OSTEOLOGICAL EVIDENCE FOR SHOREBIRD AFFINITIES OF THE FLAMINGOS

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ALTHOUGH once widespread, flamingos are survived today by only four species (six of some authors) that occur in rather remote regions of the earth. Flamingos or flamingolike birds are well documented in the fossil record, extending well back into the late, and perhaps early Cretaceous (Brodkorb 1963); however to date the fossil record has failed to provide any conclusive evidence concerning the relationships of this enigmatic group. Sibley et al. (1969), in reviewing the classification of the flamingos, listed 15 separate taxonomic treatments. In each case, the flamingos are placed somewhere near the anseriforms (ducks, geese, and swans) or the ciconiiforms (storks, ibises, and herons). Sibley et al. (1969: 155) stated that, "The question is, are the flamingos most closely related to the herons and storks and merely convergent to the anseriform birds in certain characters or were they derived from the ducks and geese and later converged toward the ciconiiform birds?" Alliance with the ducks and geese has been based primarily on the structure of the bill and feet, voice, development of the young, and the mallophagan parasites, while general anatomical similarity has been used to indicate alliance with the Ciconiiformes. On the basis of the protein evidence, Sibley et al. (1969: 176) concluded that the flamingos (Phoenicopteriformes), Ciconiiformes, and Anseriformes are related to one another and that the flamingos and Ciconiiformes are closer to one another than either is to the Anseriformes. These are conclusions similar to those of many authors, but Sibley et al. (1969: 155) cautioned that, "A third possibility is that they were derived from some other group and are similar to both geese and herons by convergence."

During the course of an investigation of a fossil nesting colony of Eocene age in Wyoming (McGrew and Feduccia 1973, Feduccia and McGrew 1975), I reexamined specimens described as flamingolike waders from South America, *Telmabates antiquus* Howard (1955) and *Telmabates howardae* Cracraft (1970), and the form described as a recurvirostrid, *Presbyornis pervetus* Wetmore (1926), from the Eocene of Utah. The latter is from the same geologic formation as the newly discovered Wyoming nesting colony. The conclusions were that the Eocene nesting colony from Wyoming was composed entirely of a single species of small flamingolike wader, slightly smaller than, but very close morphologically to the South American *Telmabates antiquus*; we (Feduccia and McGrew

1975) recommended that the Green River fossil be considered conspecific (at least osteologically) with the small species, *Telmabates howardae* Cracraft, of the same locality as *T. antiquus*. We also discovered that several fossils described previously from the Green River Formation were the same as the new Green River wader; they included probably two auks (*Nautilornis avus* and *N. proavitus*, though the material is not very good for comparison and may be unassignable on its own merit), and a species of recurvirostrid, *Presbyornis pervetus*, described by Wetmore (1926) as representing a new family, Presbyornithidae. We recommended that it would be most appropriate to use the family name Presbyornithidae in place of Telmabatidae, and the name *Presbyornis pervetus* for the Green River flamingo and the small form of *Telmabates*, *T. howardae* Cracraft.

It was not surprising to discover that the two Green River auks were in reality not properly assigned, because the material is so poorly preserved. However that the so-called recurvirostrid from the Green River was misidentified was surprising as it was represented by a very well-preserved tarsometatarsus and other taxonomically useful elements. This led me to reexamine the position of the presbyornithids (including now *Telmabates* (= *Presbyornis*) *antiquus*). Indeed, Wetmore's description of the Green River wader as a shorebird rather than a flamingo has now opened up an entirely new view of flamingo relationships that I present in the present paper. This new view, which is supported primarily by evidence from osteology, indicates that the living flamingos and the presbyornithids are mosaics, adding an anseriformlike skull onto post-cranial characters of the shorebirds.

In the following osteological analysis I attempt to show that the flamingos (including the fossil forms) exhibit important and previously unnoticed similarities with the Charadriiformes, and show very little osteological similarity with the Ciconiiformes.

Character Analysis

In describing *Telmabates* (= *Presbyornis*) *antiquus*, Howard (1955) compared the fossil primarily with the living flamingos, swans and geese, and the ibises, in addition to the fossils *Apatornis* and *Palaelodus*. She stated (p. 3) that, "Resemblance to living birds is distributed among several groups: the flamingos, the swans and geese, and the ibises. Minor similarities to the shorebirds were noted in a few instances." All in all, her analysis was in line with what one would have expected from a fossil of a primitive phoenicopterid when one considers the consensus of opinion for relationships of modern flamingos. Howard lacked good material of two of the major elements that are morphologically

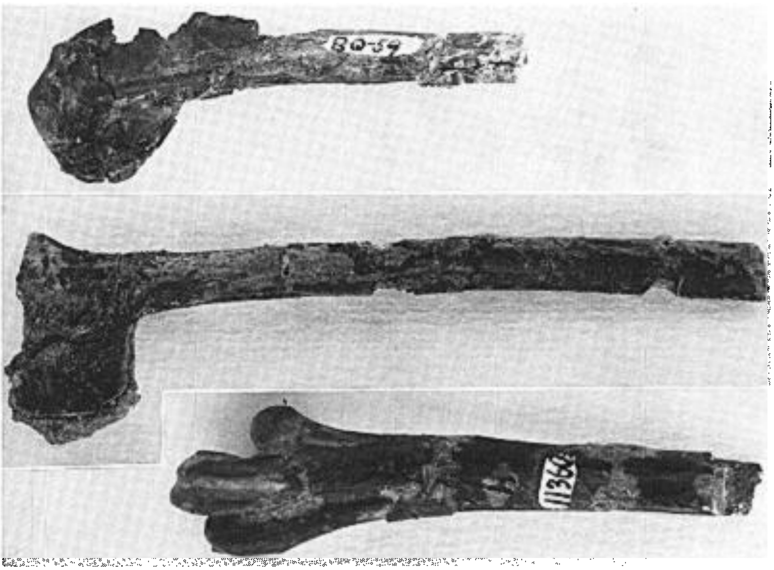

Fig. 1. Fossil bones of *Presbyornis pervetus* Wetmore from the Eocene of the Green River Formation of Wyoming and Utah. From top to bottom: anconal view of the proximal end of the right humerus (Univ. Wyoming, Mus. Paleontology, BQ-59), actual length, 72 mm; internal view of the proximal end of the right tibiotarsus (Univ. Wyoming, Mus. Paleontology, BQ-50), actual length, 69.7 mm; anterior view of the distal end of the right tarsometatarsus (Carnegie Mus., n. 11360; distal pieces of type of *P. pervetus*), actual length 42.4 mm.

similar to the shorebirds, especially the recurvirostrids; these elements are the tibiotarsus (proximal end), and the tarsometatarsus (distal end). Other characters, such as the sternum and proximal end of the humerus show similarities to the recurvirostrids, but are less convincing.

Tibiotarsus (Figs. 1, 2).—The proximal end of the tibiotarsus presents one of the most convincing cases of flamingo affinity to the shorebirds, and relationship of the presbyornithids to the above modern groups.

The inner cnemial crest in modern flamingos and presbyornithids and recurvirostrids (and many other shorebirds) is a very large, almost rectangular piece of bone, which projects slightly upward. In the presbyornithids, the crest is more nearly at a right angle with the shaft of the tibiotarsus, but overall closely resembles that of recurvirostrids. In both herons and ibises there is only slight development of the inner cnemial crest, and in anseriforms it is considerably smaller than that of flamingos, recurvirostrids, or presbyornithids. Certain of the gruiforms exhibit a well-developed inner cnemial crest, but to a lesser extent than shorebirds, presbyornithids, or flamingos.

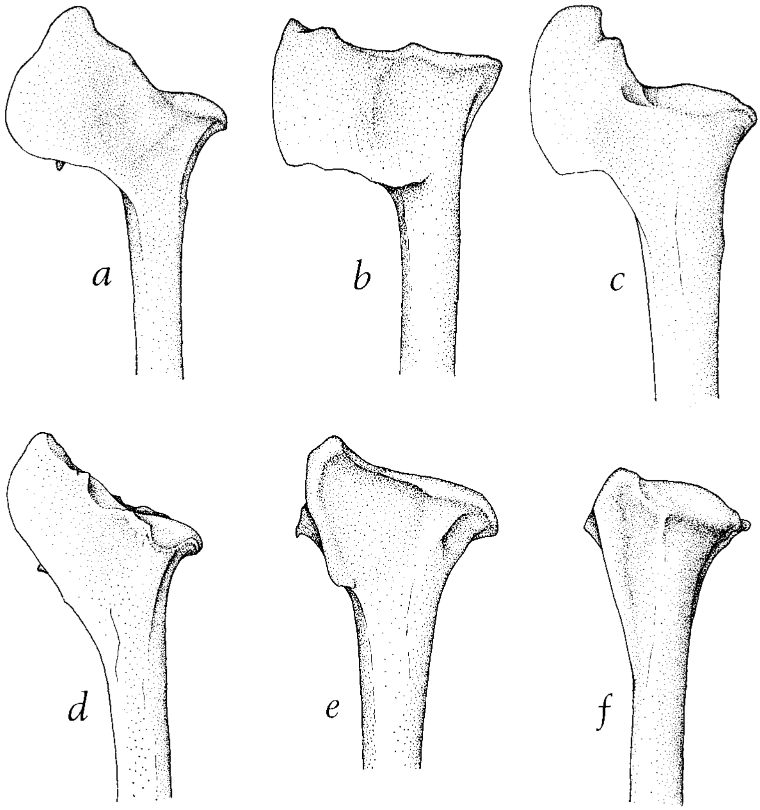

Fig. 2. Upper: internal views of the proximal ends of right tibiotarsi of a, recurvirostrid (*Recurvirostra americana*); b, presbyornithid (*Presbyornis pervetus*); c, flamingo (*Phoeniconaias minor*); d, duck (*Anas rubripes*); e, ibis (*Eudocimus ruber*); and f, heron (*Egretta caerulea*). All specimens in this and the following drawings are drawn to the approximate same size.

The form of the outer cnemial crest is not very diagnostic. It should be noted that the flamingos, recurvirostrids, ducks, ibises, and presbyornithids are fairly similar in having the crest curved, with a slight hook at the distal extremity; but in recurvirostrids the crest is slightly more developed, having a greater downward slope and a more highly developed hook. Presbyornithids are more similar to modern flamingos in having the crest less curved with less development of the distal hook. Again, the ciconiiforms have a very poorly developed outer cnemial crest, and of the groups under consideration probably represent the primitive condition for the outer cnemial crest.

The large, rectangular inner cnemial crest in modern flamingos, recurvirostrids, and the presbyornithids is a significant derived condition, which is here interpreted as an indication of common ancestry.

Howard (1955) had good material of only the distal end of the tibiotarsus for *Telmabates* (= *Presbyornis*) *antiquus*. She stated (p. 17) "This element combines characters found in *Paloelodus* [*sic*], the geese, and certain shorebirds, but does not resemble that of the highly specialized *Phoenicopterus*." However it should be noted that in modern anseriforms, the tendency of the distal end to thrust to the internal side is very marked. In the presbyornithids, modern flamingos, and modern recurvirostrids this tendency is only slight. The posterodistal aspect of the tibiotarsus is very similar in modern flamingos and recurvirostrids, with a deep sulcus present between high ridges of the internal and external condyles. This is true also of presbyornithids, but to a lesser degree.

In modern flamingos, recurvirostrids, and the presbyornithids, the internal condyle extends anteriorly beyond the external condyle although in modern flamingos the anterior extent is slight. In flamingos and recurvirostrids the condylar fossa is deeply excavated; in the presbyornithids the fossa is less deeply excavated. The distal end of the tibiotarsus is strikingly similar between modern flamingos and recurvirostrids, with the presbyornithids intermediate between the two in many features. These three groups are much more similar to one another than any is to the ciconiiforms or the anseriforms.

Tarsometatarsus (Figs. 1, 3, 4).—Another character that shows convincing morphological similarity between the flamingos, recurvirostrids, and the presbyornithids is the form of the trochleae on the distal end of the tarsometatarsus.

Herons have the trochleae for digits II, III, and IV nearly equal in their distal extents; they are also equal in their anteroposterior axes, being nearly level with the shaft of the tibiotarsus. In all the other birds under consideration, the middle trochlea (trochlea for digit III) remains in the same position, as though it comes straight out of the shaft of the tarsometatarsus, while trochleae for digits II and IV vary considerably in their relative position. Ibises (and most other birds) have the trochlea for digit II thrust posteriorly; the trochlea for digit IV is also thrust posteriorly and is nearly equal in its posteroproximal extent with the trochlea for digit II.

In describing the tarsometatarsus of *Telmabates* (= *Presbyornis*) *antiquus* Howard (1955: 19) stated "The position of the internal condyle (sloping sharply towards the medial line posteriorly) parallels the condition found in *Phoenicopterus* and in shorebirds such as *Limosa*, *Numenius*, and *Recurvirostra*; in *Paloelodus* [*sic*] the slope is less marked."

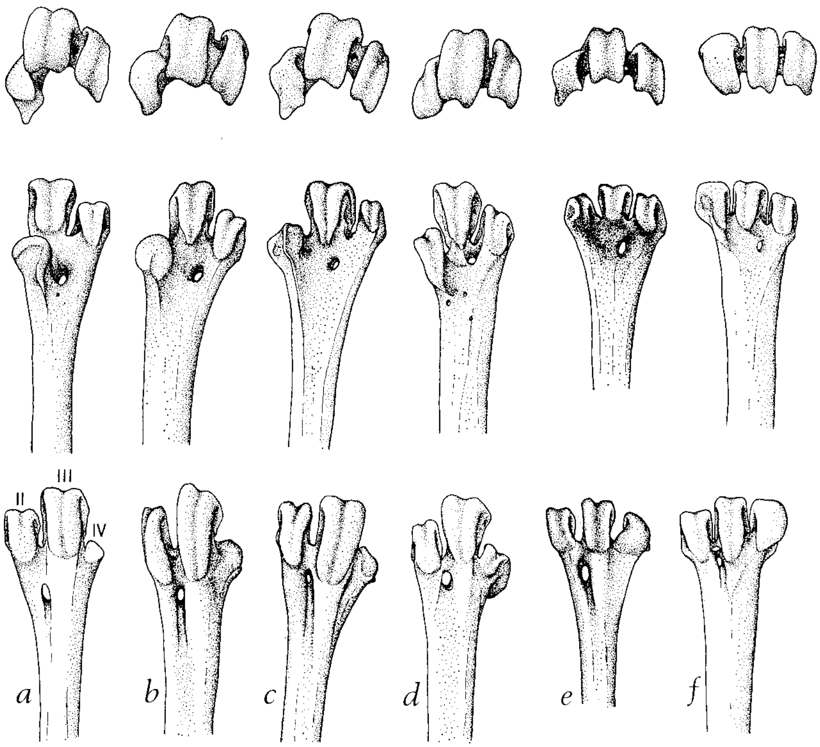

Fig. 3. From bottom to top: anterior, posterior, and distal end views of left tarsometatarsi of a, recurvirostrid (*Recurvirostra americana*); b, presbyornithid (*Presbyornis pervetus*); c, flamingo (*Phoeniconaias minor*); d, duck (*Anas rubripes*); e, ibis (*Threskiornis aethiopica*); and f, heron (*Egretta caerulea*).

In anseriforms the trochlea for digit II is thrust less posteriorly, being nearly parallel with the trochlea for digit III; the trochlea for digit IV is thrust posteriorly, and is greater in its posterodistal extent than the trochlea for digit II; however it has only a very slight medial slope. In addition, anseriforms have the distal foramen located more distad than in any of the other groups under consideration.

In lateral view of the internal condyle another aspect of this character complex is visible in the form of the trochlea for digit IV. In herons it is quite rounded and is nearly equal in extent with the other trochleae. In ibises, this trochlea has a slight posteroproximal thrust. In modern flamingos the posteroproximal thrust is such that all but the posteriormost region of the middle trochlea (for digit III) is visible in lateral view; in addition the posterodistal extent of the trochlea is not rounded,

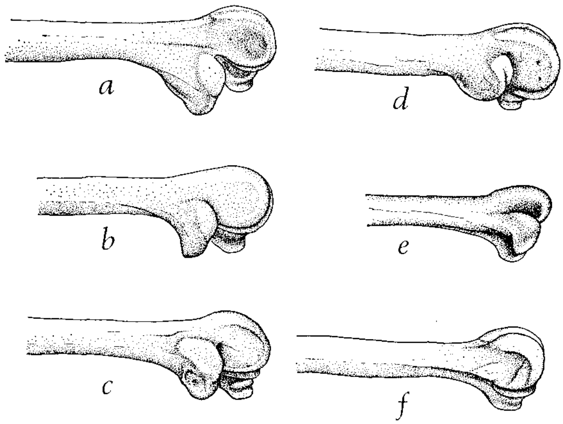

Fig. 4. Internal views of left tarsometatarsi of a–e, same as in Fig. 3.

but tapered towards the distal extreme. In anseriforms the trochlea for digit IV is not thrust so posteriorly (though about the same as flamingos and presbyornithids proximally) and is rounded so that it appears as a large half circle. In the shorebirds (especially recurvirostrids) the trochlea for digit IV has a great thrust posteroproximally so that the entire trochlea for digit III plus part of the shaft of the tarsometatarsus is visible in lateral view; in *Presbyornis* the morphology of the trochlea for digit IV is very close to both modern flamingos and modern recurvirostrids, appearing somewhat intermediate, but the posteroproximal thrust is not quite as great as that of the recurvirostrids; as in flamingos and recurvirostrids the internal trochlea shows a decided slope towards the medial line posteriorly.

It should be noted that some of the gruiform birds exhibit not only a fairly well-developed inner cnemial crest of the tibiotarsus but a distal tarsometatarsus that in many respects resembles that of the flamingos and shorebirds, but in gruiforms the shaft of the tarsometatarsus is relatively wider as it merges into the distal end. In addition the space between the trochleae is relatively greater, the trochleae are more laterally spread, the external trochlea is relatively broader, and the internal trochlea typically shows relatively little mesial inflection. Gruiforms are not included in the overall analysis because of the heterogeneity of the order and their lack of large numbers of characters in common with the flamingos and presbyornithids. Galliforms have a tarsometatarsus somewhat similar to that of charadriiforms, but are distinctive in a number of characters (cf. Olson and Farrand 1974). Among the Charadriiformes many forms exhibit some of the derived characters under consideration

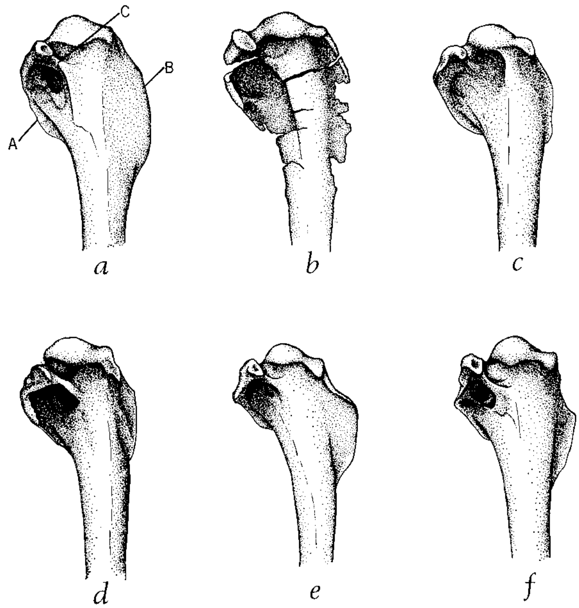

Fig. 5. Anconal views of the proximal ends of right humeri of a, flamingo (*Phoeniconaias minor*); b, presbyornithid (*Presbyornis pervetus*); c, recurvirostrid (*Recurvirostra americana*); d, duck (*Anas rubripes*); e, ibis (*Eudocimus ruber*); and f, heron (*Egretta caerulea*). Abbreviations are as follows: A, bicipital crest; B, deltoid crest; C, median crest.

here, but only in the recurvirostrids is the total combination present, along with a general body form similar to that of the flamingos.

Humerus.—The humerus (Figs. 1, 5) shows some characters of interest. In both the presbyornithids and the modern flamingos the deltoid crest is relatively long and is smoothly curved into the shaft, unlike the condition found in the other groups under consideration. In the region of the bicipital crest the humerus of *Presbyornis* is most similar to the shorebirds. It has a large, broadly curved bicipital crest, with a deeply excavated subtrochanteric fossa without fossae or foramina. Howard (1955: 12) pointed out that a distinguishing characteristic of *Telmabates* was the shape and simplicity of the subtrochanteric fossa; she stated that it had no counterpart in any species compared. Yet, the recurvirostrids seem clearly in line with this character, having a simple, deeply excavated fossa, devoid of the complexities of the other groups under consideration. *Telmabates* has a well-developed median crest; in recurvirostrids it is less well developed.

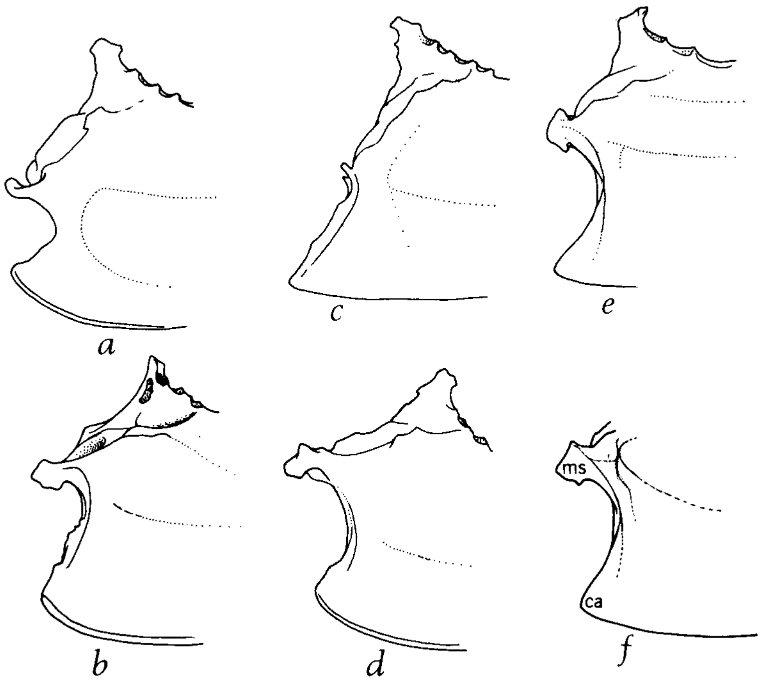

Fig. 6. Lateral views of the anterior aspect of the sterna of A, a heron (*Egretta caerulea*); B, an ibis (*Threskiornis aethiopica*); C, a duck (*Aythya affinis*); D, a flamingo (*Phoenicopterus ruber chilensis*); E, a recurvirostrid (*Recurvirostra americana*); and F, *Presbyornis*. Abbreviations: ms, ventral manubrial spine; ca, carinal apex.

Miscellaneous postcranial characters.—The sternum of *Presbyornis* (Fig. 6) has a well-developed ventral manubrial spine, very much like those of modern flamingos, ibises, and shorebirds. In anseriforms, the ventral spine is not well developed except in *Anas* and some geese, and in herons it is present as a long straight process, rather than as a nearly square bony block. The anseriforms also differ in the form of the anterior carinal margin. In most of the forms under consideration and the presbyornithids, the margin is extended ventrally, with a slight anterior curve; in anseriforms the margin extends in a straight line anteroventrally. The sternal characters do not appear to be very constant within the groups being considered.

In the presbyornithids the trochanter of the femur is highly raised above the iliac crest. This character is present in modern flamingos, recurvirostrids, ibises (but not herons), but absent in anseriforms.

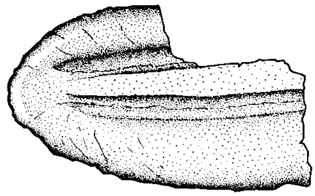

Fig. 7. Dorsal view of the bill of *Presbyornis pervetus* Wetmore (Univ. Wyoming, Mus. Paleontology, BQ-250). Actual length of specimen, 38.4 mm.

In the presbyornithids, the coracoid has a deep undercut below the furcular facet and the neck is excavated below the head with a diagonal rise separating the regions. Living recurvirostrids show a deep excavation beneath the furcular facet, but the rise is only slightly developed. Modern flamingos, anseriforms, and herons lack the combination of coracoid characters enumerated above, but ibises approach the presbyornithid condition.

Pelvic characters are, with a few exceptions, not very diagnostic of the groups under consideration. The pelvises of flamingos, ibises, herons, shorebirds, and presbyornithids are fairly similar. Anseriforms have a distinctive pelvis. In presbyornithids the ischiopubic fenestra is a long opening, its length approximately three times its height; of the groups under consideration the recurvirostrids most closely approximate this condition. In modern flamingos and most ciconiiforms (except ibises) the fenestra is more rounded.

Skull.—The skull of *Presbyornis* (Figs. 7, 8) is similar to that of modern flamingos in the region of the nasal-frontal hinge, but has a straight ducklike bill, and the posterior orbit and postorbital process are

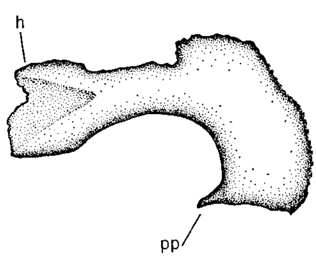

Fig. 8. Lateral view of the posterior region of the skull of *Presbyornis pervetus* Wetmore (Univ. Wyoming, Mus. Paleontology, BQ-550). Abbreviations: pp, postorbital process; h, nasal-frontal hinge. Measurements: distance from postorbital process to anterior extent of nasal-frontal hinge, 21.6 mm; width across supraorbital area of frontal bone, 5.5 mm.

also ducklike. The Green River bird appears to have been a straight-billed form, but this cannot be established unequivocally. The bill is flat and very ducklike in general appearance. It shows no real signs of tapering until the very distal extent, at which point it is rounded but with a slight dip at the tip, as in most ducks. A general mesial depression with a ridge along the middorsal line is bordered by small furrows on either side. Some modern ducks (e.g. *Spatula clypeata*) have similar but smaller furrows.

The area of the nasal-frontal hinge is not drastically different from that of modern flamingos, although ducks are similar to flamingos in many characters of this region. Facets for the articulation of the lacrimal bones are present laterally on the anterior regions of the frontals, as in modern flamingos; in anseriforms, the lacrimals are typically fused to the frontals. In *Presbyornis*, as in modern flamingos, an anterolateral flaring of the frontals at the region of the nasal-frontal hinge leaves a slight depression in the middle of the hinge region. This flaring gives a V-shaped appearance to the anterior region of the frontals at the area of the hinge. Unlike modern flamingos, but as in modern anseriforms, the supraorbital region of the frontals is very constricted (in modern flamingos, the area above the orbit is relatively wider, sloping off gradually to the sides).

The foramina of the orbit vary greatly within modern orders of birds, and within the order Anseriformes; within the orbit are no characters to preclude affinities of *Presbyornis* with any number of modern avian orders.

The posterior part of the skull is anseriformlike in appearance. The posterior orbital wall is rounded with the postorbital process turning back anteriorly, as in modern ducks. In modern flamingos the postorbital process points almost ventrally. In addition, the interorbital septum slopes upward toward the nasal-frontal hinge at an angle of approximately 45°, as in most ducks and many other modern orders; in modern flamingos the slope is much steeper.

A final and striking ducklike character in *Presbyornis* is the form of the occipital condyle. In modern birds the condyle may be either rounded (as in shorebirds) or rounded ventrally and flat dorsally with a slitlike depression middorsally as in modern ducks. Modern flamingos have the flat dorsal region with only a slight indication of the slitlike depression characteristic of the anseriforms and a number of other modern orders (e.g. some ciconiiforms).

In summary, while the skull of modern flamingos is highly specialized, that of *Presbyornis* is decidedly anseriform, but exhibits some flamingo-like characters in the region of the nasal-frontal hinge.

PARASITES

The mallophaga of flamingos are most like those of ducks (Clay 1957), but the tapeworms are related to those of the Charadriiformes (Baer 1957).

SWIMMING BEHAVIOR

The ability of the adults to swim has often been used to support an affinity of flamingos with the anseriforms, but the recurvirostrids are able swimmers and have the feet "webbed" as in the flamingos. The presbyornithids had a flamingo webbing to the feet, as indicated by tracks of Lower Eocene age (see photograph in Kahl 1970).

THEORETICAL CONSIDERATIONS

The foregoing osteological analysis has been based on overall similarity of certain characters of bones that are presumably derived character states. I agree in theory with those who would use a method of character analysis involving primitive-derived character sequences (see Hennig 1966, Cracraft 1972), but I doubt that a methodology exists for actually determining primitive-derived sequences in more than a handful of cases in the entire class Aves. In comparisons across broad groups of birds it may be impossible to determine unequivocally which character states are primitive and which are derived, and phylogenies based on a small number of shared, derived characters may be entirely misleading or absolutely incorrect. The insidious trap of convergence lies baited, just as it always has.

Great caution must be exercised in determining primitive-derived sequences, for seemingly irrefutable phylogenies may be established by using the Hennig methodology, but may be so tenuous that one or several mistakes in assessing primitive-derived sequences can throw off the entire phylogeny in a completely different direction.

With respect to the characters under consideration here, one would presume that in Figs. 2 and 3, a, b, and c probably represent the most highly derived types illustrated. In Fig. 2, e and f probably represent the primitive condition, though possibly they could be derived types. In Fig. 3 e appears to be the more generalized character state and therefore presumably the primitive condition; f probably represents another derived character state, but conceivably f could represent the primitive condition. With respect to the humerus (Fig. 5) and the sternum (Fig. 6) determining primitive-derived sequences could be anyone's guess. In essence, what I have done is to attempt an osteological comparison based on overall similarity of a number of elements, and have attempted not to use or weight characters that could represent the primitive condition.

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SUMMARY AND CONCLUSIONS

The presbyornithids are flamingolike waders from the Lower Eocene of North and South America that exhibit a mosaic of osteological characters of a number of living orders. When taken in combination, the characters are shared most closely with the living flamingos, shorebirds, and anseriforms, suggesting a close affinity of those living groups. Evolutionary affinity of the Phoenicopteriformes and Charadriiformes is also strengthened by the similarity of their cestode parasites. The Gruiformes have some of the postcranial characters used in this paper to indicate affinity of the shorebirds and the flamingos, but they lack the total combination of characters present in the shorebirds, and particularly the recurvirostrids. Gruiforms are probably closely allied to the Charadriiformes and, judging from the large number of living relict groups, may be of earlier origin. In general appearance, flamingos and recurvirostrids also resemble one another; both groups are gregarious, and both groups are good swimmers with well-developed webbing in the feet. The extremely close similarity of particularly the tibiotarsus and tarsometatarsus of flamingos and recurvirostrids might suggest convergent evolution, but the major characters of these two bones, except for the general form (they are long, slender bones in both groups), are shared by diverse members of the Charadriiformes with divergent forms of locomotion.

The following conclusions based on osteology seem reasonable. Ibises and herons are quite distinctive; the two groups are probably not closely related, and neither is closely allied with the flamingos. Flamingos are probably more closely related to the Anseriformes and Charadriiformes than to any other living orders of birds. Many of the osteological characters not shared by living flamingos and living recurvirostrids are bridged by the Eocene fossil *Presbyornis* Wetmore, a form originally described as

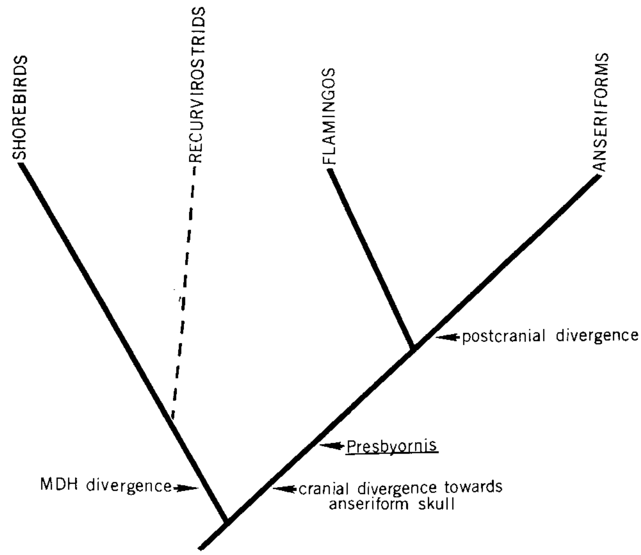

Fig. 9. Hypothetical phylogeny illustrating major cladistic events in the evolution of flamingos. MDH divergence refers to the divergence of the S form of malate dehydrogenase which has a unique mobility in all shorebirds (Kitto and Wilson 1966), and argues strongly for their monophyly.

an extinct recurvirostrid, which is actually a charadriiform-anseriform mosaic.

The flamingos are a very ancient group survived today by a small group of highly specialized relicts. Because of the antiquity of the group they possess a mosaic of characters shared with a number of modern orders, but most closely with the Anseriformes and the Charadriiformes.

A classification reflecting the views of this paper is shown below; it involves placing the flamingos in their own order, Phoenicopteriformes, between the Charadriiformes and the Anseriformes:

Gruiformes
Charadriiformes
Phoenicopteriformes
Anseriformes

A hypothetical phylogeny illustrating the possible major cladistic events in the evolution of modern flamingos is illustrated in Fig. 9.

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