowl; see fig. 3) can be inferred by the presence of a prominent crista fossa parabasalis of the exoccipitale (derived state for character 2 of Livezey, 1997) and a prominent processus coronoideus of the mandible (derived state for character 18 of Livezey, 1997). A sister group relationship between *Anatalavis, Presbyornis,* and the clade Anatidae (true ducks) can be hypothesized because of the presence of a spina externa (as a compressed phlange) on the rostral end of the sternum (derived state for character 60 of Livezey, 1997), and an elongate acromion on the cranial end of the scapula (reversal within Anseriformes for character 68 of Livezey, 1997).

Both of the features discussed by Olson (1999) in support of the referral of *Anatalavis* to the Anseranatidae were included within the osteological character matrix of Livezey (1997) and have been demonstrated to have a wider distribution within Anseriformes. The presence of a hypocleideum on the furcula (character 67 of Livezey, 1997), although seen in *Anatalavis* and *Anseranas,* is hypothesized to have been present primitively within the group: this character, tested by the congruence of others, has been secondarily lost in *Anhima, Chauna, Presbyornis,* and the Anatidae. The second of the two features discussed by Olson (1999), the presence of a foramen pneumaticum on the dorsal surface of the coracoid (character 70 of Livezey, 1997), is hypothesized to diagnose the clade Anseriformes + Galliformes and is lost in *Presbyornis* and the Anatidae. Hence, both of the osteological features presented by Olson (1999) in support of the referral of *Anatalavis* to the Anseranatidae are primitive among Anseriformes.

Headonornis Harrison and Walker, 1976

Headonornis hantoniensis (Lydekker, 1891); Harrison and Walker, 1976

Agnopterus? *hantoniensis* Lydekker (1891)

Agnopterus? *hantoniensis* Lydekker; listed by Lambrecht (1933)

Agnopterus? *hantoniensis* Lydekker; listed by Brodkorb (1964)

Headonornis hantoniensis Harrison and Walker (1976)

The genus *Agnopterus* was erected by Milne-Edwards (1869–1871) for the reception of the distal portion of a right tibiotarsus from the Upper Eocene of Montmartre, France. Milne-Edwards (1869–1871) named the species *Agnopterus laurillardi* on the basis of this material, and he noted a resemblance with the extant *Phoenicopterus* (flamingo). Later, Lydekker (1891) named the species *Agnopterus*? *hantoniensis* on the basis of a partially complete right coracoid (BMNH PAL 30325; fig. 4A), and referred a cast of a proximal left femur (BMNH PAL 144) to this taxon. Harrison and Walker (1976) removed this material from the genus *Agnopterus,* making the coracoid the holotype of the new genus and species *Headonornis hantoniensis* within the Anseriformes. They also referred an incomplete right humerus (BMNH A 3686; fig. 4B). The specimen (BMNH PAL 144) is a cast of an original held in the Institute of Geological Sciences, London (IGS GSM 113109; formerly the Geological Survey Museum, London; Harrison and Walker, 1976).

MATERIAL: BMNH PAL 30325, a partially complete right coracoid lacking extremities of processus lateralis and angulus medialis

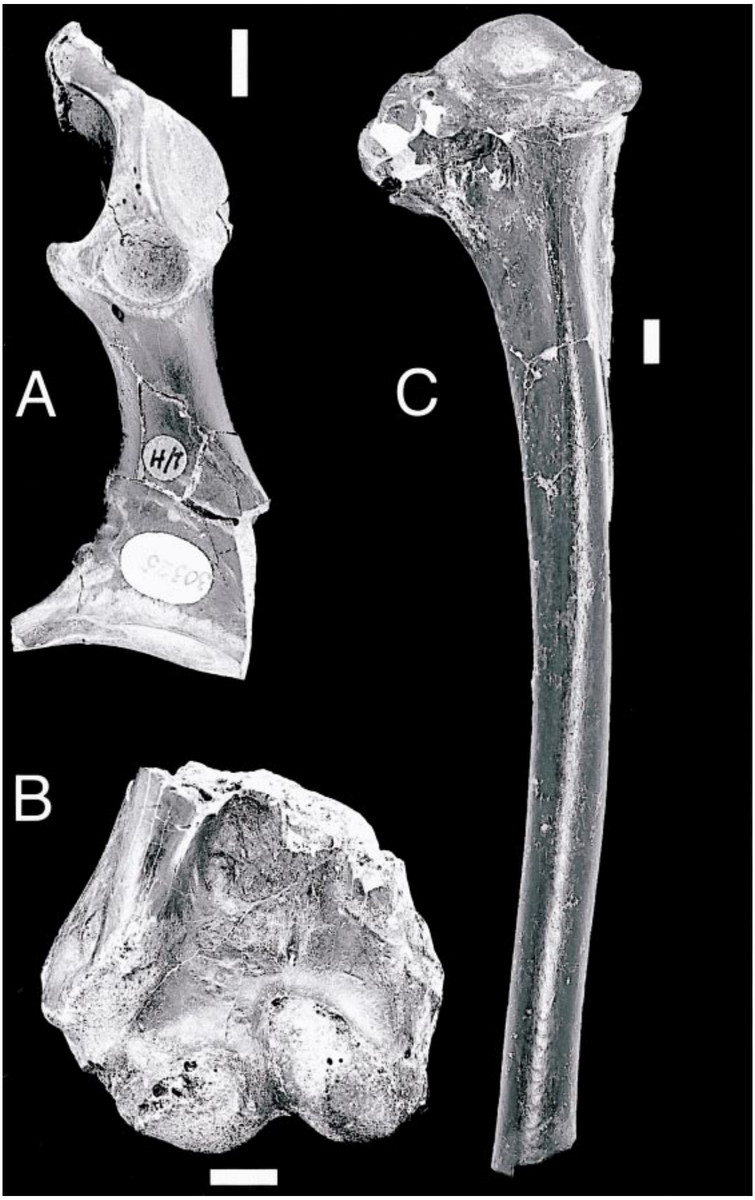

Fig. 4. Some of the fossil material referred to *Headonornis hantoniensis* Harrison and Walker. **A,** holotype right coracoid in dorsal view (BMNH PAL 30325); **B,** referred distal end of left humerus in cranial view (BMNH PAL 5105); **C,** referred right humerus in caudal view (BMNH PAL 3686). Scale bars are 5 mm.

(holotype; Harrison and Walker, 1976; fig. 4A), purchased from the Hastings Collection in 1855 but collected sometime prior to this from the Upper Eocene of Hordle (Hordwell), Hampshire. BMNH PAL 3686, an incomplete right humerus lacking the distal end (referred specimen: Harrison and Walker, 1976; fig. 4B), collected from Upper Eocene deposits near Milford, Hampshire, and presented by J. Athersuch in 1970. BMNH PAL 4989, the proximal end of a right scapula (referred specimen: Harrison and Walker, 1979a), collected from the Lower Oligocene Hampstead Beds on the Isle-of-Wight by S. L. Wood in 1925 (presented in 1933). SMC C20412, the sternal end of a coracoid (referred specimen: Harrison and Walker, 1979a; collection data unknown). As noted by Harrison and Walker (1979a), this specimen was described by Seeley (1866) under the generic name *Ptenornis* (no species name given), that was later regarded by Lydekker (1891) as a nomen nudum. BMNH PAL 5105, the distal end of a left humerus (referred specimen: Harrison and Walker, 1979a; fig. 4C), collected from the Lower Oligocene Bembridge Marls at Burnt Wood, Isle of Wight, by R. Ford in 1978.

TAXONOMIC REMARKS: As discussed above, the original holotype specimen of *H. hantoniensis* is a partially complete right coracoid (Harrison and Walker, 1976).

As noted by Harrison and Walker (1976), this specimen is very similar to the coracoids of Recent anseriforms, such as *Cygnus* and *Anseranas*. The cotyla scapularis is deep and rounded (as appears to be primitive for modern birds in general; Mayr, 1999), the impressio m. sternocoracoidei is poorly developed and shallow, and the processus procoracoideus is blunt, having some ventral curvature at its tip. The morphology of this specimen agrees with that of *Presbyornis pervetus* (as coded by Livezey, 1997, and figured by Ericson, 1999a) in the presence of a small foramen pneumaticum on the processus procoracoideus and in the absence of a large and excavated foramen on the sternal face (dorsal surface). More generally, BMNH PAL 30325 has a small and semi circular processus acrocoracoideus and a non excavated articularis clavicularis. With respect to these specific features, and overall, this element is very similar (other than in size) with the known coracoids of *P. pervetus* (Ericson, 1999b). Hence, the holotype of *H. hantoniensis* can be referred to the family Presbyornithidae Wetmore.

A similar-sized member of this family is known from the Tertiary of North America. Olson (1994) described a ‘‘giant’’ species of the genus *Presbyornis*, *P. isoni*, on the basis of a left humerus lacking the distal end (USNM 294116: holotype) and the left phalanx of the alar digit (USNM 294117) from the Palaeocene of Maryland. Olson (1994) noted that, in the morphology of the distal humerus, this species does not differ from *P. pervetus* other than in size and the distinctiveness of the fossa olecrani. The latter character may also be related to the large size of the specimen. In particular, on the distal end of the humerus of both *Presbyornis pervetus* and *P. isoni*, the fossa m. brachialis is deep and marked, and the condylus dorsalis is prominent and strongly developed proximally (Olson, 1994; Ericson, 1999a).

Harrison and Walker (1979a) noted that *Headonornis* from the London Clay is ‘‘a member of the Presbyornithidae’’. However, on the basis of the material avialable to them at the time, their conclusion cannot be confirmed. As discussed above, since the holotype on *Headonornis hantoniensis* is a coracoid, it is not certain whether the two referred humeri (Harrison and Walker, 1976, 1979a) can be associated to the taxon on any basis other than their large size; the coracoid and humeri are clearly from birds of a similar size. Subsequent investigation, however, shows that the second referred humerus, BMNH PAL 5105 (Harrison and Walker, 1979a), is identical both in size and preserved morphology to the holotype of *Presbyornis isoni* (Olson, 1994).

At the time of his description of *P. isoni*, Olson (1994) omitted discussion of the London Clay material from his paper. However, the morphology of another specimen, BMNH PAL 6240, does serve to confirm the suspicions of Harrison and Walker (1979a) that at least some of the London Clay material should be referred to the Presbyornithidae.

BMNH PAL 6240 was collected from the Totland Bay Member of the Middle-Upper Eocene Headon Hill Formation at Hordle, Hampshire, in 1995 by A. Jord. This material consists of a partially complete, but fragmented, right humerus with both the proximal and distal ends, as well as much of the shaft. The proximal end preserves about one-third of the crus dorsale fossa (broken beneath the fossa pneumotricipitalis), and the distal end lacks the medial area lateral to the condylus dorsalis (fig. 5). Nevertheless, the morphology of this specimen confirms the association between the two specimens originally referred to *H. hantoniensis* (BMNH PAL 3686 and PAL 5105; Harrison and Walker, 1976, 1979a), as does the presbyor-

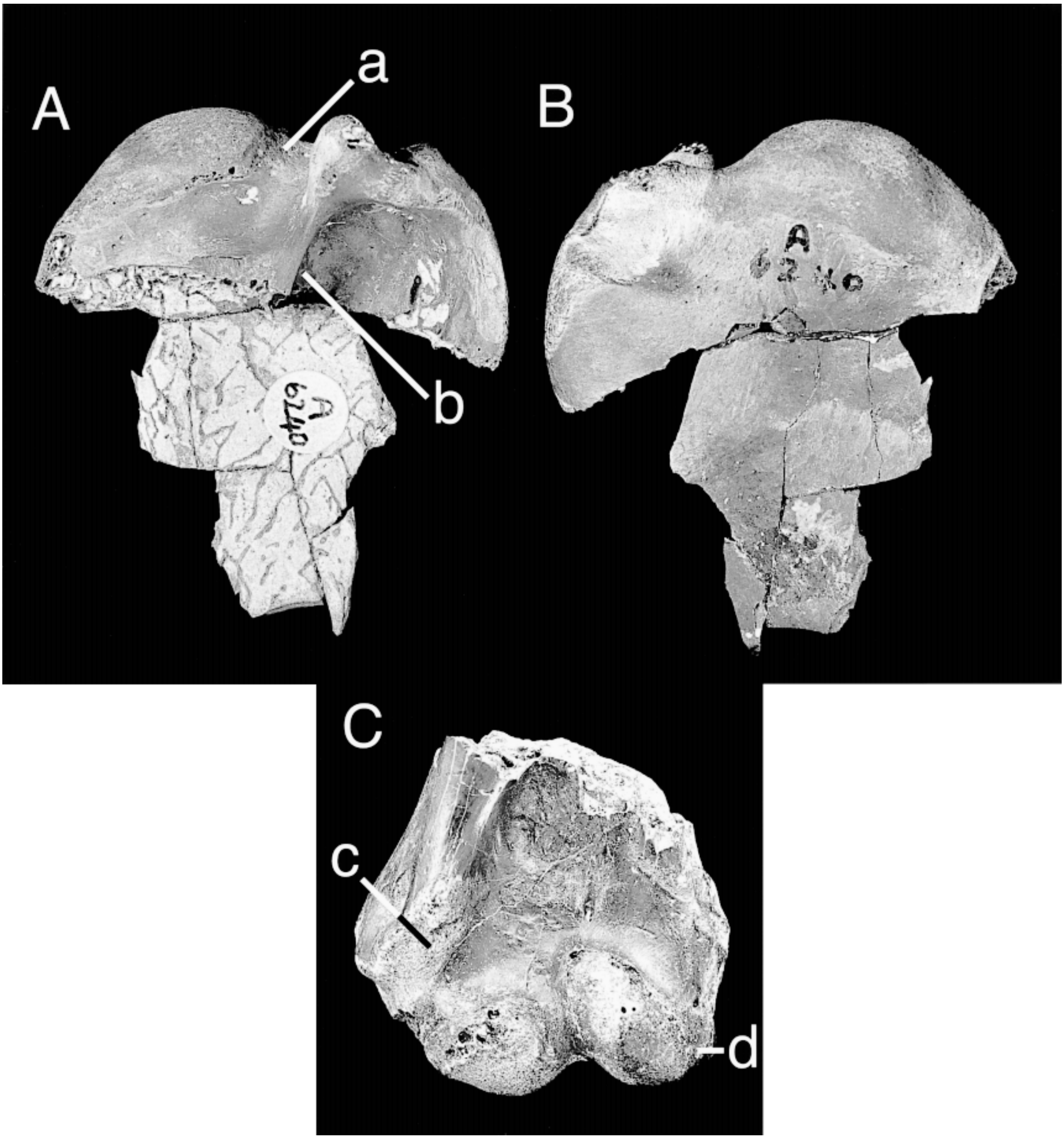

Fig. 5. Additional fossil material referred to *Headonornis hantoniensis* (BMNH PAL 6240). **A,** right proximal humerus in caudal view; **B,** cranial view; **C,** referred distal end of left humerus in cranial view (BMNH PAL 5105). Characters based on the hypothesis of Ericson (1999) are labeled. Scale bars are 5 mm. Abbreviations as follows: **a,** incisura capitis humeri; **b,** impression of M. scapulohumeralis cranialis; **c,** tuberculum supracondylare ventrale; **d,** epicondylus dorsalis.

nithid nature of this material on the basis of the osteological features discussed by Ericson (1999a). On the basis of the hypothesis of Ericson (1997, 1999a), BMNH PAL 6240 exhibits the presence of four derived presbyornithid characters (fig. 5), including the presence of an excavated area beneath the caput humeri and a prominent scar for the attachment of M. flexor carpi ulnaris.

In addition, in size and morphology

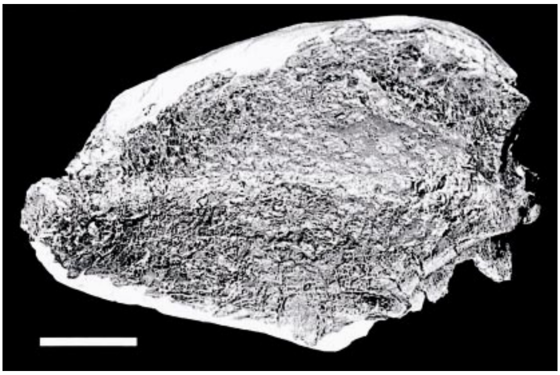

Fig. 6. The original holotype sternum of *Proherodius oweni* Lydekker (BMNH PAL 43164) in right lateral view. Scale bar is 10 mm.

BMNH PAL 6240 is identical to both the originally referred specimens of *H. hantoniensis* and the holotype of *P. isoni* (figs. 4, 5). This match is further confirmed by comparison with the illustrations of a complete (but crushed) humerus referred to *P. isoni* from the late Paleocene of North Dakota by Benson (1999).

Having confirmed that these fossil humeri from the Eocene of England are similar to those described for *Presbyornis isoni* (see Olson, 1994; Benson, 1999), the synonymy of this material remains. Since the holotype of the species *hantoniensis* within the genus *Headonornis* is a coracoid that can only be placed tentatively within the Presbyornithidae (see above) and cannot be associated with certainty to the originally referred humeri (other than by size), the original genus and species is retained here on the basis of the holotype alone. The three fossil humeri (BMNH PAL 3686, 5105, and 6240) are therefore referred to the taxon *Presbyornis isoni* Olson. It is likely, however, that the generic name *Headonornis* Harrison and Walker is a junior synonym of *Presbyornis* Wetmore, and that the species name *isoni* Olson is preoccupied by the earlier name *hantoniensis* Harrison and Walker; however, the recovery of additional fossil material will be required to confirm this.

The remaining fossil specimen referred to *H. hantoniensis* by Harrison and Walker (1979a: BMNH PAL 4989, the proximal end of a right scapula) is regarded as Aves incertae sedis. This specimen cannot be referred to the holotype of *H. hantoniensis* with certainty.

Proherodius Lydekker, 1891

Proherodius oweni Lydekker, 1891

Proherodius oweni Lydekker (1891)

Proherodius oweni Harrison and Walker (1977)

Proherodius oweni Harrison and Walker (1978)

Owen (1846) illustrated and described an incomplete cranial portion of sternum (BMNH PAL 43164; fig. 6) as a small wading bird, and he referred to the similarity of the overlapping sulcus carinae seen on the specimen to the condition seen in living herons (family Ardeidae). Owen (1846) did not name this specimen, leaving this to Lydekker (1891) who formally referred it to the family as the holotype of the taxon *Proherodius oweni*. This assignment met with the agreement of Harrison and Walker (1977), who described and re-figured the specimen after additional preparation.

TAXONOMIC REMARKS: Harrison and Walker (1978, 1979c) remarked on the possible referral of the holotype of *Proherodius oweni* to the family Presbyornithidae, and they (1979c) noted that ‘‘the shape and angle of articulation of the surfaces of the coracoid sulci, in differing from those of herons, matched those of the large *Headonornis hantoniensis* of the Upper Eocene’’. It is unclear what to make of this remark: Harrison and Walker (1976) made no mention of the referral of a sternum to *H. hantoniensis,* and no museum catalog number was given in the later paper either (Harrison and Walker, 1979c).

The possible affinity of this specimen with the family Presbyornithidae was noted by Ericson (1999b), but in this paper the taxon name *Proherodius oweni* Lydekker was incorrectly attributed to Harrison and Walker (1978). Of the features of the sternum listed by Ericson (1999b: 4), only the character ‘‘right sulcus articularis coracoideus crossing below left past midpoint of the rostrum sterni with a ridge present between the two’’ (Howard, 1955; Ericson, 1997) is preserved in *Proherodius* (Harrison and Walker, 1978, 1979c). This feature was listed by Ericson (1997: 471) as present in the members of the Presbyornithidae, as well as in *Phoenicopterus* and *Threskiornis,* but absent in remaining anseriforms. However, although this specimen is of a similar size with respect to the known specimens of *Presbyornis pervetus* (Howard, 1955; Ericson, 1999b), the presence of crossed coracoidal sulci is widespread among basal Neornithes, seen also in Lithornithidae, for example (Houde, 1988). At present, more anatomical details are required to confirm the placement of *Proherodius* within Anseriformes and Presbyornithidae (Dyke, 2000). This situation would be complicated further by the resulting synonymy of the two existing generic names—*Proherodius* Lydekker (Lydekker, 1891) would clearly have priority over *Presbyornis* Wetmore, as stated by Harrison and Walker (1978). At present, this material is considered to be Aves incertae sedis, because of the lack of diagnostic characters seen in the existing material.

Palaeopapia Harrison and Walker, 1979b

Palaeopapia eous (Harrison and Walker, 1976); Harrison and Walker, 1979b

Colymboides anglicus Lydekker (1891)

Colymboides anglicus Lydekker; listed by Lambrecht (1933)

Howardi eous Harrison and Walker (1976)

Palaeopapia eous Harrison and Walker (1979)

Lydekker (1891: 192) placed the specimen BMNH PAL 4355 (an incomplete anterior portion of sternum) within his fossil gaviiform (loon) taxon *Colymboides anglicus.* The genus *Colymboides* had been created on the basis of a humerus from the Lower Miocene of France by Milne-Edwards (1867–1871). The sternum (BMNH PAL 4355) specimen was originally cataloged as part of BMNH PAL 30330, along with a partially complete left coracoid, the holotype of *Colymboides anglicus* Lydekker. The sternum was removed by Harrison and Walker (1976), made the holotype of *Howardi eous,* and placed within the order Anseriformes. Both the specimens BMNH PAL 30330 and 4355 are from the same locality, the Upper Eocene of Hordle (Hordwell), Hampshire, and were purchased from the Hastings Collection in 1885.

When it subsequently proved that the generic name *Howardia* was preoccupied by a bug (Hemiptera), Harrison and Walker (1979b) proposed the replacement name *Palaeopapia* for this taxon. They later tentatively referred an additional specimen, an incomplete left coracoid (SMC C20949; cast BMNH PAL 4405; fig. 7A), to the genus (Harrison and Walker, 1979a) collected from the Lower Oligocene Hamstead Beds, Isle-of-Wight (date unknown).

TAXONOMIC REMARKS: Harrison and Walker (1976) noted that BMNH PAL 4355 ‘‘shows no similarity to gaviid sterna’’ but they did not dicuss this further. When Lydekker (1891) named the taxon *C. anglicus,* he noted (p. 193) that the holotype coracoid (BMNH PAL 30330) fitted perfectly into the preserved sulcus carinae of the incomplete sternum. Since this is the case, I agree with the observations of Lydekker (1891) that this specimen must be retained as the single referred specimen of *C. anglicus,* placed within the Gaviidae until further material pertaining to this taxon becomes available. The incomplete left coracoid tentatively referred to *Palaeopapia eous* by Harrison and Walker (1979a) is not diagnostic at the ordinal level and is regarded here as Aves incertae sedis. Although this specimen is very similar to the coracoids of the Recent teal (e.g., *Anas*), having both a cup like cotyla scapularis and an oblique facies articularis sternalis (fig. 7A), neither of these characters has been hypothesised as a synapomorphy of Anseriformes

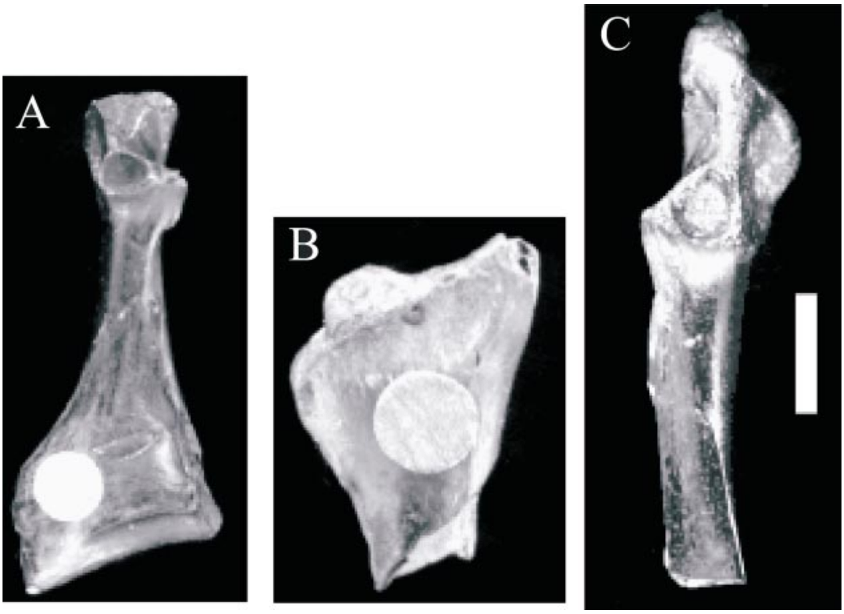

Fig. 7. Additional specimens pertaining to named fossil waterfowl taxa from the Eocene of England. **A,** BMNH PAL 4405 (cast of SMC C20949), left coracoid in dorsal aspect (specimen referred to *Palaeopapia eous* Harrison and Walker); **B,** BMNH PAL 4412, proximal right scapula in medial view (holotype of *Palaeopapia hamsteadiensis* Harrison and Walker); **C,** BMNH PAL 4407, proximal right coracoid in dorsal view (holotype of *Paracygnopterus scotti* Harrison and Walker). Scale bar is 10 mm.

(Livezey, 1997). Indeed, both have a wider distribution within basal Neornithes (Mayr, 1999).

Palaeopapia hamsteadiensis Harrison and Walker, 1979

The taxon *Palaeopapia hamsteadiensis* was erected by Harrison and Walker (1979a) on the basis of a single specimen, the incomplete proximal end of a right scapula (BMNH PAL 4412; fig. 7B). This specimen was collected from the Lower Oligocene Hampstead Beds, Yarmouth, Isle-of-Wight by S. L. Wood in 1925 (presented in 1933).

TAXONOMIC REMARKS: Harrison and Walker (1979a) did not present much discussion of this material except to remark that the lateral elongation of the tuberculum coracoideum of BMNH PAL 4412 seemed to correspond with the elongation of the facies articularis scapularis seen on the referred specimen (SMC C20949) of *Palaeopapia eous* (see above). I have been unable to find any osteological characters on this material that would permit the placement of this taxon within order Anseriformes. Referral of BMNH PAL 4412 to the genus *Palaeopapia* cannot be confirmed because of the lack of overlapping elements between the two species of the genus: this material is considered Aves incertae sedis.

Paracygnopterus Harrison and Walker, 1979a

Paracygnopterus scotti Harrison and Walker, 1979a

This taxon was created by Harrison and Walker (1979a), again on the basis of only a single specimen, the incomplete proximal portion of a right coracoid and associated portion of shaft (BMNH PAL 4407; fig. 7C). The specimen was collected from the Lower Oligocene Hampstead Beds, Yarmouth, Isle-of-Wight, by S. L. Wood in 1925 (presented in 1933).

TAXONOMIC REMARKS: Harrison and Walker (1979a) noted that the holotype specimen of *Paracygnopterus scotti* resembles closely the morphology of the Recent whistling-duck

Dendrocygna. However, this material does not preserve any characteristic osteological features since it is broken at about the midpoint of the facies articularis humeralis. From comparisons, I have been unable to find any characters that would permit the referral of this material to the level of the order Anseriformes. At this stage, the specimen must be classified Aves incertae sedis.

SYSTEMATIC CONCLUSIONS

On the basis of the fossil waterfowl material discussed in this paper, a number of specific taxonomic and phylogenetic conclusions are presented:

(1) The preserved morphology of the holotype specimen of *Anatalavis oxfordi* Olson (BMNH PAL 5922) does not confirm the hypothesis of Olson (1999) that this taxon is closely related to the extant Magpie Goose (*Anseranas*). Parsimony analysis, including this material and using the osteological data set presented by Livezey (1997), leads to the alternative hypothesis that *Anatalavis* is the sister taxon to the fossil *Presbyornis* Wetmore and the extant clade Anatidae (true ducks).

(2) The two partial humeri (BMNH PAL 3686 and 5105) referred by Harrison and Walker (1976, 1979a) to the taxon *Headonornis hantoniensis* (Lydekker) Harrison and Walker are referred to *Presbyornis isoni* Olson within the anseriform family Presbyornithidae Wetmore on the basis of the more complete specimen BMNH PAL 6240.

(3) The holotype specimen of *Headonornis hantoniensis* (Lydekker) Harrison and Walker, a partial right coracoid (BMNH PAL 30325), is referred to the anseriform family Presbyornithidae Wetmore. The referral of a second, incomplete sternal end of coracoid (SMC C20412) to this taxon by Harrison and Walker (1979a) is retained. The original genus and species name are retained on the basis of the holotype and newly referred coracoids because definite associations with the referred specimens cannot be confirmed.

(4) The holotype specimen of *Proherodius oweni* Lydekker is regarded here as Aves incertae sedis. The suggested referral of this specimen to the Presbyornithidae Wetmore, as well as the associated questions of the synonymy of the genus *Presbyornis* (Harrison and Walker, 1978), must await the recovery of additional fossil material.

(5) The holotype specimens of *Palaeopapia* (*Howardia*) *eous* Harrison and Walker, *Palaeopapia hamsteadiensis* Harrison and Walker, *Paracygnopterus scotti* Harrison and Walker, are regarded as Aves incertae sedis.

(6) The proximal end of a right scapula (BMNH PAL 4989), referred to *Headonornis hantoniensis* by Harrison and Walker (1979a), cannot be associated with the remaining material of this taxon or, because of the absence of diagnostic characters, be placed with confidence within the order Anseriformes. At this stage, this specimen must be classified as Aves incertae sedis.

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APPENDIX 1

The Preserved Osteological Characters of *Anatalavis oxfordi* Olson (based on the phylogenetic analysis of Livezey, 1997).

Ossa cranii

1. Os basioccipitale, condylus occipitalis, modal conformation in caudal view: b, strongly bilobate with lobes showing marked, lateral divergence dorsally, producing ''kidney-shaped'' aspect.
2. Os exoccipitale, fossa parabasalis, crista fossa parabasalis: b, prominent.
3. Os exoccipitale, processus paraoccipitalis, ventral prominence relative to plane of os paraspenoidale, lamina basiparasphenoidalis: b, long, and terminating ventrad. This character reduced to two binary states, based on uncertain distribution with respect to *Anatalavis.*
5. Os supraoccipitale, fonticulus occipitale: b, present (pronounced above foramen magnum).

Ossa mandibulae

18. Mandibula, processus coronoideus: b, prominent.
20. Mandibula, true, blade like processus retroarticularis: b, present. This character reduced to

two binary states because of uncertainties regarding the correct coding for *Anatalavis.*

21. Mandibula, ramus mandibulae, extremitas caudalis mandibulae, recessus conicalis: a, absent.

Ossa cinguli membri thoracici

60. Sternum, rostrum sterni, spina externa: b, present as a compressed phlange.
61. Sternum, rostrum sterni, spina communis, foramen rostri: a, absent.
62. Sternum, corpus sterni, trabecula lateralis: a, absent.
67. Furcula, extremitas sternalis claviculae, apophysis claviculae (hypocleideum): b, present.
68. Scapula, extremitas cranialis scapulae, acromion: a, elongate.
69. Coracoideum, extremitas omalis coracoidei, processus procoracoideus, foramen pneumaticum: a, present.
70. Coracoideum, extremitas sternalis coracoidei, facies dorsalis, foramen pneumaticum: b, present.

Ossa membri thoracici

71. Humerus, extremitas proximalis humeri, crista deltopectoralis, facies caudalis: b, concave.
72. Humerus, extremitas proximalis humeri, crista deltopectoralis, terminus distalis, prominent tuberculum m. pectoralis subcutanea thoracica: a, absent.
73. Carpometacarpus, extremitas proximalis carpometacarpi, processus extensorius, prominent, pointed calcar alae: b, present.
74. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, processus intermetacarpalis: a, absent.
75. Carpometacarpus, corpus carpometacarpi, os metacarpale minus, conspicuous craniocaudal curvature of corpus relative to os metacarpale majus: b, absent.
76. Carpometacarpus, extremitas distalis carpometacarpi, processus articularis digitalis major, prominent, cranially directed calcar alae: b, present.

Ossa cinguli membri pelvici

81. Os coxae, pubis, apex pubis, ventral component to otherwise caudomedial orientation: a, absent.
84. Ilium ala postacetabularis ilii, margo lateralis, crista iliaca dorsolateralis, vertex craniolateralis: a, inconspicuous.

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