The Anseriform Relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a New Species from the Lower Eocene London Clay

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ABSTRACT

An associated partial skeleton, including the skull but lacking legs, from the lower Eocene London Clay of Essex, England, possesses derived characters of the coracoid and furcula that show it to belong to the Anseranatidae, which previously had no fossil record. Except for its much larger size, the humerus of this specimen is identical to that of *Anatalavis rex* (Shufeldt) from the late Cretaceous or early Paleocene of New Jersey. The Eocene specimen is described as a new species, *Anatalavis oxfordi,* and the genus *Anatalavis* is transferred from the form-family Graculavidae to a new subfamily, Anatalavinae, of the Anseranatidae. *Anatalavis* is characterized by a very broad duck-like bill, a proportionately very short and robust humerus, and an anterior portion of the pelvis resembling that of ibises and other wading birds more than that of any known anseriform. Other features of its osteology are unique within the order.

Introduction

Waterfowl of the order Anseriformes are among the best known and most distinctive groups of modern birds. Although waterfowl are abundantly represented by Neogene fossils, much of their early evolutionary history has remained obscure. The most informative fossils until now have been the Paleocene and early Eocene remains of *Presbyornis* and its close relatives, which were nearly cosmopolitan in the early Paleogene. *Presbyornis* was shown to have a duck-like skull on the body of a long-legged wading bird and was interpreted as showing a derivation of the Anseriformes from a charadriiform-like ancestor (Olson and Feduccia, 1980b) rather than from the Galliformes, as had been postulated previously. The

more recent studies of Ericson (1996, 1997) confirmed the lack of relationship between the Anseriformes and Galliformes, but the ancestry of the Anseriformes was unresolved beyond a complex of various groups of wading birds, including Charadriiformes. *Presbyornis,* however, was determined to have branched off within the order and constitutes the sister group of the Anatidae proper, with the Anhimidae and Anseranatidae being the primitive outliers of the Presbyornithidae/Anatidae clade.

The giant Paleocene and Eocene groundbirds of the genus *Diatryma,* once thought to have been predatory descendants of crane-like birds, also may be part of the anseriform radiation (Andors, 1988, 1992). The dietary habits of *Diatryma,* however, have been equivocated (Andors, 1992; Witmer and Rose, 1991).

Although no fossils of screamers (Anhimidae) had hitherto been reported, a somewhat more primitive genus is now known from the middle Tertiary of Brazil (Alvarenga, this volume), and I have examined excellent fossils, as yet undescribed, from the lower Eocene Willwood Formation of Wyoming and from the contemporaneous London Clay of England. Thus, of the three major lineages of living Anseriformes, the only one with no early Tertiary (or later) fossil representative is the Anseranatidae, with its sole member being the Magpie Goose, *Anseranas semipalmata,* of Australia.

Two bones from the Hornerstown Formation of New Jersey, a deposit of debated Late Cretaceous or early Paleocene age (Olson, 1994; Hope, this volume), were thought to show some similarities to the Anatidae, but in the absence of associated material they were assigned to the form-family Graculavidae, which contains various taxa resembling primitive Charadriiformes (Olson and Parris, 1987). A new fossil from the London Clay consisting of much of a skeleton, although lacking legs, permits positive identification of the New Jersey fossils as not only belonging to the Anseriformes but belonging to the family Anseranatidae. Thus, the New Jersey and London Clay fossils

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provide the first record of this family, as well as the earliest certain occurrence of the entire order.

The present paper is intended to provide a name for the new fossil from the London Clay and to place on record its more salient osteological features. Full analysis of anatomical details and phylogenetic significance will have to await the appearance of information not presently available for certain extant but sequestered fossils, especially those of Eocene Anhimidae.

Nomenclature for species' binomials and English names of modern birds herein follows Sibley and Monroe (1990).

Order ANSERIFORMES

The primary adaptation of the order Anseriformes is the modification of the bill so that the upper jaw houses an enlarged tongue, which functions as a double-piston pump used in filter-feeding (Olson and Feduccia, 1980a), giving rise to a characteristic "duck-billed" shape that may be modified secondarily for other feeding functions. The following features also are characteristic of the Anseriformes, some being convergent with Galliformes (Olson and Feduccia, 1980b; Ericson, 1996): the configuration of the quadrato-mandibular articulation; the enlarged, deep, curved, blade-like retroarticular process of the mandible; and the enlarged rounded or ovoid "basipterygoid process" on the parasphenoid rostrum, with a corresponding enlarged facet on the pterygoid. These characters are practically all that exist to demonstrate the anseriform relationships of both living and fossil screamers (Anhimidae), in which the bill has either lost or never had the adaptations for filter-feeding. The holotype of the new species described below has a skull with all of the features typical of the order Anseriformes, to which it clearly belongs.

Family ANSERANATIDAE

Recognition of the living Australian Magpie Goose, *Anseranas semipalmata,* as a monotypic family of Anseriformes has been supported by several anatomical studies (e.g., Verheyen, 1953; Woolfenden, 1961; Livezey, 1986), and the distinctiveness of this species is confirmed by DNA sequencing as well (Michael Sorensen, University of Michigan, pers. comm., 1996). Two presumably derived characters group the fossil genus *Anatalavis* in the same family as *Anseranas*. The first is the unique V-shaped furcula with a large, deep symphysis. In other members of the order the furcula is an unelaborated U-shaped structure with a symphysis that is scarcely, if at all, larger than the rami. I interpret the former condition to be a derived character within the Anseriformes. If it is primitive, the only outgroups that show any similarity (and this only in a general way) are storks (Ciconiidae) and, to an even lesser extent, herons (Ardeidae). The second character is the presence of a distinct, large pneumatic foramen in the dorsal surface of the sternal end of the coracoid. Although a similar condition exists in modern Anhimidae, 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 (pers. obs.). Therefore, the condition in modern screamers is obviously independently derived and is not an indication of relationship with the Anseranatidae.

Subfamily ANSERANATINAE

INCLUDED GENUS.—*Anseranas* Lesson.

DIAGNOSIS.—Subfamilial characters are intended as diagnostic only within the Anseranatidae. Rostrum strong, deep, and hooked; frontal area with a large bony casque; attachment for M. depressor mandibulae not greatly developed. Humerus of normal anseriform proportions. Pelvis with anterior portions of the ilia narrow.

Subfamily ANATALAVINAE, new subfamily

INCLUDED GENUS.—*Anatalavis* Olson and Parris, 1987.

DIAGNOSIS.—Rostrum very broad and shallow, not hooked; frontal area without bony casque; attachment for M. depressor mandibulae greatly enlarged. Humerus proportionately very short and extremely robust. Pelvis with anterior portions of ilia markedly expanded and rounded.

Anatalavis Olson and Parris, 1987

TYPE SPECIES.—*Telmatornis rex* Shufeldt, 1915.

INCLUDED SPECIES.—*Anatalavis rex* (Shufeldt), *Anatalavis oxfordi*, new species.

The genus *Anatalavis* was proposed for the species *Telmatornis rex* from the Hornerstown Formation in New Jersey, which differed from the type species *Telmatornis priscus* Marsh in the proportionately much shorter, more robust, and curved shaft of the humerus (Olson and Parris, 1987). *Anatalavis rex* is known so far only from two humeri lacking the proximal ends and was assigned to the form-family Graculavidae, which was used to include various fragmentary postcranial fossils showing similarities to the Presbyornithidae, Burhinidae, and other families. At the time, it was recognized that if cranial material could ever be associated with any of the genera of Graculavidae, it would probably prove possible to refer them to various other families or orders (Olson and Parris, 1987). The age of the fossil birds from the Hornerstown Formation remains controversial, being either latest Cretaceous or early Paleocene (Olson and Parris, 1987; Olson, 1994).

The fossil from the London Clay is herein assigned to *Anatalavis* because the humerus is identical in proportions and has the same distinctive curvature and robustness as that of *A. rex* (Figure 8), which it matches in all details except size. At the time the genus *Anatalavis* was proposed, it was thought that the humerus appeared somewhat duck-like, hence the name, and this is fully borne out by the associated fossil from the London Clay.

Anatalavis oxfordi, new species

FIGURES 1–9

HOLOTYPE.—Partial, associated skeleton, BMNH Department of Palaeontology registry number A5922. Collected 12 October 1991 by Andrew Oxford and Michael Daniels.

TYPE LOCALITY.—Tidal mudflats and basal cliffs at Walton-on-the-Naze, Essex, England.

HORIZON.—London Clay (Ypresian), lower Eocene.

MEASUREMENTS OF HOLOTYPE (in mm).—*Skull* (measurements taken from ventral aspect): Total length from posterior of cranium to tip of bill as preserved, 100 (measurement longer than it should be due to separation of cranium and rostrum); length from posterior of cranium to apparent nasofrontal hinge, 46.5; length and width of right nostril, 8.6 × 5; length from an-terior margin of nostril to bill tip, 34; maximum width of bill as preserved, 27.5.

Skull (measurements taken from dorsal aspect): Width of interorbital bridge, 21.5; width of frontals at nasofrontal hinge, 12.7; dorsal length and width of narial opening, 12.0 × 6.5; width of internarial bar, ~2.5; width of cranium across squamosal protuberances, 25.3; depth (including occipital condyle) and width (across occipital condyle) of area of cervical muscle attachment, 18.5 × 19.3.

Mandible: Length of retroarticular process, 11.0; depth of retroarticular process at midpoint, 6.9.

Pterygoid: Total length, 11.4; greatest diameter of basipterygoid facet, 4.6.

Atlas: Depth, 9.8; width, 8.5.

Axis: Length of centrum, 12.2; depth, 10.8.

Thoracic Vertebra (19th?): Length of centrum, 10.9.

Caudal Vertebra: Width (double the distance from tip of transverse process to midline), 17.8; length of centrum, 6.7.

Furcula: Length from apex of right ramus to farthest extent of symphysis, 53.7; depth of symphysis, 14.4; width and depth of ramus at broadest point, 7.0 × 2.1.

Coracoid: Length from head to internal angle, 48.0; width and depth of shaft at approximate midpoint (narrowest point below procoracoid process), 8.7 × 4.5; depth through head, 9.3; distance from distal margin of procoracoid foramen to internal angle, 29.0; width of sternal articulation, 22.3.

Scapula: Length from acromion to posterior tip, ~79; width of articulation including acromion, 12.5; depth of articular end, 4.4; greatest width of shaft, 7.0.

Sternum: Anterior depth through carina, 39.3; estimated width through third costal facet, 42.5; width of anterior base of carina, 5.6.

Pelvis: Width across antitrochanters (estimated by doubling distance to midline), 46; length from anterior margin of iliac shield to posterior margin of antitrochanter, 52; anterior depth of synsacrum, 24.

Humerus: Length, 119.3; length from head to distal margin of pectoral crest, 41.7; width and depth of shaft at midpoint, 9.7 × 7.8; depth through internal tuberosity, 20; distal width and depth, 22.3 × 11.7; length of radial condyle, 11.6.

Ulna: Width and depth of shaft at approximate midpoint, 6.6 × 6.8; distal depth ~13; distal width, 10.7+.

Ulnare: Greatest diameter, 13.5.

Carpometacarpus: Length, 69.5; length from proximal symphysis to distal end, 43.8; length of intermetacarpal space, 32.8; length of distal symphysis, 11.0; proximal depth, 18.5; width of trochlea, 9.7; distal width, 10.0; greatest width of major metacarpal, 6.9.

Alular Digit: Length, 21.3.

Major Digit, Phalanx 1: Length, 30.2; proximal width, 8.0; distal depth, 7.8.

Major Digit, Phalanx 2: Length, 22.7.

Minor Digit: Length, 15.2.

ETYMOLOGY.—Dedicated to the collector and donor, Andrew Oxford, of Great Mongeham, Kent.

DIAGNOSIS.—Much larger than *Anatalavis rex* (Table 1).

PRESERVATION OF THE HOLOTYPE.—The holotype is essentially an associated, partially articulated skeleton lacking the posterior half of the pelvis, the tail (except one caudal vertebra), and both hindlimbs. The skull, vertebral column, pectoral girdle, and wings are present, although in various states of preservation and with some elements missing (e.g., the right wing is missing except the proximal two-thirds of the humerus and one phalanx).

Cranium and Bill (Figures 1, 2): The skull is considerably distorted through compression and by having been pushed into other bones. Although the rostrum and cranium appear to be continuous, they are actually no longer articulated and have bone, mostly of the palatal region, in the intervening space. The cranium is abraded along the left (dorsal) margin, the palatines are crushed and distorted and are pushed over to the right of the midline. The right quadratojugal is present and more or less in place. What may be most of the left quadratojugal was broken off and is present as a separated bone. The left pterygoid is well preserved as a separate bone (Figure 3). The

TABLE 1.—Comparative measurements (mm) of the humerus of the two species of *Anatalavis* (*A. rex*, holotype and paratype, from Olson and Parris, 1987).

Measurement	A. rex	A. oxfordi
Length from distal end of pectoral crest to ulnar condyle	49.1, 50.7	80.0
Shaft width at midpoint	5.4, 5.6	9.7
Width of shaft at proximal extent of brachial depression	7.2, 7.5	13.2
Depth through radial condyle	7.3, 7.5	12.1
Distal width	3.6, 13.2	22.3

rostrum has portions of the left margin abraded. The entire bill is turned upward through compression, having been pressed into an underlying portion of humerus that has made a great depression in the left dorsal surface, which is seen as a large tumescence in ventral view. As seen in dorsal aspect, crushing has produced a large, somewhat triangular pit in the cranium just anterior to the parietals. The nasal part of the nasofrontal articulation is very badly crushed and distorted on the left side but is somewhat better preserved on the right. The left nostril is crushed and almost obliterated, whereas the right one is almost undistorted.

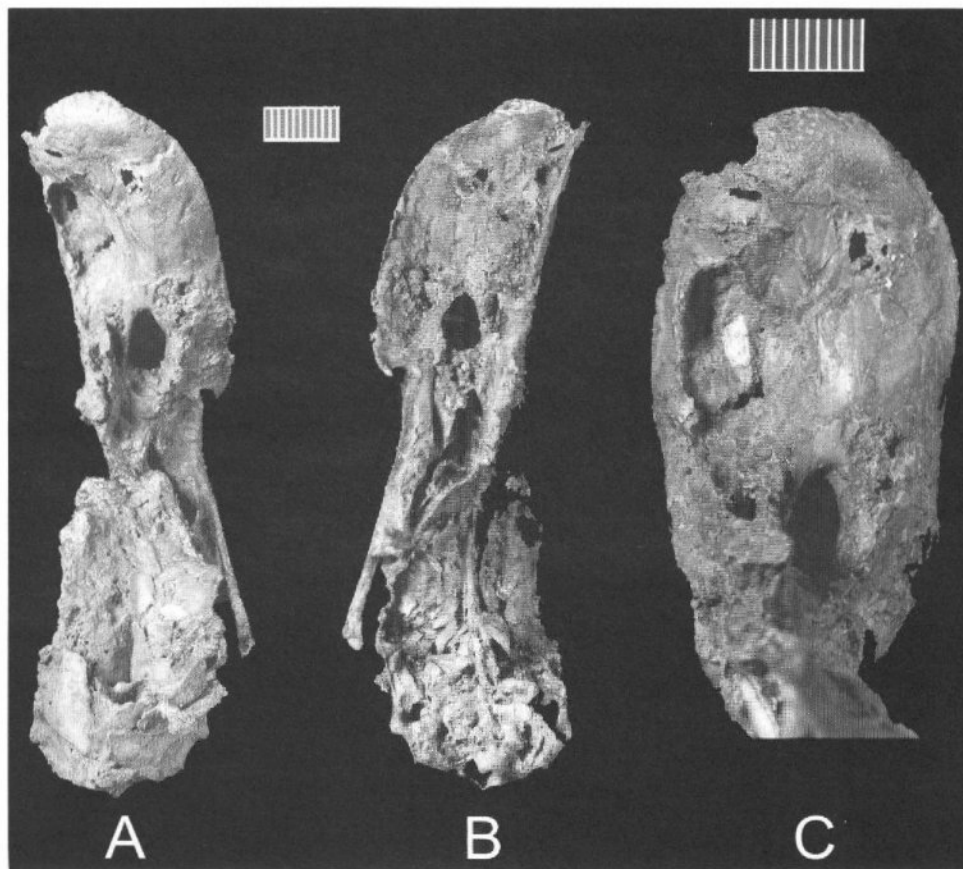*Lacrimal?:* What is possibly a portion of the right lacri-

FIGURE 1.—Skull with rostrum of *Anatalavis oxfordi* (holotype, BMNH A5922): A, dorsolateral view; B, ventrolateral view; C, rostrum in direct dorsal view. Scales in mm.

mal was found under the right orbit, but it is so fragmentary that no interpretation can be made of it. Regardless, it is clear from the cranium that the lacrimal was not fused.

Mandible (Figure 4):   The mandible appears to have slipped forward during burial, and most of it has been eroded off the original block of matrix. Only the right articular por-
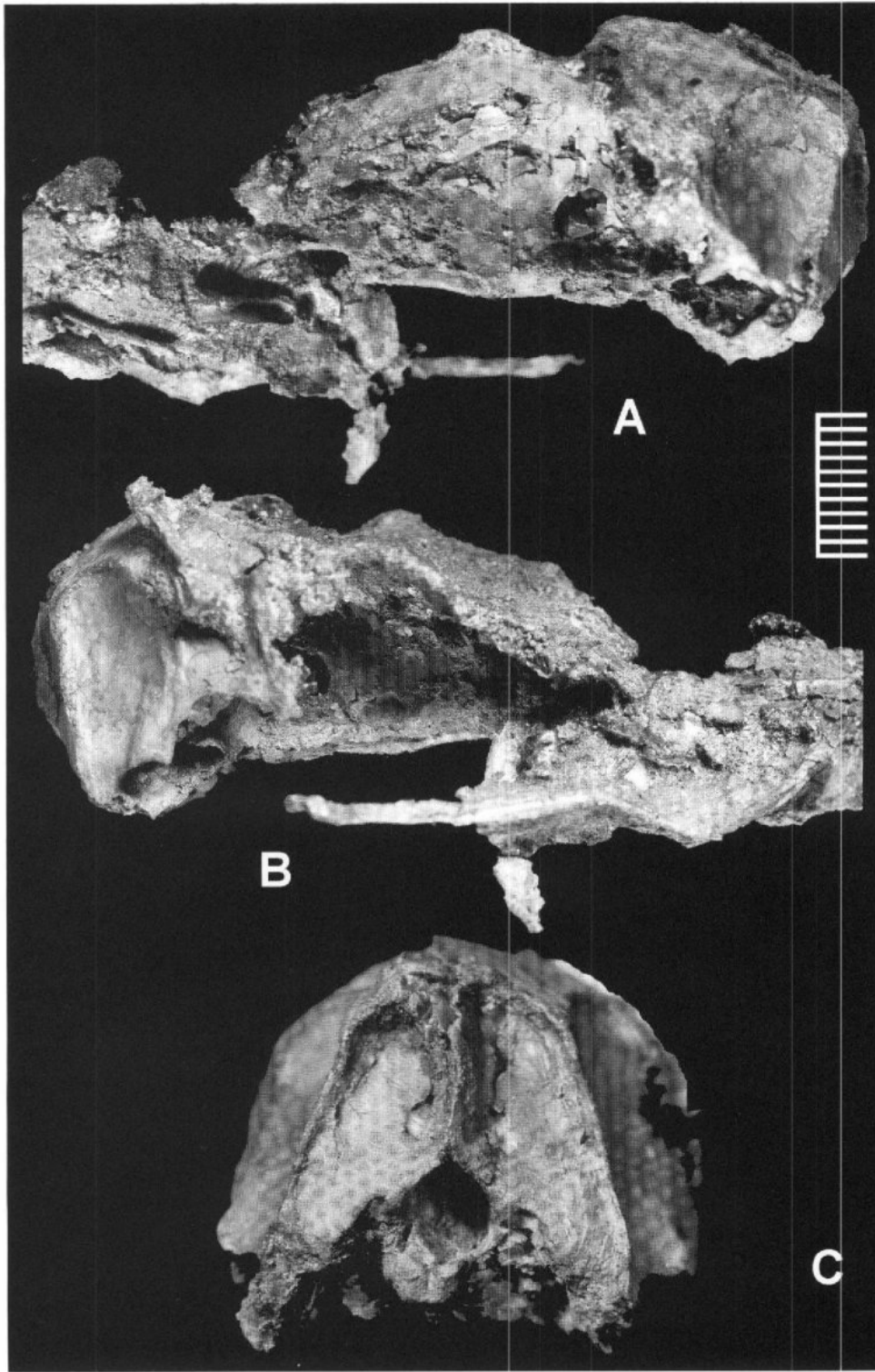
FIGURE 2.—Cranium of *Anatalavis oxfordi* (holotype, BMNH A5922): A, left lateral view; B, right lateral view; C, posterior view. Scale in mm.

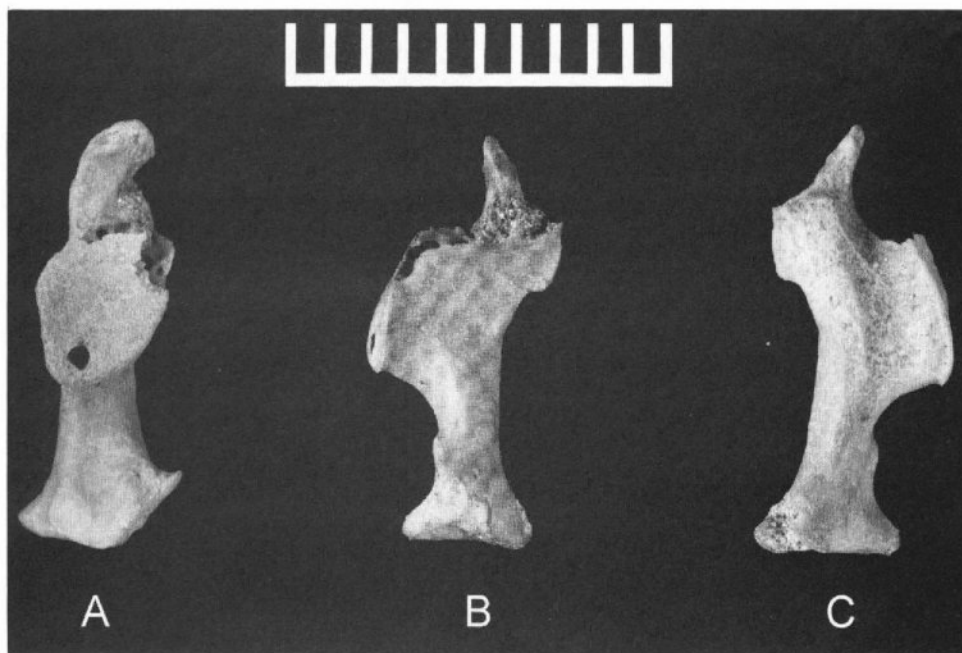FIGURE 3.—Left pterygoid of *Anatalavis oxfordi* (holotype, BMNH A5922): A, medial (internal) view; B, dorsal view; C, ventral view. Scale in mm.
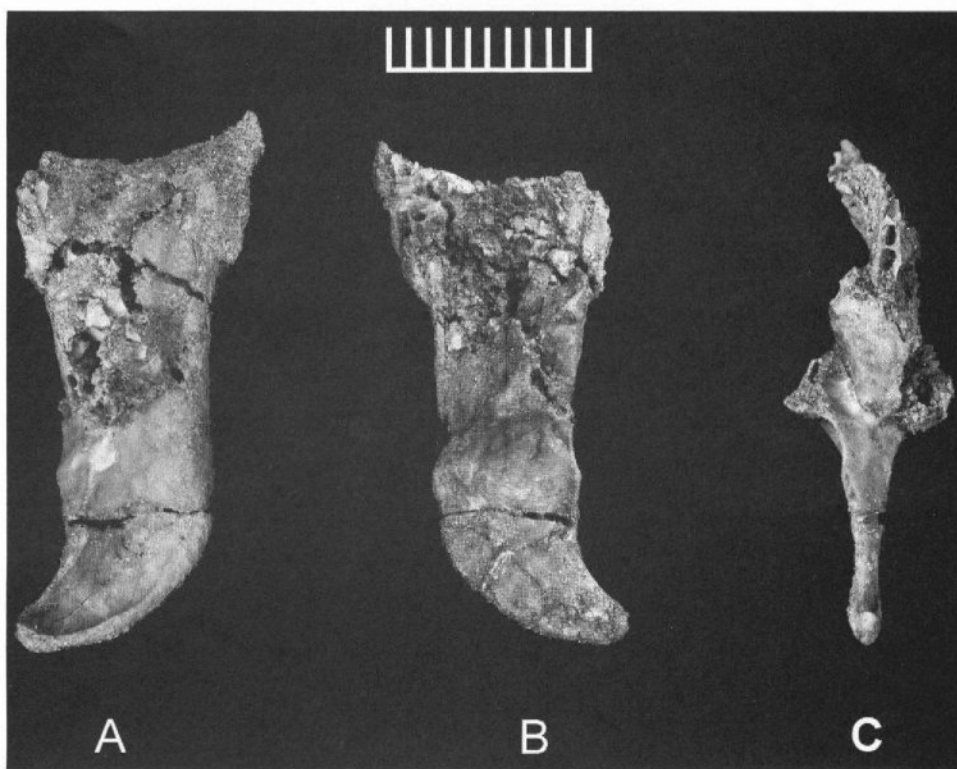

FIGURE 4.—Right articular portion of the mandible of *Anatalavis oxfordi* (holotype, BMNH A5922): A, lateral (external) view; B, medial (internal) view; C, dorsal view. Scale in mm.

tion, with retroarticular process and an unidentified adherent piece of bone, was preserved with the specimen, lying under the rostrum.

Vertebrae: Vertebrae 1 through 4 are present, as are at least four thoracics, fragments of other vertebrae, and a single caudal lacking most of the right transverse process and neural crest. There also are various fragments of ribs and other pieces of unidentified bone.

Furcula (Figure 5): Complete except lacking the very tip of the left ramus and showing some lateromedial distortion.

Coracoids (Figure 6A–F): The right coracoid lacks the external angle and the tip of the procoracoid process. The left lacks the head and the tip of the external angle.

Scapulae (Figure 6G): Both are present and complete except the left lacks much of the coracoidal articulation.

Sternum (Figure 7): This lacks the posterior one-third or so, with much of the left side being badly damaged. The anterior part of the carina is well preserved. The sternocoracoidal processes are variously damaged or obscured, and the dorsal surface of the anterior portion is obscured by the anterior part of the pelvis and matrix.

Pelvis (Figure 7): This consists of the anterior half or more. The right side is lacking posterior to the anterior iliac shield, and the left side is obscured anteriorly by the sternum but posteriorly preserves the dorsal part of the acetabulum, antitrochanter, and part of the posterior portion of the ilium.
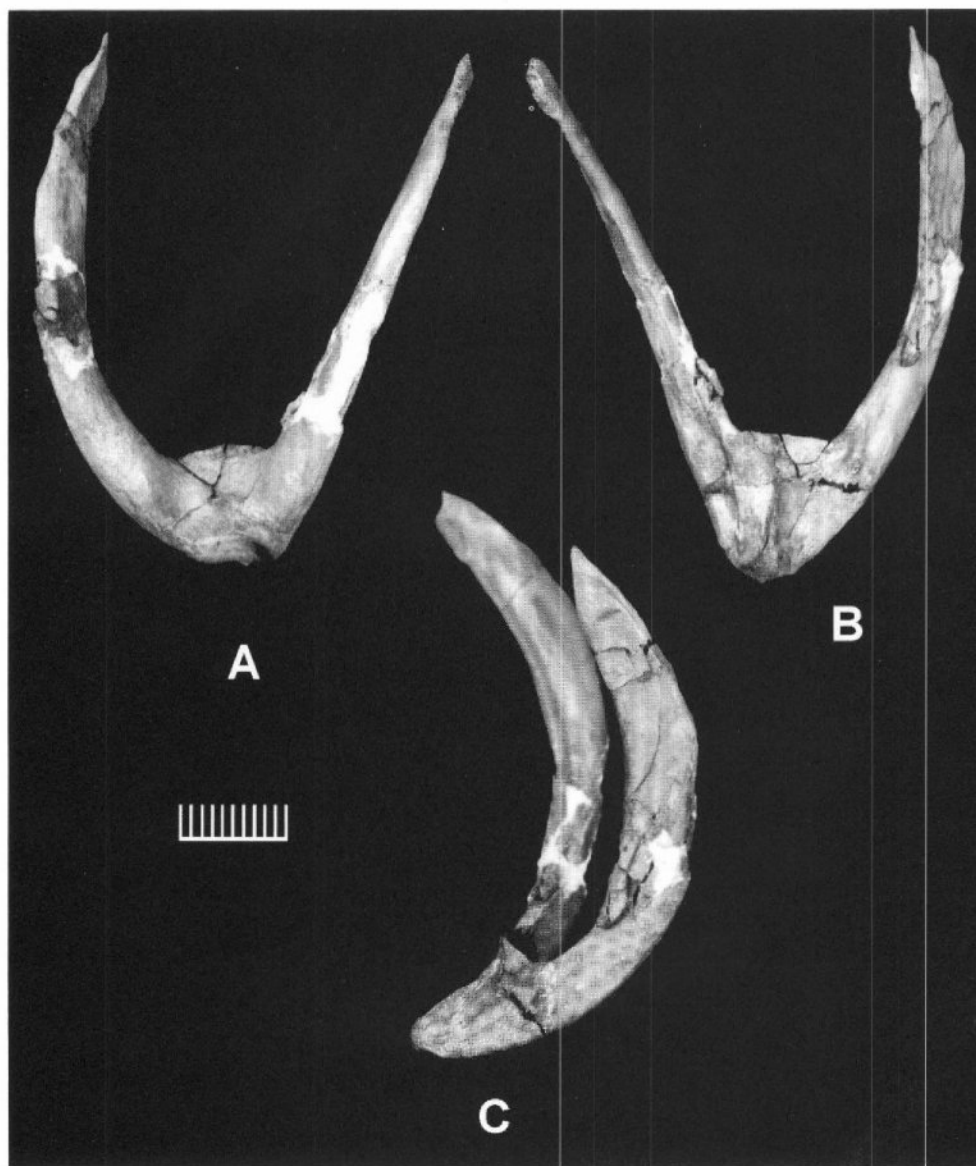

FIGURE 5.—Furcula of *Anatalavis oxfordi* (holotype, BMNH A5922): A, anterior view; B, posterior view; C, right lateral view (rotated slightly clockwise). Scale in mm.
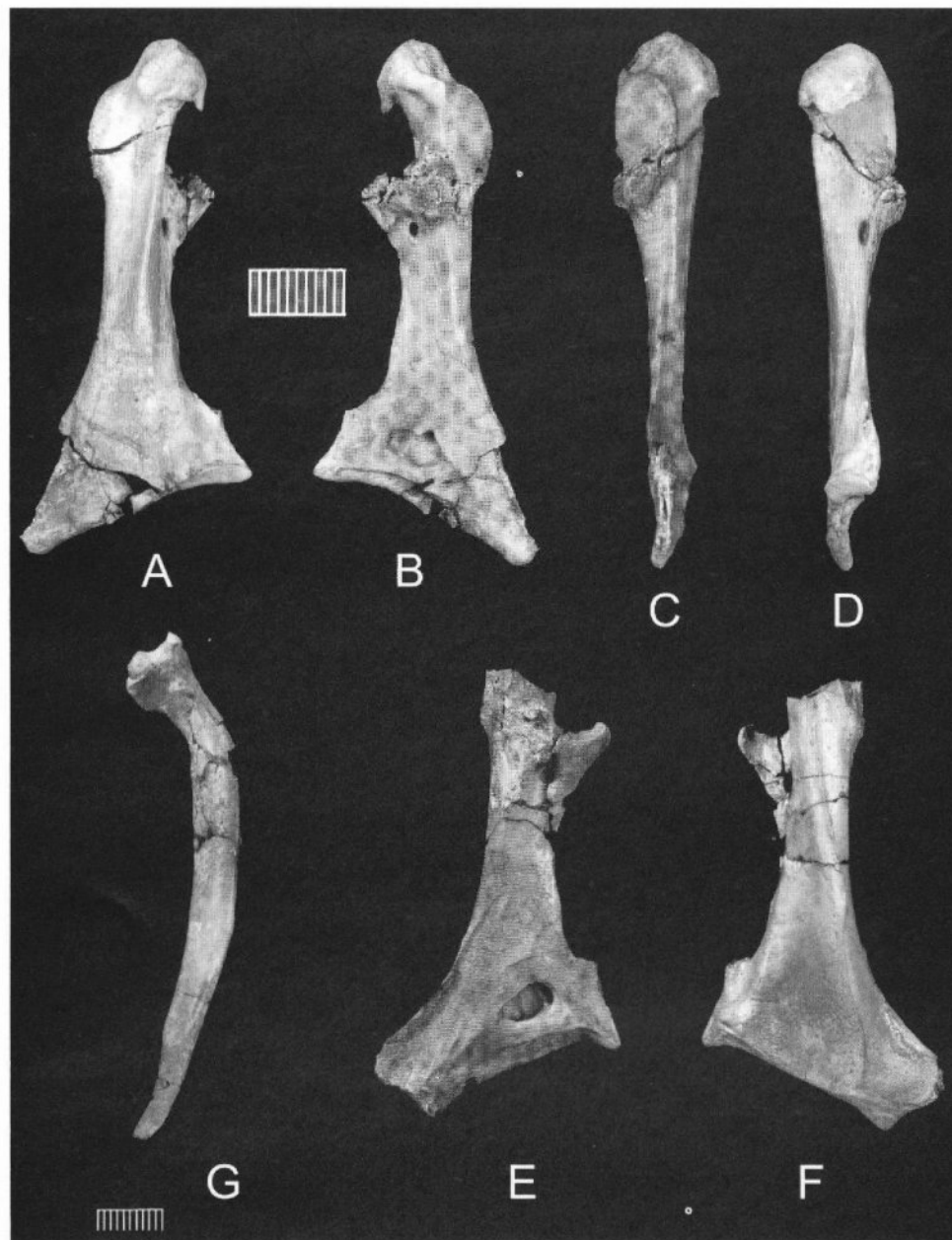
FIGURE 6.—Coracoids and scapula of *Anatalavis oxfordi* (holotype BMNH A5922): A–D, right coracoid in (A) ventral view, (B) dorsal view, (C) lateral (external) view, (D) medial (internal) view; E,F, left coracoid in (E) dorsal view, (F) ventral view; G, right scapula in ventral view. Scales in mm.

Humeri (Figure 8): The left is complete, lacking a bit of the pectoral crest and has the proximal end somewhat crushed and distorted. The right lacks the distal one-third and is much crushed and obscured by adhering matrix and bone.

Radius and Ulna: These are represented only by the distal two-thirds or more of the left radius and ulna. The radius lacks much of the articular end, and the ulna has the internal condyle broken and the distal end obscured by an adhering piece of bone.

Carpal Bones: Only the left ulnare (Figure 9) was located and identified.

Carpometacarpus (Figure 9): The right is lacking. The left is complete, having been broken and repaired, with a small piece of the major metacarpal missing and the whole element showing some compressional distortion.

Alar Phalanges (Figure 9): All phalanges of the major and minor digits of the left wing are present, as is phalanx 1 of the right major digit. The single alular digit is presumably that of the left side as well.
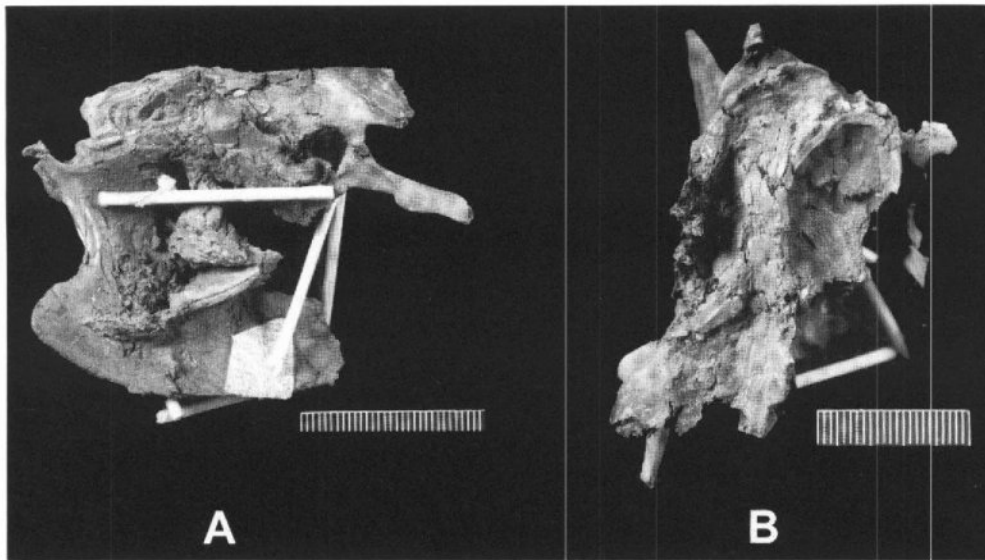
FIGURE 7.—Sternum and pelvis of *Anatalavis oxfordi* (holotype, BMNH A5922): A, left lateral view; B, dorsal view. Scales in mm.
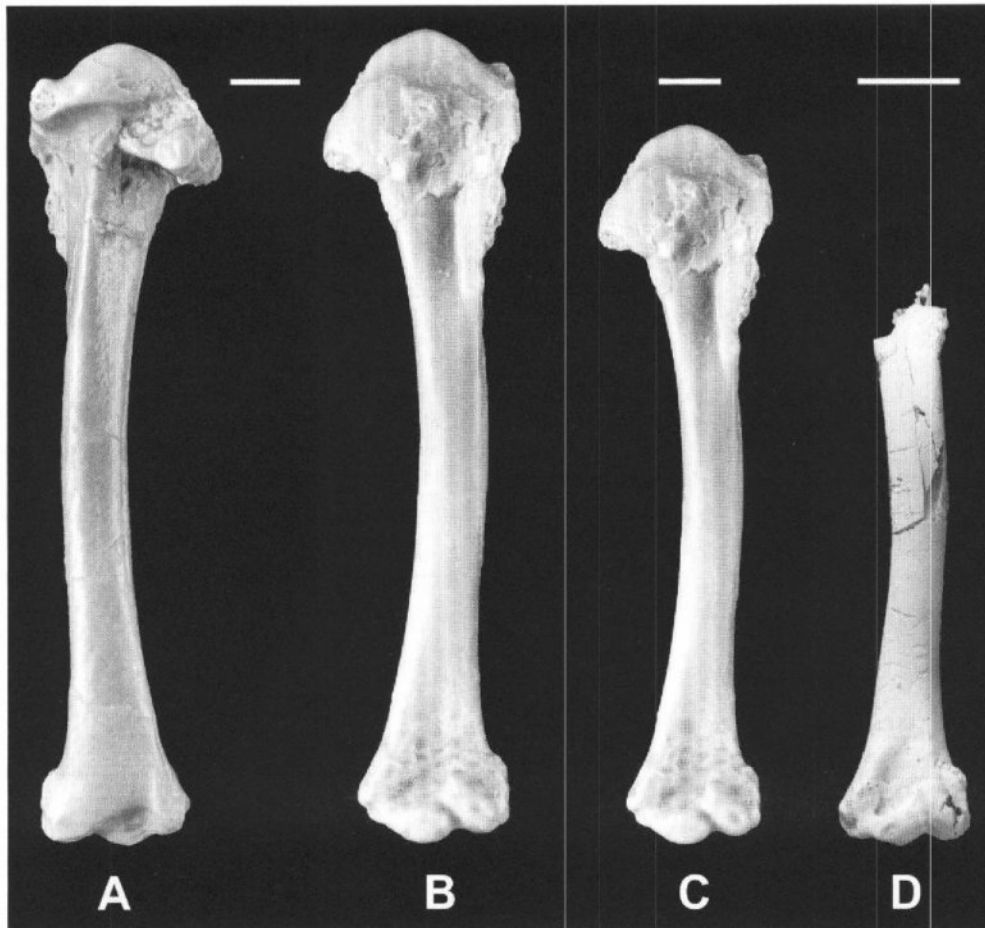
FIGURE 8.—Left humeri of *Anatalavis*. A–C, *A. oxfordi* (cast of holotype, BMNH A5922) in (A) anconal view, (B) palmar view, and (C) palmar view, at lesser magnification. D, *A. rex* (paratype Yale Peabody Museum 948), enlarged for comparison with C. The slight differences are mainly due to slightly different rotation of the specimens. Scale bars=1 cm.

FIGURE 9.—Left manus (ulnare, carpometacarpus, and phalanges) of *Anatalavis oxfordi* (holotype, BMNH A5922) in (A) dorsal view and (B) ventral view (bottom). Scale in mm.

Description and Comparisons

Direct comparisons were made with the three major groups of living Anseriformes. Anhimidae: *Chauna chavaria* male, BMNH S/1954.3.3. Anseranatidae: *Anseranas semipalmata* male (by skull morphology), BMNH 1891.7.20.110; female (by skull), BMNH 1862.7.6.6 (Vellum catalog 441c). Anatidae: *Dendrocygna bicolor* male, BMNH S/1952.1.163; *Anser fabalis*, BMNH 1930.3.24.204.

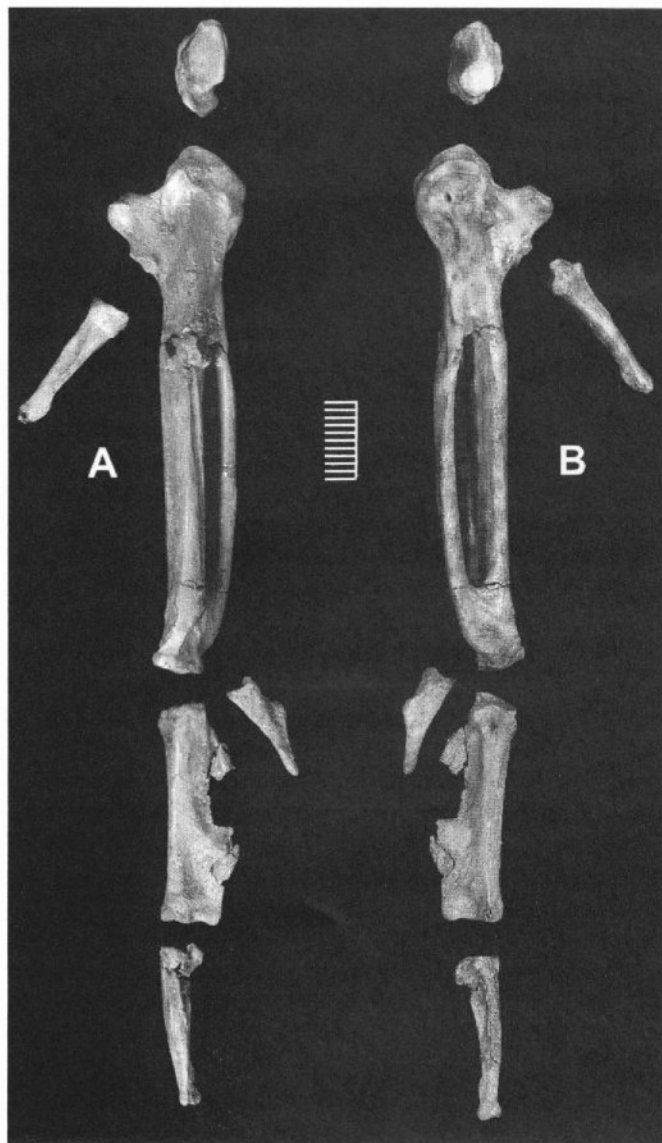Using the descriptions and photographs, further comparisons were made with various other taxa of Anseriformes and with Eocene fossils assigned to the Anhimidae and Presbyornithidae, using collections of the National Museum of Natural History,

Smithsonian Institution, Washington, D.C., and of Michael Daniels.

CRANIAL ELEMENTS

SKULL (Figures 1, 2).—There is so much crushing and distortion of the skull that interpretation of many of its aspects is often very difficult. The bill is obviously very different from that of *Anseranas* in being short and very wide, with the bone being quite thin. How concave the ventral surface may have been is now difficult to say, but it cannot have been as deeply excavated as in *Anseranas*. The tip is extremely broad and rounded, quite unlike the pointed, nail-like tip of *Anseranas*. The nostrils are very short, broad, and rounded compared with any other anseriform. The internarial bar is very narrow. As preserved, the nostrils in ventral view are almost completely exposed, there apparently being no roofing over of bone (secondary palate) by the maxillopalatines. If this is not the product of breakage, then the condition is unlike that of *Anseranas* or the Anatidae and is more like that in the Anhimidae. The posterior flange of the rostrum below the anterior articulation of the quadratojugal bar is reasonably well developed, about as in *Dendrocygna*, and is not as large, elongated, and pointed as in *Anseranas*.

The interorbital bridge is much wider than in *Anseranas* and bears no hint of the bony casque of that species. From the appearance of the left side, the lacrimals must have been unfused, as in *Anseranas*, which is the primitive condition shared with *Presbyornis* and Anhimidae, as opposed to the Anatidae, in which the lacrimals are fused.

The postorbital process is quite short and blunt, unlike any of the anseriforms compared (smaller in *Chauna*, but pointed). The posterior portion of the temporal fossa bears extremely broad, nearly rectangular scars indicating great development of M. depressor mandibulae, perhaps more so than in any extant waterfowl. In *Anseranas* these scars are narrow and are much less distinct. The anterior temporal fossa is hardly distinguishable in the fossil, however, indicating lesser development of the mandibular adductors. The combination of the deep scars of the depressor mandibulae and the well-developed area of attachment of the cervical musculature produces very distinct nuchal crests on the occiput (Figure 2C). The occipital area may have been crushed lateromedially, thus reducing the size of the foramen magnum, which seems comparatively small, although the occipital condyle is large relative to that of *Anseranas*. There are two vertically oriented, narrow, elongate foramina situated where the large, oval occipital fontanelles occur in most Anseriformes, the two presumably being homologous. It is not clear whether these are evolutionarily incipient fontanelles or whether the fontanelles have become mostly closed by bone, as occurs in certain modern waterfowl.

PTERYGOID (Figure 3).—By virtue of the distinctive facet for articulation with the basipterygoid process of the parasphenoid rostrum, the pterygoid of *Anatalavis* is recognizably anseriform, yet it differs markedly from modern members of the or-

der. The bone is very short and robust, with the basipterygoid facet proportionately very large but nearly round in shape rather than being an elongate oval as in *Anseranas* and *Anser.* The quadrate articulation is much larger and more expanded, and the palatine articulation is completely offset laterally from the main (long) axis of the bone, rather than being in a line with it as in other anseriforms.

MANDIBLE (Figure 4).—Only the right articular is preserved, and this has a large, blade-like retroarticular process that curves upward at the tip. It is very anseriform in appearance but is shorter, deeper, and thicker than typical forms, looking more like that in *Chauna,* although it is relatively larger. The medial process, although broken, is very small, unlike any modern anatid, and the lateral process is likewise not nearly as well developed. Although partly obscured by an adhering piece of bone, the articular surface looks typically anseriform, perhaps most similar to that in *Chauna.* The ramus seems to rise immediately to a deep coronoid process.

The recessus conicalis is absent. This is a deep conical hollow extending on the medial side from the retroarticular process anteriorly under the articulation. It represents a derived character uniting the Presbyornithidae and Anatidae, but it is lacking in *Anseranas* and the Anhimidae (Ericson, 1997).

AXIAL POSTCRANIAL SKELETON

THORACIC VERTEBRA.—The best-preserved thoracic vertebra appears to be equivalent to the 19th of *Anseranas* (which is the sixth in front of the sacrum and the first with a full thoracic rib, but no sternal attachment, so that technically this would be the last cervical). This is very similar to that in *Anseranas* except that the sides of the centrum are concave, with a small pneumatic foramen that is lacking in *Anseranas.* Evidence from various Eocene waterbirds suggests that the condition of having concavities on the centrum, which is characteristic of the Charadriiformes, for example, may be primitive.

FURCULA (Figure 5).—The furcula is absolutely distinctive in being V-shaped and having a long, broad symphysis, thus resembling only *Anseranas* among the Anseriformes, which otherwise have a simple U-shaped furcula. The fossil differs from *Anseranas* in that most of the symphysis is a thin, nearly translucent sheet of bone with a sharp, low crest running down the midline on the posterior face, whereas in *Anseranas* the symphysis has become thickened and pneumatized, with a pneumatic foramen on the dorsal surface and the posterior crest much less distinct. In lateral view the fossil is wide throughout but is thin and flat lateromedially, whereas in *Anseranas* the rami become narrower toward the symphysis but are much thicker lateromedially than in the fossil. The ramus in the fossil comes to a very sharp point dorsally but is not expanded into an angular flange on the anterodorsal edge as in *Anseranas,* which gives the ramus in the latter a more curved appearance.

The furcula in both *Anatalavis* and *Anseranas* differs from that in the Anatidae in being less curved, with the portion pos-

terior to the articulation not forming an angle and extending posteriorly. The modern Anhimidae are utterly different from any of these in having a furcula that is very broad, flat, and pneumatic posteriorly on both rami.

CORACOID (Figure 6A–F).—The fossil has a narrow, pointed procoracoid process, whereas in *Anseranas* this is much broader, blunter, and extends farther sternally. The procoracoid process in *A. oxfordi* has a distinct circular foramen. This is the primitive condition that in Anseriformes is retained in *Anseranas,* Eocene and modern Anhimidae (in the latter it may sometimes be absent; see Alvarenga, this volume), and the Presbyornithidae. The procoracoid foramen has been lost in all Anatidae. Although a similar structure appears in the New Zealand fossil genus *Cnemiornis* and in some individuals of *Cereopsis* (Livezey, 1989), this probably evolved secondarily through ossification of ligaments.

On the internal dorsal surface of the sternal end of the coracoid of the fossil there is a large, sharply delimited, ovoid pneumatic foramen. This also is found in *Anseranas,* where it may vary from a larger, although less distinctly edged, foramen, to a depression with only a pinhole foramen. A very large pneumatic foramen occurs in about the same place on the coracoid of modern Anhimidae, but this is entirely absent in the Eocene members of the family and must therefore have evolved independently as a result of the extreme pneumatization of the skeleton in modern screamers.

The whole sternal end of the bone in the fossil is more expanded, with the external angle a longer, sweeping wing. There also is a distinct projecting angle on the medial edge just above the internal angle that is not found in *Anseranas.* In sternal view the medial part of the sternal articulation is not nearly as deep and expanded as in *Anseranas.*

SCAPULA (Figure 6G).—This bone appears to be relatively longer than in the Anatidae but is not as narrow as in *Anseranas* and apparently has the acromion narrower and more pointed.

STERNUM (Figure 7).—In lateral view the sternum differs from that of *Anseranas* in having the apex of the carina more rounded and undercut by a broad, rounded notch. The distinctly projecting, blunt, triangular manubrial spine in the fossil is lacking in *Anseranas.* In these respects the sternum in the fossil is more similar to that in *Chauna;* however, in *Chauna* the manubrium is shorter and blunter.

PELVIS (Figure 7).—The remaining portion of the pelvis is very different from that in any known member of the Anseriformes because the preacetabular portion is relatively short and the anterior iliac shield is very broad, rounded, and deeply excavated for the iliotrochantericus muscles, leaving a broad, well-defined dorsal ridge. In overall appearance, the pelvis in the fossil is more like that in certain wading birds, such as ibises (Plataleidae) and other Ciconiiformes, or Charadriiformes, than in any anseriform. The acetabulum in the fossil is relatively larger than in *Anseranas.*

The ilia appear to be fully fused to the sacral vertebrae, as in all living Anseriformes, which makes the unfused innominates of *Presbyornis* seem all the more anomalous.

PECTORAL APPENDAGE

HUMERUS (Figure 8).—The humerus is characterized by the extremely short, robust shaft with markedly sigmoid curvatures both anteroposteriorly and lateromedially. The total length of the bone is 33% shorter than in *Anseranas*, yet the shaft is slightly wider, indicating very different proportions and presumably a much different flight pattern. The pectoral crest is very broad and rounded, unlike *Anseranas* or the Anatidae, but is somewhat similar to *Chauna*. The head and internal tuberosity are massive, and the capital groove is extremely wide and deep, unlike other anseriforms. The orientation of the internal tuberosity may have been distorted by compression and perhaps pushed distally; regardless, it overhangs the tricipital fossa, which is small and may not have been pneumatic (obscured by pyrite). The capital ridge is very well defined.

The distal end is expanded and flattened compared with most Anatidae but is generally similar to that of *Anseranas* except that the brachial depression is longer and narrower, the radial condyle is longer, and the olecranal and tricipital fossae are slightly deeper. The twisting of the shaft is remarkable because it appears as though the distal end has been rotated clockwise about the long axis of the bone by perhaps 15° or more.

RADIUS AND ULNA.—In their incomplete condition there is little to be said about these elements. Compared with *Anser*, the fossil radius agrees with *Anseranas* in the more expanded distal end and more slender shaft, which is more sharply angular in cross section, with more flattened surfaces than in *Anseranas*.

CARPOMETACARPUS (Figure 9).—This element agrees with that of *Anseranas* in being short and stout, although it is more robust even than that in *Anseranas*. It is intermediate in length between the male and female specimens compared. The alular metacarpal is more vertically oriented than in *Anseranas* and is more like that in the Anatidae. It also is much blunter, with a larger digital facet.

ALAR PHALANGES (Figure 9).—Phalanx 1 of the major digit is relatively short and stout, as in *Anseranas*, but the proximal articulation is wider and not as deep. Phalanx 2 of the major digit and the minor digit are each relatively shorter, the former much more so, than in *Anseranas*.

Discussion

The two species of *Anatalavis* provide the only recognized occurrence of the family Anseranatidae in the fossil record. *Anatalavis rex*, from the Hornerstown Formation of New Jersey, whether Late Cretaceous or early Paleocene in age, also provides the earliest certain record of the entire order Anseriformes. The material of *Anatalavis oxfordi*, from the lower Eocene London Clay, is more complete than that of any early

Tertiary anseriform yet described, apart from *Presbyornis*, and provides us with a new set of clues regarding early evolution in waterfowl.

The skull in *Anatalavis oxfordi* indicates that it was most likely an obligate filter feeder. The bill is very broad yet is thin and weak. The retroarticular process of the mandible is quite well developed, although not nearly to the extent observable in the more extreme members of the Anatidae, yet the massive development of M. depressor mandibulae shows it to have been more adapted for straining, as opposed to grasping, in which the mandibular adductors play a greater role (Goodman and Fisher, 1962). This is practically the opposite of its nearest presumed relative, the Australian Magpie Goose (*Anseranas semipalmata*), in which the bill is strong, deep, and hooked and is used in digging out tubers and other plant material (Frith, 1967).

Although the palate is very poorly preserved in the holotype of *A. oxfordi*, the fundamentally different morphology of the pterygoid compared with modern Anseriformes suggests that aspects of the organization and function of the skull in *Anatalavis* may have differed considerably from that in living waterfowl.

In the shoulder girdle, the peculiar structure of the furcula and the pneumatic foramen in the dorsal surface of the sternal end of the coracoid are considered to be derived characters uniting *Anatalavis* and *Anseranas* in the family Anseranatidae. The two otherwise have very little else in common that is not generally present in most of the rest of the order.

The proportionately short and very robust, twisted humerus of *Anatalavis* is unique in the order and bespeaks a different mode of flight that probably was very strong and rapid. Many extant waterfowl are strong, fast fliers without having such a robust humerus, however. The overall proportions of the humerus are more like those of a falcon (*Falco*, Falconidae), although why a filter feeder would need such a wing is not easily envisioned.

The pelvis of *Anatalavis* is likewise peculiar for an anseriform in the short, expanded anterior portions of the ilia, whereas in all other waterfowl, including the Anhimidae, the preacetabular part of the pelvis is longer and narrower. From its resemblance to such wading birds as ibises (Plataleidae) and other Ciconiiformes, the pelvis of *Anatalavis* is presumably primitive within the order. The innominate bones, however, are fused to the sacrum, which is a more derived condition also found in Ciconiiformes and other Anseriformes except *Presbyornis*. In the lack of fusion of the innominates, *Presbyornis* more nearly resembles the Charadriiformes.

With the recognition of *Anatalavis* as a member of the Anseranatidae, we can trace each of the three major modern lineages of Anseriformes back to the early Eocene, or earlier in the case of *Anatalavis*. According to the phylogeny developed by Ericson (1997), the Presbyornithidae, which were probably world-wide in distribution in the early Tertiary, are on the lineage leading to the Anatidae proper. As yet unpublished early

Eocene records of the Anhimidae from Wyoming and England establish that this group was in existence at the same time and occurred outside of South America, the modern members of the family evidently being highly derived relicts. *Anseranas* in Australia likewise now appears to be a rather specialized relict of a once more diverse family Anseranatidae.

Although the Anatidae proper probably existed in the Paleogene, they do not appear with any certainty or regularity in the Northern Hemisphere until the Miocene, from which it has been presumed that the family probably originated in the Southern Hemisphere (Olson, 1989). Possibly the Anseranatidae was the more diverse family in the Northern Hemisphere in the Paleogene, and the possible affinities of such taxa as the late Eocene *Romainvillia* Lebedinsky (1927), from France, and *Cygnopterus* Lambrecht (1931), from the early Oligocene of Belgium, with the Anseranatidae should be investigated.

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