

Presbyornis and the Origin
of the Anseriformes
(Aves: Charadriomorphae)

STORRS L. OLSON
and
ALAN FEDUCCIA

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ABSTRACT

Olson, Storrs L., and Alan Feduccia. *Presbyornis* and the Origin of the Anseriformes (Aves: Charadriomorphae). *Smithsonian Contributions to Zoology*, number 323, 24 pages, 15 figures, 1980.—Evidence purportedly allying the Anseriformes with the Galliformes is discredited. The discovery of vestigial lamellae in the Anhimidae, in addition to the characters these birds share with the anomalous Australian Magpie Goose (*Anseranas*), proves their anseriform relationship; within the order Anseriformes, the Anhimidae are highly derived and not representative of the ancestral condition in the order. The abundant Eocene fossil *Presbyornis* combines the body of a shorebird with a duck-like head and shows the Anseriformes to have evolved from the Charadriiformes. The unique filter-feeding apparatus of *Presbyornis* and the Anatidae was the key adaptation that led to the radiation of the order Anseriformes. The skull of *Presbyornis* has its greatest similarity to that of the living Australian duck *Stictonetta*, which on other grounds has been considered primitive. This suggests that a rearrangement of the subgroups of Anatidae may be needed. The fossil record shows that no certain Anseriformes are known before the early Oligocene, indicating a probable mid-Tertiary date for the major radiation of Anatidae. The ancestors of ducks were Charadriiformes that adapted originally for life in shallow saline lakes, where selection pressure for filter-feeding would have been strong. The Anseriformes should be maintained as a separate order following the Charadriiformes. *Presbyornis* is considered still to have had a charadriiform grade of morphology and for the present is retained in the Charadriiformes.

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FRONTISPIECE.—Provisional reconstruction of the skeleton of *Presbyornis* to show proportions and the duck-like head. Details of vertebrae and other lesser skeletal elements remain to be determined.

Presbyornis and the Origin of the Anseriformes (Aves: Charadriomorphae)

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Introduction

The waterfowl (Anseriformes) are among the best known of all groups of birds. The order traditionally consists of two distinctive families, the nearly cosmopolitan Anatidae (ducks, geese, and swans), and the South American Anhimidae (screamers). Members of the Anatidae generally may be recognized by their broad, straight, spatulate bill equipped with lamellae or some modification thereof. Most have short legs and fully webbed toes. The three species and two genera of Anhimidae are large birds with short, somewhat fowl-like bills and rather long legs, with long toes having vestigial webs; considerable morphological differences exist between the two genera, *Anhima* and *Chauna* (Beddard and Mitchell, 1894).

Although much has been written on the relationships among the genera of Anatidae, there is a great deficiency of information on the origin of the Anseriformes and their possible relationships to other orders of birds. A review of the literature (Sibley and Ahlquist, 1972) shows that no conclusive evidence has ever been set forth on the sub-

ject. Speculations on the affinities of the Anseriformes have almost always been made with reference to the attributes of the Anhimidae, which are invariably regarded as primitive within the order, rather than addressing the characteristics and adaptations of the Anatidae. Yet at the same time, it is usually admitted that the Anhimidae are referred to the Anseriformes only for lack of "evidence linking them to some other order" (Sibley and Ahlquist, 1972:87).

At times it has been suggested that the Anseriformes may be related to the flamingos (Phoenicopteridae), but until recently the affinities of this family were equally uncertain. Resemblances between flamingos and ducks are superficial and flamingos have been shown conclusively to belong in the order Charadriiformes, near the Recurvirostridae (Olson and Feduccia, in press). The only other hypothesis with any currency proposes a relationship between the Anseriformes and the chicken-like birds of the order Galliformes. In view of the manifest dissimilarity of these two orders, such an alliance must seem strange to those not acquainted with the antiquated traditions of ornithological systematics. The anseriform-galliform theory of relationships is founded almost entirely on a single morphological character—the supposed similarity in the pterygoid-

Storrs L. Olson, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Alan Feduccia, Department of Zoology, University of North Carolina, Chapel Hill, North Carolina 27524.

parasphenoid articulation. Yet for lack of an alternative, this peculiar idea has been perpetuated and even today has tenacious adherents.

Excellent fossil material of the Eocene bird *Presbyornis* provides strong evidence for a derivation of the Anseriformes from the Charadriiformes (Feduccia, 1978). This mosaic is a true "missing link" without which the origins of the Anseriformes might have remained obscure indefinitely. We intend to undertake detailed studies of the osteology and origins of *Presbyornis* itself in a future paper. For the present we shall review and dispose of the evidence hitherto cited in connection with the extraordinary relationships of the Anseriformes, show the anseriform affinities of the Anhimidae and their proper place in the classification of the order, and discuss the overall morphology of *Presbyornis* with regard to its significance in the evolution of the Anatidae.

ACKNOWLEDGMENTS.—We are grateful to A. R. McEvey, National Museum of Victoria, Melbourne, for supplying skeletons of *Stictonetta*, and John Farrand, Jr., American Museum of Natural History, New York, for a fluid-preserved head of *Anhima*, kindly transported by Richard L. Zusi. Don Baird, Princeton University, made the type of *Eonessa anaticula* available for study.

Robert J. Emry provided Olson with transportation, supplies, hard labor, and good company while aiding in the collection of specimens of *Presbyornis* in 1977. One of these, an intact skull, was expertly prepared by Arnold D. Lewis. In connection with our studies of *Presbyornis* we have repeatedly benefitted from the generous assistance of Paul O. McGrew.

Illustrations are by Jaquin B. Schulz and photographs are by Victor E. Krantz. We gratefully acknowledge David W. Steadman, Glen E. Woolfenden, and George R. Zug for their criticisms of the manuscript.

Review of Previous Ideas of Anseriform Relationships

The history of classification of the Anseriformes was summarized by Sibley and Ahlquist (1972). As mentioned above, most of the literature on

this subject has to do with generic relationships within the Anatidae and very little has been written on the origins of the order as a whole.

Huxley (1867) noted that in the large, rounded parasphenoid articulations for the pterygoids and the strong, upcurved retroarticular processes of the mandible, screamers appear to resemble both the Anatidae and the Galliformes. He remarked on features of the skull in Galliformes that set them apart from either screamers or ducks and placed the last two together in his order Chenomorphae. Despite his conclusion, Huxley's reference to Galliformes in his discussion of the Anhimidae was probably a major factor influencing subsequent taxonomists.

The early work of Garrod (1873, 1874) on thigh muscles of birds produced a classification so completely artificial that it never merited any serious consideration. He placed the Anhimidae in an order Galliformes, but his concept of this order also encompassed the Psittacidae, Cuculiformes, the so-called ratites, the Tinamidae, Rallidae, and Otidae, as well as the true gallinaceous birds. His order Anseriformes included penguins, loons, and grebes as well as ducks. "Common sense revolts at the acceptance of any scheme which involves so many manifest incongruities" (Newton, 1896: 93 [intro.]). Later, Garrod (1876) examined the Anhimidae in more detail and adopted the view that they could not be placed among the Anseriformes. However, most of the features he cited as being unlike ducks are also those, such as the pterylosis, that are unique to screamers and hence also unlike any other birds. Garrod noted similarities in the digestive tract of the Anhimidae to *Struthio* and *Rhea*, while admitting that the trachea and the retroarticular processes of the mandible were duck-like. Garrod also perceived in screamers what he believed to be similarities to Galliformes, all of these being in the skull; nevertheless, in his summary paragraph (1876:199) he stated that "their osteology points in no special direction."

Seebohm (1889) regarded the Anhimidae, although closest to the Anatidae, as forming a connecting link with the Galliformes, this conclusion being based entirely on the same skull char-

acters noticed by Huxley (1867). Shufeldt (1901) in a very general way compared the osteology of screamers with that of anseriforms and galliforms; he considered most features to be anseriform except for several aspects of the skull in which he perceived galliform characteristics. This notwithstanding, he concluded (p. 461) that the screamers were an "independent group standing between the [Anseres] and the ostrich types of birds." No reason was proffered for this last statement. Simonetta (1963), also on the basis of the pterygoid-parasphenoid articulation, postulated a common origin for Anseriformes and Galliformes. Bock (1969; 1970:67) considered "waterfowl and gallinaceous birds . . . to be closely related." Although he stated that "all aspects of their cranial morphology support this conclusion," he cited only "the common possession of a peculiar and unique basiptyergoid articulation" as evidence for this assertion. He also regarded the Anhimidae as being intermediate between the two orders.

The electrophoretic patterns of egg-white proteins of Anseriformes indicated a close relationship among members of the Anatidae but were not conclusive in showing extraordinary affinities (Sibley and Ahlquist, 1972). Nevertheless, these authors still favored the old idea that the Anseriformes might be related to the Ciconiiformes through the flamingos.

The most current hypothesis is that the Anseriformes are related to the Galliformes. As we have seen, the morphological basis for this rests on the alleged similarities in the pterygoid-parasphenoid articulation and the retroarticular processes of the mandible in the two groups. Were it not for this and the superficially fowl-like appearance of the bill of screamers, it is extremely doubtful that a relationship between ducks and galliforms would ever have been entertained, for all other aspects of their morphology are so utterly different.

Galliformes are archetypal fissipedal land birds that scratch and peck for their food. Not one shows the slightest approach towards an aquatic or filter-feeding existence. On the other hand, all members of the Anseriformes are web-footed

swimming and diving birds that are filter feeders or are derived from aquatic filter feeders. Anseriformes differ from Galliformes in almost every anatomical feature imaginable and there is not the slightest resemblance between the two groups in their postcranial osteology. The following tabulation compares a few aspects of the morphology of Galliformes and Anseriformes. In it we have outlined some of the characters that were often used by nineteenth-century anatomists to define higher taxa of birds, though the utility of many of these characters is nil. To these we have added a few of the major postcranial osteological differences. This list could be extended almost indefinitely, but even in this brief form it should indicate that there never has been sufficient reason to regard these two orders as being in any way related.

GALLIFORMES	ANSERIFORMES
Lamellae absent	Lamellae present
Feet unwebbed	Feet webbed
Schizognathous	Desmognathous
Aftershaft present	Aftershaft rudimentary or absent
Syrinx tracheal	Syrinx bronchial
Crop present	Crop absent
Eutaxic	Diastataxic
Deep flexors type 1	Deep flexors type 2 or 4
Intestine type 5	Intestine type 3
Nostrils imperforate	Nostrils perforate
Supraorbital glands absent	Supraorbital glands present
Sternum 4-notched	Sternum 2-notched
Furcula Y-shaped, hypocleidium large	Furcula U-shaped, hypocleidium absent
Coracoid long, narrow, sternal end arched	Coracoid short, wide, sternal end flat
Humerus short, stout, curved	Humerus long, slender, straight
Ulna bowed, internal side flat	Ulna straight, terete
Carpometacarpus short, bowed, usually with an intermetacarpal tubercle	Carpometacarpus long, straight, never with a tubercle
Femur long and narrow	Femur short and stout
Inner cnemial crest of tibia poorly developed	Inner cnemial crest large

Bock's (1970:70) statement that "all aspects of . . . cranial morphology" support a relationship between Anseriformes and Galliformes is abso-

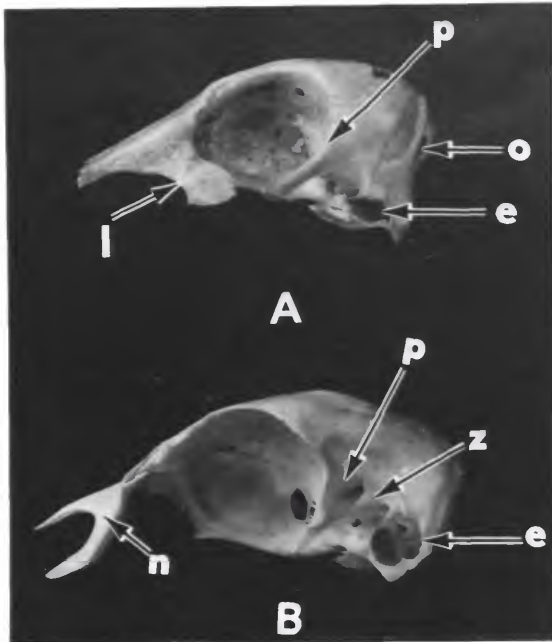


FIGURE 1.—Left lateral view of the cranium and associated fused bones in a duck, *Anas luzonica* (a), and a galliform, *Gallus gallus* (b). Note presence of distinctively forked nasals (n) in *Gallus*; presence of a large, fused lacrimal (l) in *Anas*; fusion of postorbital (p) and zygomatic (z) processes in *Gallus* (zygomatic absent in *Anas*); presence of occipital fontanelles (o) in *Anas*; and the completely different structure of the ear region (e) in these two birds.

lutely false. In Galliformes, unlike most other birds, including Anseriformes, there is typically little or no fusion of the rostral elements. The premaxilla is free because the joints with the nasals, jugals, and palatines do not ossify. The nasals are only lightly fused to the frontals posteriorly, and anteriorly they form characteristic bipronged forks that are particularly apparent in macerated specimens because the premaxilla falls away (Figures 1, 3). The lacrimals are fused in all Anseriformes except *Anseranas*, but are unfused in all Galliformes. The tip of the postorbital process fuses with that of the zygomatic process in Galliformes, leaving a foramen, whereas in the Anseriformes the zygomatic process is absent (Figure 1). Occipital fontanelles are present in almost all Anseriformes but invariably are absent in Galli-

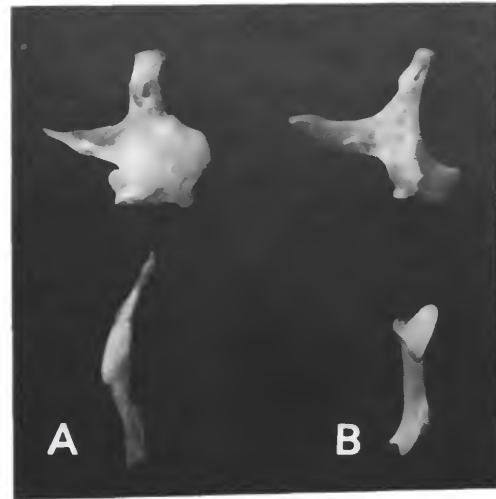


FIGURE 2.—Medial views of right quadrate (top row) and right pterygoid (bottom row) of *Anas luzonica* (a) and *Gallus gallus* (b) to show the total lack of similarity between Anseriformes and in Galliformes in these elements.

formes (Figure 1). There are no similarities between the Galliformes and Anseriformes in the palatines, quadrates (Figure 2), pterygoids (Figure 2), or in the auditory region (Figure 1), and the differences in the bill are too obvious to merit discussion.

Even the supposed similarities of the pterygoid-parasphenoid articulation in Anseriformes and Galliformes are nowhere near as great as implied in the literature. In the Anseriformes the articulating facets on the parasphenoid are very distinct, almost pedicellate, elliptical surfaces with a projecting lip all around (Figure 3). A like facet occurs on the medial surface of the pterygoid (Figure 2). In Galliformes these facets are best developed in the Cracidae and those on the parasphenoid are much more elongate, less distinctly set off from the rostrum, and situated farther posteriorly than in Anseriformes. Those in the Phasianidae are, in fact, rather indistinct and cannot in any way be likened to the condition in ducks and screamers (Figure 3). Furthermore, the facet on the pterygoid is located at the anterior end of the bone in Galliformes, rather than on the medial surface, and is not shaped at all like

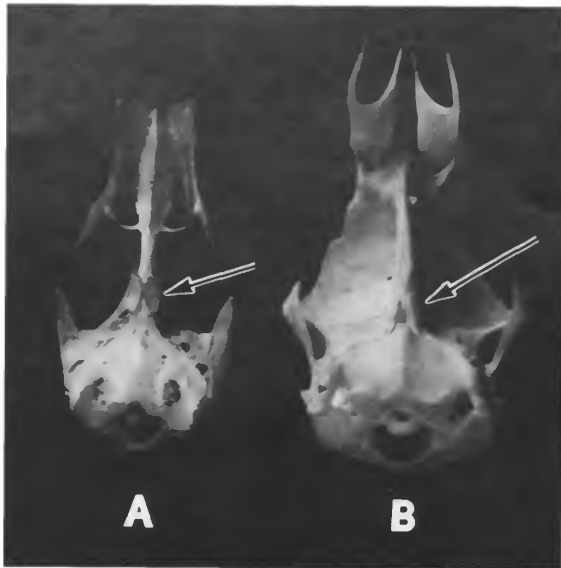


FIGURE 3.—Ventral view of the cranium of a duck, *Anas luzonica* (a), and a galliform, *Gallus gallus* (b), to show the differences in the structure and placement of the so-called basipterygoid processes (arrows).

that of Anseriformes, in which the pterygoid has a large anterior spine, a structure absent in Galliformes (Figure 2).

Although the articular facets on the parasphenoid of Anseriformes and Galliformes are almost always referred to as the “basipterygoid processes,” McDowell (1978) has shown that the so-called basipterygoid processes in birds are not homologous to the structures of the same name in reptiles. He suggested that the avian structures may be neomorphous and that they may have arisen several times within the class.

We dissected an embryo of a duck (*Aythya* sp.) and a young galliform (*Gallus gallus*) to ascertain the nature of these processes in the early stages of development. In the duck, the parasphenoid articulations were oval cartilaginous pads that were entirely free from each other and were only lightly attached to the ossified parasphenoid rostrum. When these pads were removed, the parasphenoid rostrum appeared completely normal and bore no sign of any bony processes or articulations with the pterygoid. Thus, these processes appear

to have arisen completely independently of the rest of the bony structure of the skull, and they become ossified only late in development. In the galliform, the parasphenoid articulations were also cartilaginous but, as in adults, were of a different shape and in a different position from those of Anseriformes. The cartilages were joined at the midline anteriorly and were not as easily removed, leaving distinct, bordered impressions on the parasphenoid rostrum, quite unlike the condition in the duck. There can be little doubt that these structures are not homologous between Anseriformes and Galliformes. They are simply *de novo* surfaces that evolved independently to facilitate the sliding of the pterygoid during cranial kinesis. They are probably not homologous even with the “basipterygoid processes” of other birds.

Nor are the retroarticular processes of the mandible of Galliformes really comparable to those of Anseriformes. Although long and upcurved, these processes in Galliformes are rather slender and rounded and not like the laterally compressed bladelikey hooks characteristic of Anseriformes (Figure 4).

The idea that the anseriform skull is similar to that of Galliformes can have arisen and been perpetuated only as a result of extremely perfunctory examination of specimens. In the skull, as in the rest of their anatomy, the Anseriformes differ altogether from the Galliformes. Although aberrant within the Anseriformes, the Anhimidae are in no way intermediate between ducks and galliforms and share none of the peculiarities of the latter.

Recently, certain biochemical information has been cited as confirming a relationship between Anseriformes and Galliformes. Jollès et al. (1976: 59) determined the amino acid sequence of lysozyme c in eight species of birds, all of which were either Galliformes or Anseriformes. From this they concluded that lysozyme c in the chachalaca *Ortalis vetula*, (Cracidae) “differs from other avian lysozymes c by 27 to 31 amino acid substitutions” and that “the lineage leading to chachalaca lysozyme c separated from that leading to other galliform lysozymes c before the duck lysozyme c

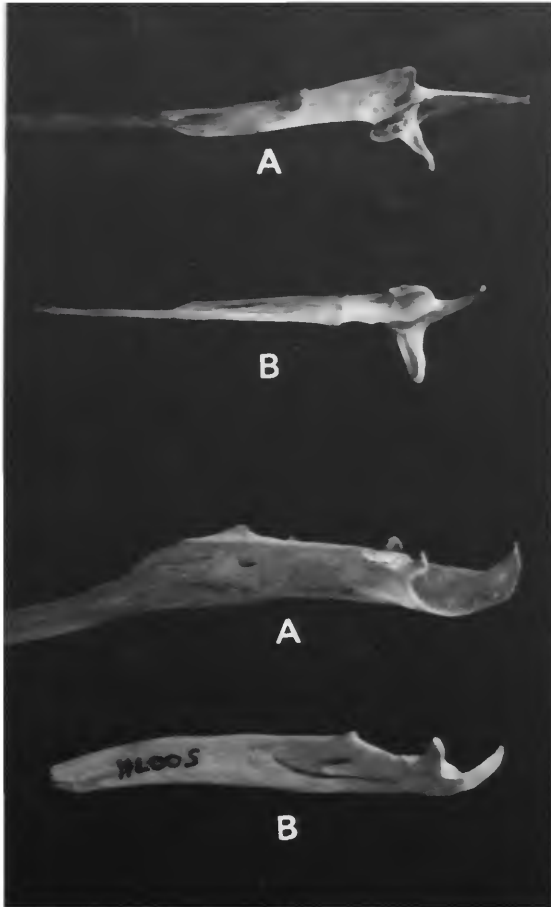


FIGURE 4.—Dorsal (*top*) and medial (*bottom*) views of the right mandibular articulation of a duck, *Anas luzonica* (*a*), and a galliform, *Gallus gallus* (*b*), showing the very different structure of the retroarticular processes and the articulation in general.

lineage did." The other taxa included in their study were "chicken, bobwhite quail, Japanese quail, turkey, and guinea fowl" (presumably *Gallus gallus*, *Colinus virginianus*, *Coturnix coturnix*, *Meleagris gallopavo*, and *Numida meleagris*, respectively, although this is not stated), also "Duck II and Duck III," no indication being given even as to whether these represent different species or not. Outgroup comparisons were made with humans and baboons. Now this may be good biochemistry, but it is not systematics; many more taxa of

birds would have to be studied in order to put this information in its proper phylogenetic context. Nevertheless, Mayr and Cottrell (1979:v) state that the work of Jollès et al. (1976) "has already demonstrated conclusively that the Anseriformes are a side branch of the galliform birds." It seems to us that this optimistic assessment goes well beyond the biochemical data or the conclusions that Jollès et al. themselves drew from it. We doubt that Mayr and Cottrell would have received this paper so enthusiastically had it not been for the long, but unsubstantiated, tradition of a galliform-anseriform relationship found in the earlier literature, or if the paper had been based on a morphological study restricted to the same taxa.

If biochemical studies should suggest a relationship between the Anseriformes and Galliformes, they shall also have to account for the fact that there is not a single bit of evidence from morphology or paleontology that supports such a hypothesis. We cannot imagine any reasonable hypothetical sequence of evolutionary events that could produce a duck from a galliform.

The Anseriform Affinities of the Anhimidae

Because the anseriform affinities of the Anhimidae have at times in the past been doubted, we intend to show that the Anhimidae are indeed related to the Anatidae, but within the Anseriformes they are among the most derived rather than the most primitive members.

In their overall appearance the screamers do not look much like ducks and they possess a number of structural peculiarities that set them apart, not only from the Anatidae, but from other birds as well. These include a thick layer of subcutaneous air-cells, nearly continuous feathering on the body with the apteria vestigial or absent, paired spurs on the carpometacarpus, the absence of uncinat processes on the ribs and the apparently correlated presence of a unique muscle, the *M. costisternalis externus*, running diagonally across the rib cage (Beddard and Mitchell, 1894:540). It should be noted that wing spurs also occur in certain Anatidae, whereas when spurs

are present in the Galliformes, they are always on the tarsometatarsus.

According to Parker (1863), the Anhimidae had once been thought to be gruiform. He remarked on the similarity of the skull and sternum of screamers to the Anatidae and he also suggested that there were similarities to the Galliformes. There is little specific detail in Parker's paper, in which he also finds screamers to "come nearer, in certain important points, to the Lizard," and suggests they might be "one of the nearest living relatives of the marvellous *Archaeopteryx*" (page 518), along with other useless observations.

Aside from the anseriform characters noted by the early anatomists (see above), additional evidence linking the screamers to the Anatidae exists in morphological and behavioral similarities to the Australian Magpie Goose, *Anseranas semipalmata*. The singularity of *Anseranas* has long been recognized by many taxonomists. It has usually been placed either in a monotypic subfamily of the Anatidae or in a family of its own. Of the external features discussed by Delacour (1954), those that are most distinctive and tend toward an anhimid-like condition are: bill with rostral nail large, strong, and overhanging the mandible; lamellae much reduced; much of lower part of tibia unfeathered; toes very long and slender with the webbing greatly reduced; hallux long and not elevated. The trachea is coiled in part externally, lying superficial to the breast muscles, a condition in waterfowl otherwise found only in *Stictonetta*. Additionally, the wing molt is gradual, unlike the Anatidae, in which the remiges are molted simultaneously. Delacour (1954) cites S. MacDowall [sic = McDowell] as providing six distinguishing osteological features of *Anseranas*, five of which are stated to approach conditions met with in the Anhimidae. Woolfenden (1961) enumerated many salient osteological features in virtually all of the skeletal elements of *Anseranas* and vigorously advocated its elevation to full family rank. He, too, noted similarities between *Anseranas* and the Anhimidae, particularly in the humerus, carpometacarpus, sternum, coracoid, and skull, as well as in external features. To these we would

add that the tarsometatarsus in *Anseranas* is quite different from that of other Anatidae and bears a close resemblance, particularly in the distal end, to the Anhimidae.

According to Beddard (1898), in all Anatidae there is a muscular slip from M. biceps femoris (= M. iliofibularis) attaching to M. gastrocnemius pars lateralis, whereas this is absent in the Anhimidae, in which the insertion of M. iliofibularis is typical. We dissected a specimen of *Anseranas semipalmata* and found no connection between M. iliofibularis and M. gastrocnemius. Thus, in this respect it differs from other Anatidae and agrees with the Anhimidae, although there can be little doubt that this is the primitive condition.

Sibley (1960) found that the electrophoretic pattern of egg-white proteins of *Anseranas* was readily distinguished from those of other Anatidae, all of which were quite similar to one another. Boetticher and Eichler (1952) discovered *Anseranas* to be uniquely parasitized by the mallophagan genus *Heteroproctus*. Johnsgard (1961a, 1961b) has remarked on behavioral peculiarities of *Anseranas*, such as parental feeding of young and the building of brood nests for the young after hatching. He also noted that the downy plumage was unlike that in any of the Anatidae, as is the fact that *Anseranas* assumes a juvenal and an immature plumage before acquiring the definitive adult plumage. Certain aspects of behavior, such as mutual preening at the nest, are shared with the Anhimidae and Johnsgard considered *Anseranas* as intermediate between the screamers and typical waterfowl.

Despite the overwhelming body of evidence pointing to the anomalousness of *Anseranas*, Davies and Frith (1964:265) maintained that the outstanding features of the genus are all probably "adaptive," its distinctiveness being a "consequence of becoming a resident bird in a tropical swamp." We reject such a simplistic interpretation and consider *Anseranas* to stand significantly apart from the remainder of the Anatidae. Although differing from the Anhimidae in many respects, *Anseranas* certainly represents a morphological stage similar to that through which the



FIGURE 5.—View of the inside of the mouth of *Chauna torquata* (Anhimidae) to show the row of vestigial lamellae (arrow) on the inside of the upper jaw.

Anhimidae must have passed in becoming increasingly terrestrial (as shown by the reduction of webbing in the feet) and in relinquishing filtering as a means of feeding (as shown by the strong nail and reduced lamellae of the bill).

We have discovered in the Anhimidae an overlooked character that strongly supports their anseriform derivation, namely the presence of vestigial lamellae. Although several authors (Parker, 1863; Garrod, 1876; Mitchell, 1895) have briefly noted the large fleshy tongue in *Chauna*, none seems to have detected these lamellae. Indeed, Pycraft (1910:49) specifically states that the Anhimidae lack "the lamellae along the edges of the beak, so characteristic of the Anseres." This is not the case, and in reality the screamers do retain, in a highly modified form, these most diagnostic of anseriform structures.

The tongue in *Chauna torquata* is elongate, thick, fleshy, and somewhat wrinkled, terminating posteriorly in a set of spiny papillae. It fills the mouth cavity, and although it lacks the laminae along the sides typical of anatids, the tip is fringed with distinctive keratinous bristles. In the roof of the mouth are three longitudinal ridges, the middle one of which is divided into large posteriorly-directed papillae; between these three ridges are two additional rows of papillae. On the ramphotheca along the insides of the upper jaw, extending from the commissure anteriorly to about the level of the midpoint of the nostril, is a series of small but easily discernable lamellae (Figures 5, 6a), about 17 in number. These are best developed posteriorly, becoming indistinct anteriorly. The largest is about 1.5 mm in depth.

Anhima is generally similar except that there

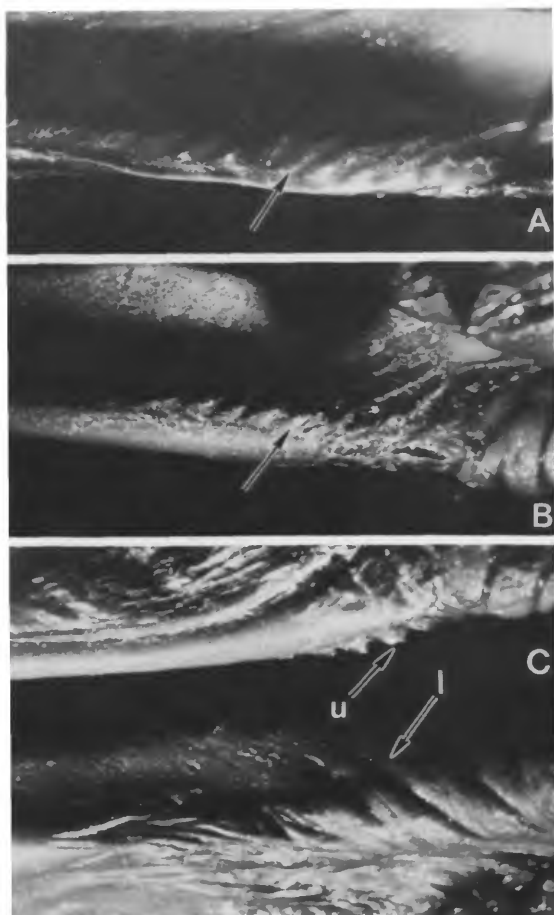


FIGURE 6.—Enlarged views of the vestigial lamellae (arrows) of screamers (Anhimidae): a, upper jaw of *Chauna torquata*; b, upper jaw of *Anhima cornuta*; c, the few lamellae in the lower jaw (l) with a different view of those in the upper jaw (u) of *Anhima cornuta*.

are vestigial lamellae in the lower jaw as well, whereas those in the upper jaw are fewer in number than in *Chauna* (Figure 6). In the specimen we examined there were four lamellae on the inside of the lower jaw about 1 cm anterior to the rictus, and seven or eight readily discernible lamellae on the upper jaw, all lying posterior to those on the lower. As with *Chauna*, these structures are not merely wrinkles in soft epidermis, but regularly spaced, hard, horny lamellae.

The modern Anhimidae are not filter feeders, nor do their habits give any indication of evolution in such a direction. Their lamellae must therefore be regarded as vestiges inherited from an ancestor in which these structures were functional. Had these lamellae been observed earlier, the ordinal affinities of the Anhimidae probably would never have been doubted.

For much of the Tertiary, South America was separated from other continental land masses (Irving, 1977) and during this time numerous organisms there, in isolation from evolutionary events taking place elsewhere, diverged wildly from their ancestors. It is evident that the Anhimidae represents one such group. The screamers are a product of an early anseriform stock for which there seems to have been little restraint on differentiation. They must be counted among the old endemic elements of the South America fauna and many of their attributes are uniquely derived features having no bearing on the major line of evolution in the Anseriformes.

Presbyornis, a Fossil Linking the Anseriformes and Charadriiformes

Having shown the supposed galliform affinities of the Anseriformes to be totally spurious, we have left the order with no known kin. An alternative theory of relationships is available, however, in the form of one of the most remarkable Tertiary birds yet discovered—*Presbyornis*—an early Eocene bird combining the body of a shorebird with a duck-like head (Frontispiece).

Presbyornis pervetus Wetmore (1926), based on a tarsometatarsus from the Lower Eocene Green River Formation of Utah, was originally described as a new family (Presbyornithidae) of Charadriiformes related to the Recurvirostridae. Subsequently, remains of *Presbyornis* have been identified from a number of localities in the Green River Formation, where they usually occur in great concentrations, at least one of which is known to represent a nesting colony (McGrew and Feduccia, 1973; Feduccia, 1978). The new material was first studied by Feduccia and McGrew (1974) who concluded that *Presbyornis*

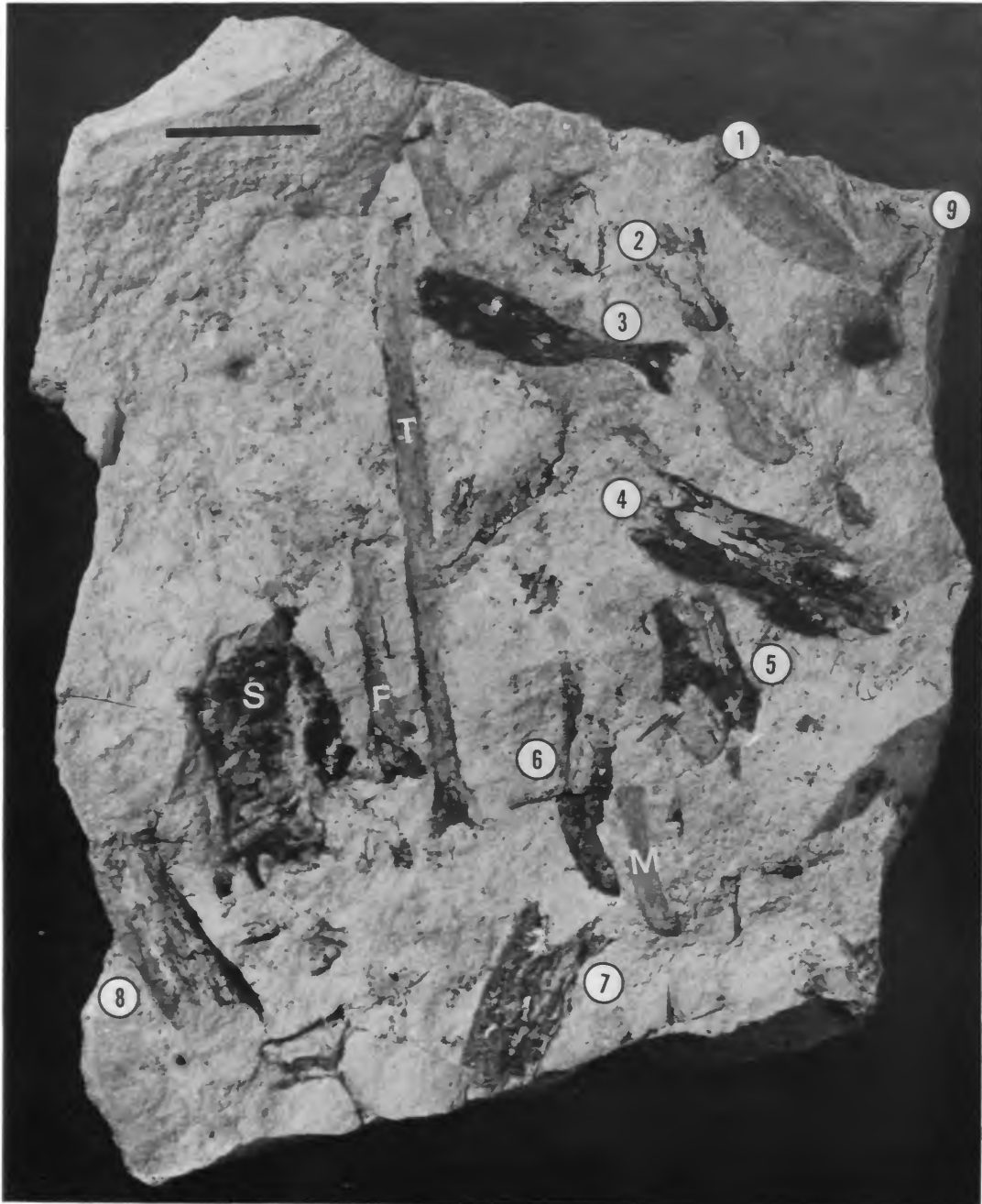
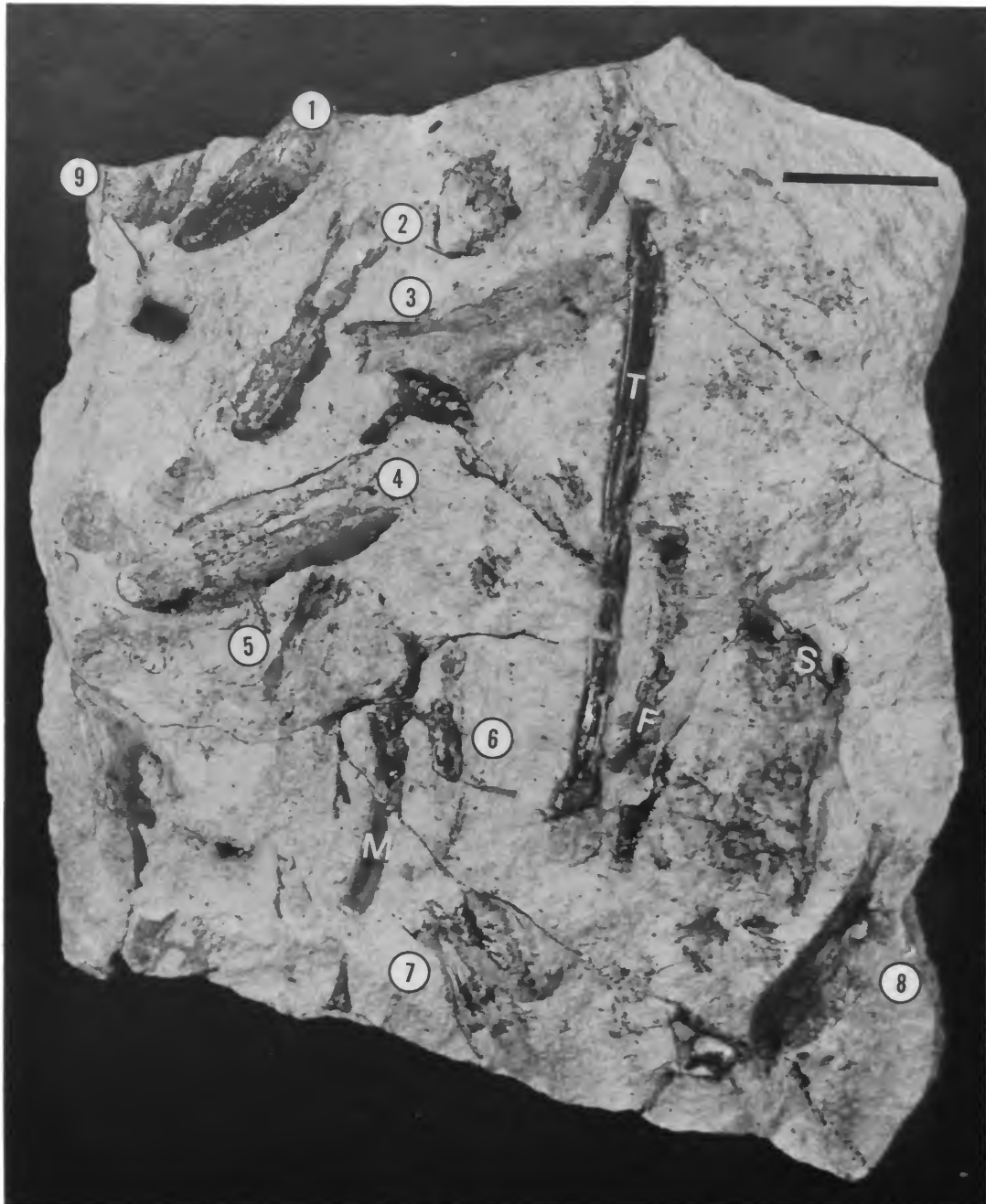


FIGURE 7.—Slab and counterslab of a small piece of rock as removed from the *Presbyornis* quarry at Canyon Creek Butte, Wyoming (see Feduccia, 1978), showing portions of nine duck-like bills (numbered) in association with a long tibiotarsus and a short, definitely four-notched sternum (seen here in dorsal view). No other kinds of bills and no duck-like postcranial elements occur



at this site and there can be no question that the shorebird-like body of *Presbyornis* is correctly associated with a duck-like head. (Scale = 3 cm; f = femur, m = mandible, s = sternum, t = tibiotalus.)

was a flamingo-like wader. They synonymized with *Presbyornis* the genus *Telmabates* from the Lower Eocene of Patagonia, which had been described in a new family, *Telmabatidae*, supposed to be related to flamingos (Howard, 1955).

Feduccia (1976) noted similarities to the Charadriiformes in the skeletons of *Presbyornis* and modern flamingos and accordingly proposed that flamingos were derived from the Charadriiformes. Bill impressions known at that time suggested, however, that the skull of *Presbyornis* may have been more duck-like than flamingo-like; this was fully confirmed by the discovery of a complete skull collected in Wyoming in 1977 by Olson and Robert J. Emry (Feduccia, 1978). Subsequent preparation of this specimen revealed that its preservation was truly exceptional, the mandible, palate, hyoid apparatus, larynx, and lacrimal being present and intact (Figures 8, 9).

Apparent similarities between *Presbyornis* and flamingos are heightened by the former having been a highly colonial inhabitant of shallow saline lakes, as are modern flamingos (McGrew and Feduccia, 1973). The habitat preferences of *Presbyornis* are substantiated by what is known of the paleoecology of parts of the Green River Formation and also by the fact that the interorbital bridge of *Presbyornis* indicates that it had well-developed salt glands (Feduccia, 1978). In the course of investigating the relationships of flamingos (Olson and Feduccia, in press), we gradually came to the conclusion, however, that *Presbyornis* does not have a direct bearing on the evolution of the Phoenicopteridae. Many of the flamingo-like features of *Presbyornis* are primitive charadriiform characters that do not necessarily indicate close relationship to flamingos, which are likewise charadriiform derivatives. *Presbyornis* lacks the cranial specializations of modern flamingos as well as the modifications of the proximal end of the humerus and the cervical vertebrae; these are among the characters used to distinguish the Phoenicopteridae, living and fossil, from other Charadriiformes (Olson and Feduccia, in press). Trackways of web-footed birds, some even including dabble marks made by the bill during feeding, are common in parts of the

Green River Formation and have been attributed to anseriform birds or flamingos (Erickson, 1967; Kahl, 1970:294). Most likely these tracks were made by *Presbyornis*. In addition to showing a fully webbed foot, they also indicate that the bird had a well-developed, somewhat elevated, hind toe, whereas in the Phoenicopteridae, the hallux is vestigial or absent.

On the basis of size differences in the material we have seen so far, it is evident that more than one species of *Presbyornis* occurs in the Green River Formation. Therefore, for the present we shall refer only to the genus *Presbyornis* and not employ any specific epithets. We shall concern ourselves here not with the origin of *Presbyornis*, but where it was leading, and in this consideration the newly acquired skull plays a most important role. When Feduccia discussed this specimen at the XVIIth International Ornithological Congress in Berlin in August 1978, considerable skepticism was expressed concerning the association of such a skull with charadriiform postcranial elements. Such doubts could result only through ignorance of the deposits of *Presbyornis*. We have collected hundreds of bill fragments and impressions, and several complete skulls, all of which are duck-like, and thousands of postcranial elements, all of which are shorebird-like. These were in direct association, with no indication of the presence of any other kind of bird (Figure 7). To raise the specter of mass burials of flocks of headless shorebirds with flocks of bodiless ducks is clearly a cause for amusement.

Most of the postcranial skeleton of *Presbyornis* is similar to that of Charadriiformes, as is testified to by the fact that the genus was originally placed near the *Recurvirostridae*. *Presbyornis* was a medium-sized bird, larger than most recent shorebirds, with long slender legs unlike any duck. Feduccia (1976, 1978) has noted some of its features that are characteristic of the Charadriiformes: sternum with well-developed blade-like manubrial spine; humerus non-pneumatic, with excavated tricipital fossae; tibiotarsus with inner cnemial crest large and rectangular, projecting far anteriorly; tarsometatarsus long and slender, with inner trochlea elevated and retracted; tro-



FIGURE 8.—Right lateral view of the skull and mandible of *Presbyornis* sp.
(Stereophotographs; specimen is 90 mm long.)

chanter of femur a well-developed crest raised above level of head. Subsequent specimens have shown that *Presbyornis* had a short, 4-notched sternum and a relatively short, shallow pelvis in which the innominate bones do not fuse to the sacrum. In all of these characters it is like Charadriiformes and unlike Anseriformes.

The skull of *Presbyornis*, on the other hand, is unmistakably duck-like (Figures 8, 9). Although showing numerous differences from most modern ducks, the rostrum of *Presbyornis* has an elongate,

hemicylindrical, subspatulate shape and the upper jaw obviously accommodated an enlarged tongue, a unique derived condition of the Anatidae (Olson and Feduccia, in press).

The mandible has the large, hooked blade-like retroarticular processes (Figure 10) typical of the Anseriformes. In the hyoid apparatus of *Presbyornis* the paraglossale is a large, elongate, spatulate structure exactly as in the Anatidae and quite unlike that in flamingos, Charadriiformes, or any other birds. Occipital fontanelles are present in



FIGURE 9.—Ventral view of the skull and mandible of *Presbyornis* sp., showing the hyoid apparatus and larynx still in position. (Stereophotographs; specimen is 90 mm long.)

Presbyornis, as in most Anseriformes. As noted by Olson (1979), these apertures are otherwise confined to the Charadriiformes (including flamingos), ibises, and the specialized gruiform families Gruidae and Aramidae. If one recognizes the Threskiornithidae as a transitional group between the Gruiformes and Charadriiformes (Olson, 1979), then every reason exists to regard the presence of occipital fontanelles as a shared derived character that is indicative of relationship.

In a specimen of *Presbyornis* with the rostrum preserved in ventral view, it is seen that the maxillopalatines are fused and extensively ossified, leaving a relatively small anterior opening for the internal nares, as is typical of the Anseriformes (Figure 11).

There are a number of differences between the skull of *Presbyornis* and that of any modern duck (Figure 12). The lacrimal is rather small and is not fused to the cranium; in addition, the area



FIGURE 10.—Mandible of *Presbyornis* sp. showing the large, blade-like retroarticular process (r) typical of Anseriformes and the point of articulation (a) with quadrate.

between the orbit and the nostril is not greatly elongated, the postorbital process is much smaller, and the temporal fossa is deeper than in modern ducks. The ventral portion of the quadrate does not have the posterior inflation characteristic of ducks and is more like that of the Charadriiformes. As far as can be determined at present, the pterygoids are short and do not have a special articular surface on the parasphenoid rostrum—also charadriiform characters. In *Presbyornis*, the Charadriiformes, and most other birds, when the skull is viewed from the side, at least part of the palate is seen to lie ventral to the jugal bar, whereas in the Anatidae the palate is entirely above the jugal bar, perhaps as another accommodation for the enlarged tongue. In *Presbyornis* even the obviously duck-like skull shows a combination of anseriform and charadriiform characters,

which is further evidence that the duck-like skull and charadriiform postcranial elements are correctly associated.

Several other features of *Presbyornis* initially appeared to be unlike modern ducks, such as the peculiarly upturned bill, with a very small rostral nail; the long, slender mandibular symphysis; and the deep groove in the ventral surface of the anterior portion of the mandibular rami. We found, however, that these features occur in one or the other of two monotypic genera of ducks in Australia: the Freckled Duck, *Stictonetta naevosa*, and the Pink-eared Duck, *Malacorhynchus membranaceus*. Of all modern ducks, only *Stictonetta* has the rostrum and mandible markedly recurved (Figure 13), the rostral nail small, and the mandibular symphysis long and narrow. The bill of *Malacorhynchus* is highly specialized in a number of re-

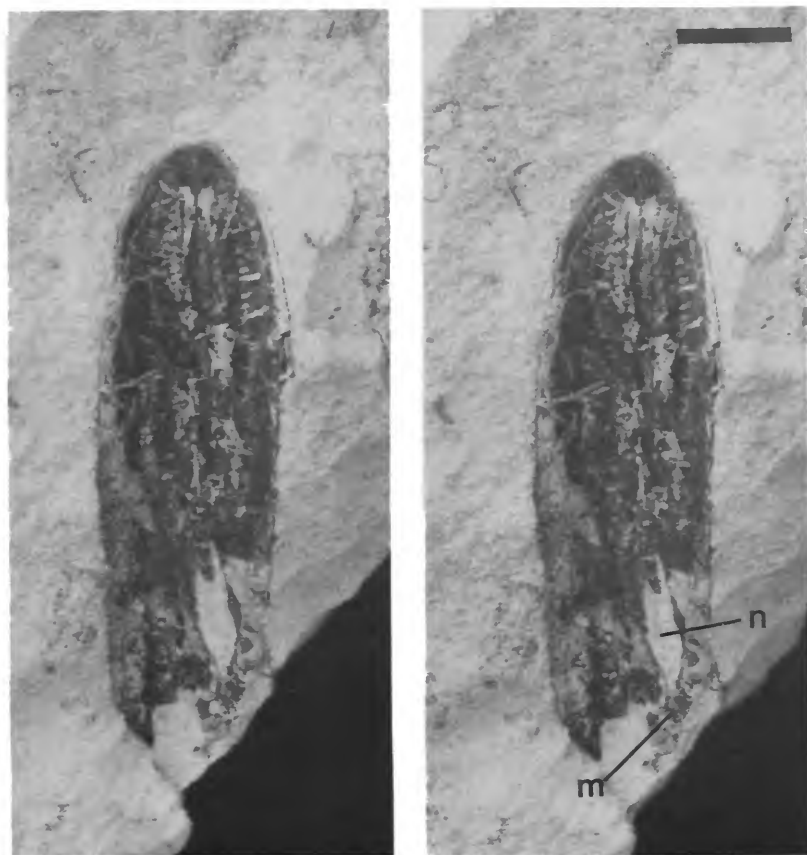


FIGURE 11—Ventral aspect of the upper jaw of *Presbyornis* sp. in matrix to show the fused maxillopalatine area (m) and the restricted internal narial opening (n) characteristic of ducks. (Stereophotographs; scale = 1 cm.)

spects, with the tip peculiarly expanded distally and bearing distinctive membranous flaps. Nevertheless, disregarding the distal expansions, the mandible is similar to that of *Presbyornis*, and unlike *Stictonetta*, in having the same characteristic grooves anteriorly and more narrowed rami posteriorly (Figure 12).

The condition of the lacrimal area in *Stictonetta* (Figure 13) is anomalous among the Anatidae and may represent the original morphological response to the elongation of the anterior portion of the cranium. In *Stictonetta*, the major part of the lacrimal is the descending process, not too unlike that of *Presbyornis* but with the body and

orbital process reduced. The lacrimal is fused to the skull and extending anteriorly from it to the naso-frontal hinge is a broad, tough membrane that covers and protects the nasal conchae. This membrane has begun to ossify in the anterior corner and is thinly ossified at the ventro-lateral corner. The whole effect is one of incompleteness and it is evident that the increased size and extent of the lacrimal in typical ducks has resulted from more extensive ossification of this membrane.

In two other respects the skull of *Stictonetta* appears primitive: in the weak ossification of the maxillopalatine area and in the similarly weak ossification of the rostrum, so that there are elon-

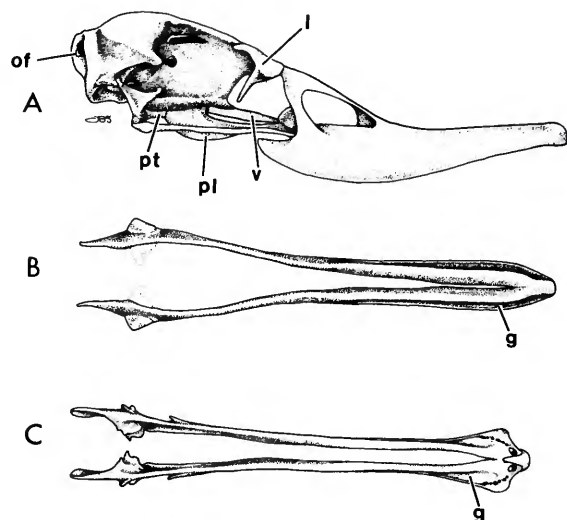


FIGURE 12.—Lateral view of skull (a) and ventral view of mandible (b) of *Presbyornis* sp. Note the characteristic groove (g) in the mandibular ramus. This is also present in the extant Pink-eared Duck, *Malacorhynchus membranaceus* (c). (l = lacrimal, of = occipital fontanelle, pl = palatine, pt = pterygoid, v = vomer.)

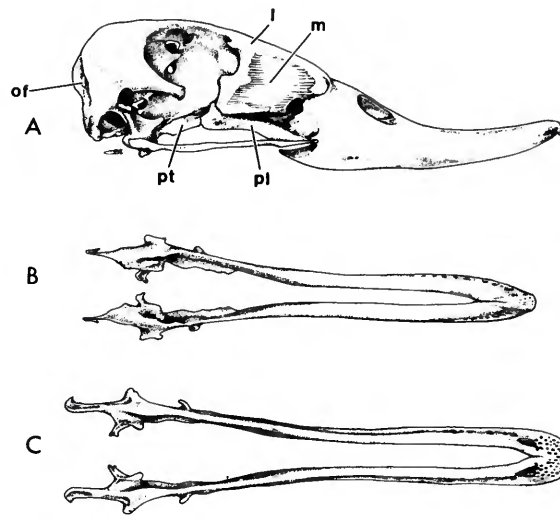


FIGURE 13.—Lateral view of skull (a) and ventral view of mandible (b) of the extant Freckled Duck, *Stictonetta naevosa*. Note the upturned bill and the long, narrow mandibular symphysis, as in *Presbyornis*, contrasted with the mandible of typical duck, *Anas platyrhynchos* (c). (Abbreviations as in Figure 12; m = lacrimal membrane.)

gate, translucent “windows” on either side of the midline. These areas are typically unossified in the charadriiform skull and would have had to fuse in order to produce the anatid condition.

Elsewhere (Olson and Feduccia, in press), we have discussed general aspects of evolution of filter-feeding in birds and shown the filtering apparatus of the Anatidae to be unique in consisting of a double-piston suction pump with the piston (the tongue) housed in the upper jaw, rather than in the lower jaw as in all other filter-feeding vertebrates. We also showed that the Red Phalarope (*Phalaropus fulicarius*) provides an excellent example of a shorebird in the beginning stages of evolving adaptations for filter-feeding and which has a broad, slightly spatulate, somewhat duck-like bill. By ossification and fusion of the maxillopalatines and much of the nostril between the dorsal and ventral rami of the premaxilla of the charadriiform skull, it would not be difficult to arrive at a substantially anseriform-like rostrum. In *Phalaropus*, the nostril has in fact

already begun to be closed over by bone in just such a manner (Figure 14). *Phalaropus*, of course, has nothing to do with the ancestry of ducks, but it does show how the anseriform cranial morphology could have evolved from that of Charadriiformes. Quite in contrast, nothing exists in the galliform skull that would predispose it towards such modification.

Because we have noted the similarity in the skull of *Presbyornis* to that of the monotypic Australian genus *Stictonetta*, the affinities of the latter merit further comment. Very little was known about *Stictonetta* until the appearance of several publications by Frith (1964a, 1964b, 1965, 1967) and Johnsgard (1965). Although having a superficial resemblance to dabbling ducks of the subfamily Anatinae, where it had formerly been placed (Delacour and Mayr, 1945), *Stictonetta* possesses the following characteristics of the swans and geese (Anserinae): tarsus reticulate; syrinx simple, without bulla; plumage simple, without speculum; slight sexual dimorphism. The color-

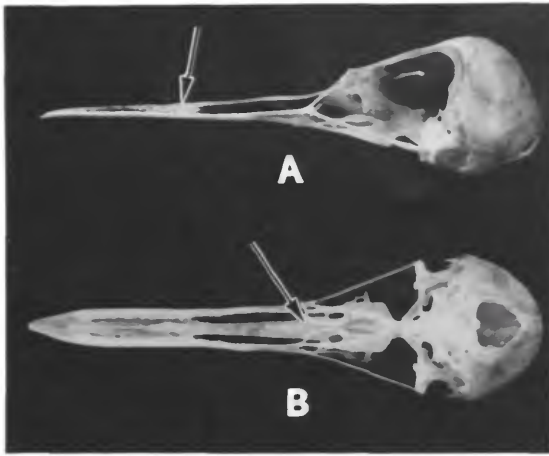


FIGURE 14.—Lateral (a) and ventral (b) views of the skull of a Red Phalarope, *Phalaropus fulicarius*, a charadriiform with rudimentary filter-feeding adaptations. By ossification of the nostrils and the maxillopalatine area (arrows), a duck-like aspect could be derived from such a bill. The nostrils of *Phalaropus* have in fact already begun such ossification.

tion and pattern of the downy young are as in the Anserinae (Frith, 1964b). The trachea in the adult male is convoluted, as in swans, and lies coiled partly outside the sternum, as in *Anseranas*. Frith (1967) regarded the behavior of *Stictonetta* as swan-like but noted that although the genus possesses some skeletal characters of the Anserinae the majority of them are like the Anatinae.

Frith (1967:114) followed Johnsgard's (1960b) suggestion of placing *Stictonetta* in a monogeneric tribe, Stictonettini, within the Anserinae, remarking that it was "not closely related to the Dendrocygnini or other tribes." Brush (1976:481) concurred in this after finding that the "electrophoretic pattern of feather proteins of the Freckled Duck was completely unlike that of the other Anatini. . . . The *Stictonetta* pattern was unique."

Frith's (1967:114) comments on *Stictonetta* seem particularly apt: "Few would deny that the waterfowl family of today passed, in evolution, through duck-like ancestors before differentiating into swans, geese, and others. The Freckled Duck is probably the closest living waterfowl to that ancestor. . . ."

The mandible of *Presbyornis* is also similar in some respects to that of *Malacorhynchus*. As with *Stictonetta*, the relationships of *Malacorhynchus* have been unclear, and it too has been classified as an aberrant member of the tribe Anatini (Delacour and Mayr, 1945). Frith (1967) reviewed the opinions concerning the classification of *Malacorhynchus*; mostly on the basis of the pattern of the downy young he considered it to be related either to the Anatini or the Cairinini. *Malacorhynchus*, however, has many of the same features that were used to distinguish *Stictonetta* from the Anatinae: lack of a speculum; lack of marked sexual dimorphism; tracheal bulla "very poorly developed, almost nonexistent" (Frith, 1967:232). The bill structure and plumage of *Malacorhynchus* are unique. It is clear that *Malacorhynchus*, like *Stictonetta*, has no close relative among extant genera of Anatidae.

On the basis of its long, narrow mandibular symphysis, *Merganetta* might also represent an early anomalous anatid offshoot. *Merganetta* is a monotypic genus of torrent-inhabiting ducks confined to South America. At times it has been recognized in a separate tribe, Merganettini, or as an aberrant member of the Anatini, but within the last group it has no obvious relatives.

Because *Stictonetta* is the only existing duck with a bill substantially like that of *Presbyornis*, it becomes of considerable interest to know something of its feeding habits. By analogy with *Presbyornis*, this could provide insight into the original anseriform adaptation. For this reason, we quote extensively from Frith's (1967:118-119) observations of *Stictonetta*.

Bottom filtering is by far the most common method of feeding; the birds wade slowly in shallow water, seldom more than two inches deep. The bill is immersed and is held immediately above the soil surface and a rapid filtering action is set up so that the fine particles of mud on the surface swirl up. It has been possible to watch this action at very close range (two feet) in perfectly clear water on several occasions. The bill has not yet been seen to enter the mud itself, but is maintained immediately above it—a true filtering, rather than a dabbling, action.

Filtering of surface water is the least frequently seen. . . . The birds swim slowly, filtering and nibbling at surface particles. Captive birds spend a great deal of time

running their bills along the edges of logs and posts and concrete walls in the water that have become encrusted with algae. The bill action is nibbling and they have been clearly seen to be feeding extensively on the algae.

Like many other ducks, Freckled Ducks up-end, but their action under water seems to be different. Captive birds . . . up-ended freely, and again it was seen that filtering was confined to immediately above the surface of the soil on the bottom. The birds did not dabble in the mud, nor did they pay attention to plants and food items on the bottom

One of the most constant sources of food was algae, nearly every stomach examined contained some and it accounted for 30 percent of the total volume; seeds of smartweeds and docks were also found in most stomachs and provided 22 percent of the food. Various aquatic grasses . . . accounted for 16 percent of the food The whole bulk of the animal food accounted for 11 percent of the total food.

We find it significant that the feeding behavior of *Stictonetta* parallels what one might have assumed for *Presbyornis*, given what is known of the paleoecology and morphology of the latter. It is noteworthy that despite its short, typically duck-like legs, *Stictonetta* generally feeds by wading rather than swimming. The bill of *Stictonetta* is used entirely in a true filtering capacity and the principal food taken is algae. In discussing the environment of a presumed nesting site of *Presbyornis*, McGrew and Feduccia (1973:164) remarked that an

interesting feature of this fossil site is the occurrence of many logs and branches that are heavily incrustated, presumably by algae The incrustations demonstrate the abundance of algae in the waters It seems reasonable that [*Presbyornis* was] feeding on algae and microorganisms. . . .

Presbyornis paralleled flamingos in its extreme coloniality and in inhabiting shallow, saline lakes, an environment in which filter-feeding is highly advantageous because it reduces salt intake (Olson and Feduccia, in press). The feeding apparatus of *Presbyornis* and ducks is, however, fundamentally different from that of flamingos. We suggest the possibility that the anseriform filter-feeding mechanism may originally have arisen as an adaptation for feeding on vegetable matter, particularly algae, whereas in contrast, the filtering mechanism of flamingos was originally an adaptation for feeding on small invertebrates.

The Recurvirostridae and *Phoenicopterus* feed mainly on animal matter, whereas only with the later development of the highly specialized, very fine straining device of *Phoenicoparrus* and *Phoeniconaias* could flamingos feed on diatoms (Jenkin, 1957), which are too small to have been taken by the filtering apparatus of *Presbyornis* or ducks. Perhaps the adaptation to two different food sources was the factor that permitted the nearly simultaneous evolution of two groups of highly derived filter-feeding shorebirds in the same limited, ephemeral environment.

The Fossil Record of the Anatidae

The early Eocene *Presbyornis* provides us with the key to the origin of the Anseriformes, but what else, if anything, does the fossil record tell us of the time of origin and radiation of the Anatidae? The earliest fossil assigned to the Anatidae is *Eonessa anaticula* Wetmore (1938), which was made the type of a new subfamily, Eonessinae. This species was based on the bones of a left wing from the Upper Eocene (Uintan) of Utah. We examined this specimen and found it to be poorly preserved, badly crushed, and of minimal diagnostic value (Figure 15). The illustrations in Wetmore (1938) are largely reconstructions and are not particularly accurate. Matrix still obscuring critical parts of the humerus was removed in 1978 to permit more careful study.

After comparing *Eonessa* with *Presbyornis* and modern ducks, we were forced to conclude that *Eonessa* is not referable to the Anseriformes. Wetmore (1938) did not explain his reasons for placing *Eonessa* in the Anatidae and there are no strong resemblances between the two. The slender proportions of the bones, noted by Wetmore himself, are not duck-like. Nor can *Eonessa* be referred to the Presbyornithidae. The external condyle of the humerus is more elongate and the shape of the proximal end of the carpometacarpus is quite different, with the ventral rim of the internal carpal trochlea flat, nearly on a line with metacarpal III, instead of rounded and projecting outward as in *Presbyornis*. We detect in such fea-

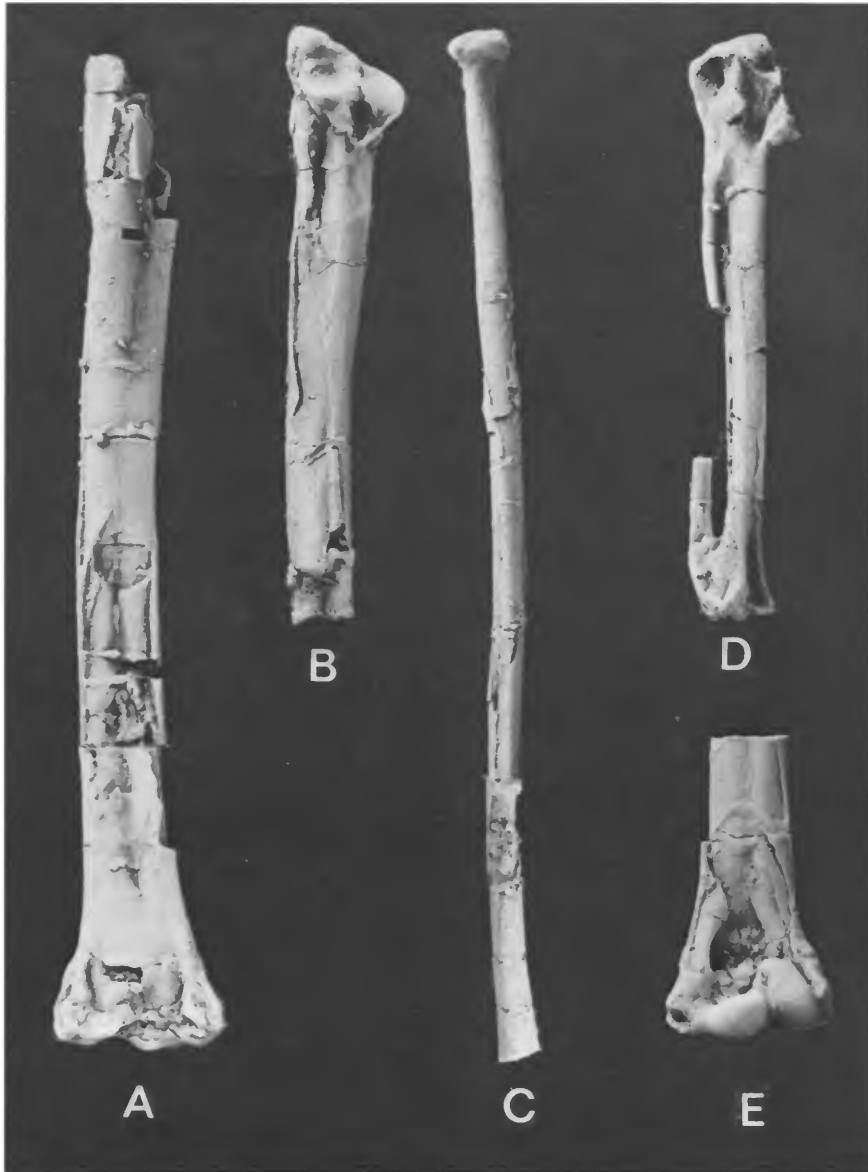


FIGURE 15.—Holotype of *Eonessa anaticula* Wetmore (Princeton University 14399): *a*, humerus in anconal view; *b*, ulna; *c*, radius; *d*, carpometacarpus; *e*, distal end of humerus in palmar view. Note the poor preservation and non-anatid proportions. Heretofore considered to be the earliest known duck, the true affinities of *Eonessa* are uncertain, but they are not with the Anatidae as originally thought.

tures as the elongate external condyle of the humerus of *Eonessa*, certain similarities to the Gruiformes, larger forms of which have been described from the same horizon in Utah (Craft, 1971). Although the true affinities of *Eonessa* are difficult or impossible to ascertain, we feel confident that it is not referable to the Anatidae.

With the removal of *Eonessa* from the Anatidae, the earliest forms referable to that family are *Romainvillia* Lebedinsky (1927), from the early Oligocene of France, and *Cygnopetrus* Lambrecht (1931) from the middle Oligocene of Belgium. A similar undescribed anseriform is known from the early Oligocene (Chadronian) of Nebraska (Larry D. Martin, pers. comm.). These were all large, goose-sized birds, the precise relationships of which have not yet been determined, although they appear to be correctly assigned to the Anseriformes.

In the late Oligocene and early Miocene, anatids appear more abundantly and a number of species have been named, many of which have been relegated to extant genera. Most of these species, however, were described prior to the use of modern generic concepts and with little reference to adequate comparative material; hence the generic identity of these mid-Tertiary anatids is problematical until they are restudied. For example, *Anas blanchardi*, a species abundant in the Aquitanian of France and known from excellent material, "clearly does not belong in *Anas*" (Howard, 1964:292, footnote) and even its tribal affinities are difficult to discern (pers. obs.).

On the other hand, a newly described fossil from the middle Miocene of Virginia, based on diagnostic associated material, is clearly referable to the Recent genus *Mergus* (Alvarez and Olson, 1978), which is among the more specialized genera of modern ducks. This suggests that the differentiation of most Recent anatid genera had occurred by mid-Miocene and that much of the radiation in the Anatidae was extremely rapid, thus possibly contributing to the propensity of modern members of the family to form intergeneric hybrids.

The known fossils of the Anseriformes, almost

all of which are from the Northern Hemisphere, would not contradict a hypothesis that early Eocene forms of Presbyornithidae were the direct ancestors of the Anatidae and that the differentiation of the latter family took place subsequent to the early Eocene. In late Neogene and Quaternary deposits, ducks are often among the most abundant of fossil birds; if true Anatidae were present in the Eocene, one would expect them to have been found in the Green River Formation and elsewhere.

Nevertheless, the ancestors of the Anhimidae, which were derived from the Anatidae, in all probability entered South America very early in the Tertiary, which suggests that the Anseriformes had differentiated from the Presbyornithidae by then. In its specialized habitat, *Presbyornis* in the early Eocene could have been a temporal relict rather than a direct ancestor. This would not, however, negate the evidence pointing towards a mid-Tertiary date for the principal radiation of modern types of Anatidae.

Conclusions

The origins of the Anseriformes may be traced back to a group of highly colonial Charadriiformes that adapted to shallow saline lakes and evolved a unique filter-feeding mechanism. In these respects the ancestors of the Anseriformes paralleled the Phoenicopteridae, which were also derived from the Charadriiformes, but which evolved a very different filtering apparatus (Olson and Feduccia, in press). The early Eocene *Presbyornis* is a representative of this ancestral anseriform type and combines a charadriiform body with a duck-like skull.

The filtering device of *Presbyornis* may possibly have evolved for feeding on algae. In any case, it proved to be a much more adaptable structure than that of flamingos and was the key adaptation that led to the subsequent divergence and radiation of the Anseriformes. Filtering represents the original feeding method of the order and departures from this such as the grazing adaptations of geese, the serrated fish-catching "teeth"

of mergansers, or the superficially fowl-like bill of screamers, are secondarily derived features.

With the knowledge afforded by paleontological evidence, and with the untenable hypothesis of galliform relationships nullified, it should now be possible to determine primitive-derived sequences within the Anseriformes more reliably. New ideas of relationships within the Anatidae already suggest themselves. For example, we have noted the similarities in the skull and mandible of *Presbyornis* to those in the monotypic Australian genera *Stictonetta* and *Malacorhynchus*. These genera, and possibly *Merganetta* as well, appear to be primitive relicts of an early anatid radiation and may be only distantly related to the remainder of the Anatidae. Significantly, these three genera have never hybridized with any other ducks. Along with *Anseranas* and the members of the Dendrocygnini and Oxyurini, they are the only waterfowl for which no intertribal or intergeneric hybrids are known (Johnsgard, 1960a). It is likely that the typical members of the "subfamily" Anserinae and the typical members of the "subfamily" Anatinae are more closely related to one another than to *Stictonetta*, *Malacorhynchus*, or *Merganetta*. A re-evaluation of the subgroups and the sequence of genera of Anatidae is in order, but this lies beyond the scope of the present work.

Preliminary indications show *Anseranas*, although having more duck-like characters than *Presbyornis*, to represent an early, very divergent offshoot that is probably on a different line altogether from that giving rise, through such forms as *Stictonetta*, to the aquatic, filter-feeding Anatidae. We agree with Woolfenden (1961) that *Anseranas* should be placed in a separate family, Anseranatidae. From a form such as *Anseranas* were derived increasingly terrestrial birds, which

in South America led to the Anhimidae, the most derived of the Anseriformes. These evolved in isolation and lost most of the identifying characters of the order, while developing many unique ones. Nevertheless, the anhimids retain traces of the original adaptation of the order in the form of vestigial lamellae.

Although specimens of Presbyornithidae are abundant in the early Eocene, it is not known when the Anatidae originally diverged, as no fossils certainly referable to this family are known before the early Oligocene. The major burst of adaptive radiation of Anatidae evidently took place in the mid-Tertiary, although the presence of the highly derived living species of Anhimidae in South America suggests that there was some divergence from the presbyornithid line earlier than this.

Until more detailed comparisons are made of the osteology of *Presbyornis*, firm recommendations as to the taxonomic status of the Presbyornithidae cannot be made. For the present, we feel that *Presbyornis* probably would have to be considered as still having had a charadriiform grade of morphology. Like the Phoenicopteridae, the Presbyornithidae appear to be Charadriiformes with a specialized feeding apparatus. The Anseriformes, as far as known, differ so much from their charadriiform ancestors in their postcranial anatomy as to have disguised their origins up to the present. For this reason, and because they represent an easily recognizable monophyletic group having a diverse radiation, they can reasonably be said to rank as a separate order of birds. The Anseriformes would constitute part of the superorder Charadriomorphae in the sense of Stegmann (1978) and should be placed immediately following the Charadriiformes.

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