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A New Wading Bird from the Eocene of Patagonia

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INTRODUCTION

The Scarritt Expeditions of the American Museum of Natural History in 1930–1934 yielded quantities of fossil bones from numerous localities in central Patagonia. Among these is a collection of bird bones taken in Chubut Territory, Argentina, in the collecting season of 1930–1931. The expedition, headed by George Gaylord Simpson, discovered the bones in Cañadón Hondo, south of the Río Chico, in a narrow deposit of green bentonite which apparently represents a local facies in the Casamayor formation of lower Eocene age.

Although the birds were the principal fossils in this deposit, there were associated with them a few other vertebrate remains, representing one amphibian (Schaeffer, 1949, p. 49), two reptiles (Simpson, 1937, 1938a; and Colbert, 1946), and a small marsupial mammal (Simpson, 1938b). In discussing the occurrence, Simpson (1938b, p. 1) refers to the deposit as "a remarkable fossil pocket only a few feet in diameter but rich in bones of highly varied character. The facies is unlike anything otherwise known in South America,[2] all the fossils found in it appear to be new, and with a single exception, none of the species, or probably genera, has ever been found except in this one minute spot in central Patagonia." (For a more detailed description of the site, see Simpson, 1946.) The deposit appears to represent a shallow, fresh-water facies in the wide-

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[2] For a review of other Tertiary vertebrate deposits of South America, see Simpson (1940).

spread volcanic ash deposits of the area, a conclusion which is borne out by the remains of the birds as well as by those of the other vertebrates noted.

The avian collection from Cañadón Hondo consists of 93 recognizable skeletal elements, plus a number of indistinguishable fragments. Ninety of the bones are assignable to a single species (new to science) which is the subject of this dissertation. Each of the other three specimens, a fragment of anterior end of very small coracoid, a proximal tip of tarsometatarsus, and a distal half of tibiotarsus, represents a distinct species. It is considered inadvisable to attempt classification of these fragments, although the tibiotarsus in many ways resembles the comparable element in the dominant species. Even in the latter, however, the tibiotarsus is not clearly distinguishable from that of several waders and swimmers, and a slight deviation might signify generic, or even greater, separation.

All the bones are highly mineralized, and most of them have suffered some distortion and fragmentation. The fortunate duplication of elements in different individuals of the dominant species has made possible the determination of normal contours in many instances. Although incomplete, the principal bones of leg, wing, and shoulder are all represented. Out of several broken bits of skull, a single fragment contributes meager information; there is no mandibular material. The manubrial area of the sternum is present in several individuals, the carina in one. Only uncommunicative fragments of furcula are available. A sacrum and fragment of pelvis and a few vertebrae are present. On the whole, the representation is an exceptionally fortunate one for so ancient a creature.

For the opportunity of studying the collection of bird bones from this deposit, and for his generous cooperation in the course of this undertaking, I wish to thank Dr. Simpson. I am also indebted to Dr. Joseph T. Gregory of the Peabody Museum of Natural History, Yale University, for the loan of specimens of Cretaceous birds from the Marsh collection, and also for his valuable assistance in the study and photography of mounted material which could not be transported. To Dr. Robert W. Wilson of the University of Kansas Museum of Natural History I extend thanks for the loan of Kansas Cretaceous bird material. Photographs were taken by Mr. Lewis Athon, Los Angeles County Museum.

DESCRIPTIONS

The 90 bones of the dominant avian species in the Patagonian material represent at least 10 individuals. For two of these individuals most of the major skeletal elements are available.

All specimens have been compared with skeletons of many different

birds, both living and extinct. 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. More significant comparisons could be made with two fossil genera, *Apatornis* (*Apatornis celer* Marsh, Order Ichthyornithiformes) of the Kansas Cretaceous, and *Paloelodus* (*Paloelodus ambiguus* and others, family Phoenicopteridae) of the European Tertiary. Specimens of *Apatornis* were examined; comparisons with *Paloelodus* were made from the illustrations presented by Milne-Edwards (1867–1871, vol. 1, pls. 82–89). Even from the fossil forms, the Patagonian bird was found to be clearly distinct. It is therefore here assigned to a new genus and species, which it is deemed advisable to describe before allocation to family or order is discussed.

TELMABATES, NEW GENUS[1]

GENOTYPE: *Telmabates antiquus*, new species.

GENERIC DIAGNOSIS: A water bird of phoenicopterid character with anseriform modifications; more primitive in structure than *Phoenicopterus;* closest similarities with *Paloelodus* and *Apatornis*. Last three thoracic vertebrae amphicoelous or opisthocoelous, fourth from last heterocoelous anteriorly, fifth completely heterocoelous; fossa below median crest of humerus well excavated but devoid of pneumatic foramina; external crest of trochlea of carpometacarpus equal in development to internal crest.

Telmabates antiquus, new species

TYPE: A.M.N.H. No. 3170, consisting of the following elements found associated:

Humerus: right and left
Ulna: distal end, left; proximal end, right
Radius: proximal and distal ends of left
Carpometacarpus: proximal and distal ends, right; distal end, left
Sternum: anterior end and fragments of costal border
Scapula: left
Furcula: fragments
Femur: proximal and distal ends, right
Tibiotarsus: distal end, left
Tarsometatarsus: fragment distal end, right
Synsacrum: nearly complete
Vertebrae: six posterior thoracic
Phalanges: one pedal, one alar

[1] From *telma*, pond, and *bates*, one who haunts.

PRINCIPAL REFERRED SPECIMEN: A.M.N.H. No. 3181, consisting of the following elements found associated:

Humerus: right and left (badly crushed and incomplete)
Radius: distal end, right
Sternum: anterior end with carina and manubrium
Furcula: fragments
Coracoid: right and left, incomplete
Scapula: right and left, incomplete
Tibiotarsus: right and left distal ends
Tarsometatarsus: proximal three-quarters of right (badly crushed)
Skull: fragments
Phalanges: four pedal

ADDITIONAL REFERRED MATERIAL: Miscellaneous elements (some associated) of at least eight individuals; all material fragmentary, as follows (all numbers refer to specimens in the collections of the American Museum of Natural History):

Sternum: Nos. 3167, 3172, 3186
Coracoid: Nos. 3172 (two), 3175, 3183, 3186
Scapula: No. 3178
Humerus: Nos. 3167 (two), 3168 (two), 3169 (two), 3171, 3173, 3174, 3177, 3179, 3180, 3184 (two)
Ulna: Nos. 3169, 3172, 3180, 3182, 3186
Radius: Nos. 3167, 3169 (two), 3171, 3178, 3186
Carpometacarpus: Nos. 3166, 3169, 3171, 3182, 3186, 3187
Femur: Nos. 3167, 3169 (two)
Tibiotarsus: No. 3180
Tarsometatarsus: No. 3171
Fibula: Nos. 3175, 3180
Pelvis: No. 3185 (fragment)
Vertebra: No. 3167
Pedal phalanx: No. 3176
Alar phalanx: No. 3180

HORIZON AND LOCALITY: Green bentonite facies in Casamayor formation, lower Eocene; Cañadón Hondo near Paso Niemann, south of Río Chico del Chubut, southern Chubut Territory, Argentina.

SPECIFIC DIAGNOSIS: Same as for genus (based on type specimen). The following characters may be added on the basis of the principal referred specimen (A.M.N.H. No. 3181): lacrimals not fused with frontals; coracoid relatively short, slender-bodied, flaring at sternal end; tarsometatarsus shorter than humerus.

DETAILED DESCRIPTION

SKULL: One fragment of frontal region (fig. 1H, I) among the miscellaneous scraps of skull in A.M.N.H. No. 3181 yields slight informa-

tion, as follows: (1) frontal area narrowing gradually to center, flaring posteriorly and anteriorly; (2) bone sloping laterally from faint longitudinal, central ridge; edges slightly striated; (3) portion of facet for attachment of lacrimal present on right side, anteriorly (bone broken in this area on left).

VERTEBRAE: Vertebrae represented in the type specimen are the last four free thoracic plus the one which is fused in articulation with the synsacrum (fig. 1J), and an additional thoracic of more anterior position. Although in a poor state of preservation, they show that the centra are not all heterocoelous. The last thoracic before that fused to the synsacrum is mildly amphicoelous (this vertebra is represented in A.M.N.H. No. 3167 also); the next two preceding are opisthocoelous; the next is heterocoelous anteriorly. The sixth specimen is typically avian at both ends. Compared with living birds, the condition is most like that found in the Charadriiformes, but is not identical. Presumably this is a primitive condition which has been held over in the charadriiforms and does not imply direct affinity with *Telmabates*. It should be noted, however, that the condition in *Telmabates* is less primitive than that found in the Cretaceous *Ichthyornis* in which the entire thoracic series is amphicoelous.

SYNSACRUM: This element is present in the type only (fig. 1B, C). It is composed of 13 vertebrae, the first vertebra incompletely separated from the preceding thoracic. Length from junction with this thoracic, to posterior tip, 63.8 mm.; greatest breadth through centrum, 7.7 mm.; breadth between facets for articulation with pelvis, 3.8 mm.; greatest depth, approximately 12.2 mm. Dorsal spine apparently low, though this area incomplete anteriorly. Extended transverse processes, if originally present, are now broken beyond recognition; first three vertebrae bear short stubs, and this stub of the third appears to be continuous with a flat facet for articulation with ilium. Fourth, fifth, and sixth vertebrae bear articular facets closely appressed to area of dorsal spine, and the fourth and fifth also bear short transverse stubs at ventral edge of centrum. Means of attachment to pelvis, of vertebrae 7 through 9, not clearly indicated; slender ridges indicate region of contact, but whether extended or appressed cannot be discerned. Vertebra 10 bears transverse stubs both dorsally and ventrally, and the last three vertebrae each have similar indications, although the ventral stubs are somewhat diagonally placed (higher posteriorly than anteriorly).

It is difficult to make comparisons in this element. The number of vertebrae (13) coincides with the number found in *Phoenicopterus* and (apparently) *Paloelodus*. A more primitive condition exists in *Telmabates*, however, in the presence of facets indicating articulation rather

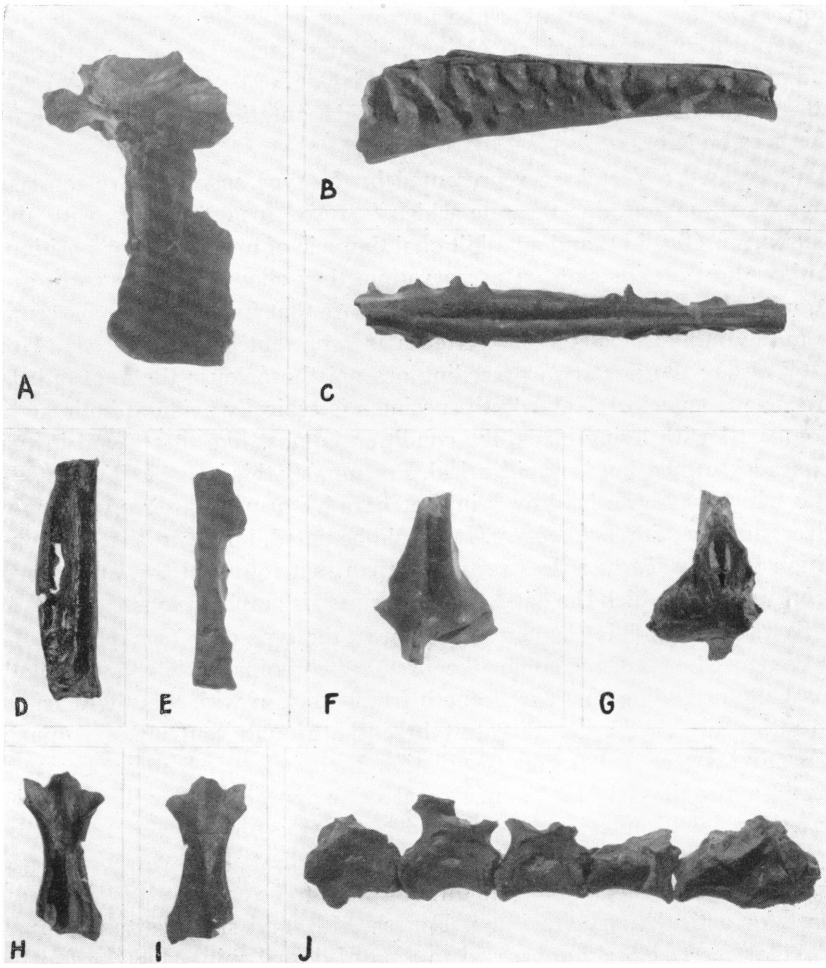

FIG. 1. *Telmabates antiquus*, new species. A. Lateral view, sternum, A.M.N.H. No. 3181. B, C. Lateral and ventral views, synsacrum, type, A.M.N.H. No. 3170. D, E. Wing phalanges, A.M.N.H. Nos. 3180 and 3170 (type). F, G. Ventral and dorsal views, anterior end of sternum, type, A.M.N.H. No. 3170. H, I. Ventral and dorsal views, frontal fragment of skull, A.M.N.H. No. 3181. J. Thoracic vertebrae, type, A.M.N.H. No. 3170. Natural size.

than fusion of pelvis with synsacrum. The condition in *Apatornis,* as depicted by Marsh (1880, pl. 28, fig. 1), is somewhat similar, though in the Cretaceous bird the facets are shown as continuing posteriorly. *Telmabates* and *Apatornis* are alike in the narrowness across the dorsal portion, neither one apparently having the broad expanse of connected transverse

processes found in the modern flamingos, ibises, and anseriforms, or the fossil *Paloelodus*.

PELVIS: The single pelvic fragment (A.M.N.H. No. 3185) appears to be a small section of ischium with lower border of ilio-ischiatic foramen and portion of acetabulum. No details of the pelvis can be described from this specimen.

STERNUM: The complete anterior border of the carina is present only in A.M.N.H. No. 3181 (fig. 1A); the manubrial area, the coracoidal sulci, and fragments of costal border are present in the type (fig. 1F, G); A.M.N.H. Nos. 3167 and 3172 have incomplete sulci and manubrium; A.M.N.H. No. 3186 includes a fragment of costal border only.

Right coracoidal sulcus crossing below left sulcus just past midpoint of manubrium, with small diagonal ridge dividing the two. Ventral edge of manubrium broadly rounded, spine well developed. Flat, shelf-like area present above dorsal lip of sulcus, 4.0–4.3 mm. wide and bordering anterior margin of sternum; behind this area, bone slopes sharply downward; single, large foramen in center of shield at this point. Carina slender but well formed; anterior border relatively straight. Height of carina from dorsal lip of sulcus, 38.5 mm. Fragments of costal border too small to indicate number of costal ridges or outer contours of sternum.

Characters of the phoenicopterids and the anseriforms are combined in the slightly crossed sulci (as in *Phoenicopterus*) and the broad, shelf-like area above them (as in the geese). In *Apatornis* the simple crossing of the sulci and the broadly rounded anterior edge are as in *Telmabates,* but the manubrial spine is apparently undeveloped; the bone is fragmented in this area in *Apatornis,* but there is no indication that a large spine was present. According to Milne-Edwards (1867–1871, vol. 2, pp. 67, 81) the degree of crossing of the sulci varies in different species of *Paloelodus*. Whereas *P. ambiguus* appears to have a condition similar to that in *Telmabates,* the crossing is much more emphasized in *P. goliath;* the anterior border of the sternum is more compressed in *Paloelodus* than in *Telmabates,* and the manubrium more pointed. Details of the area behind the sulci cannot be distinguished in either *Apatornis* or *Paloelodus*.

FURCULA: Although fragments of furcula are tentatively identified for the type and A.M.N.H. No. 3181, it is impossible to reconstruct the element sufficiently to describe it.

CORACOID (FIG. 2): The coracoids are not present in the type specimen. Characters of this element, therefore, are based on a nearly complete left and incomplete right of A.M.N.H. No. 3181 and complete (A.M.N.H. No. 3183) and incomplete (A.M.N.H. Nos. 3172, 3175, and 3186) specimens in the other assigned material.

Sternal end relatively flat dorsoventrally (very slightly bowed),

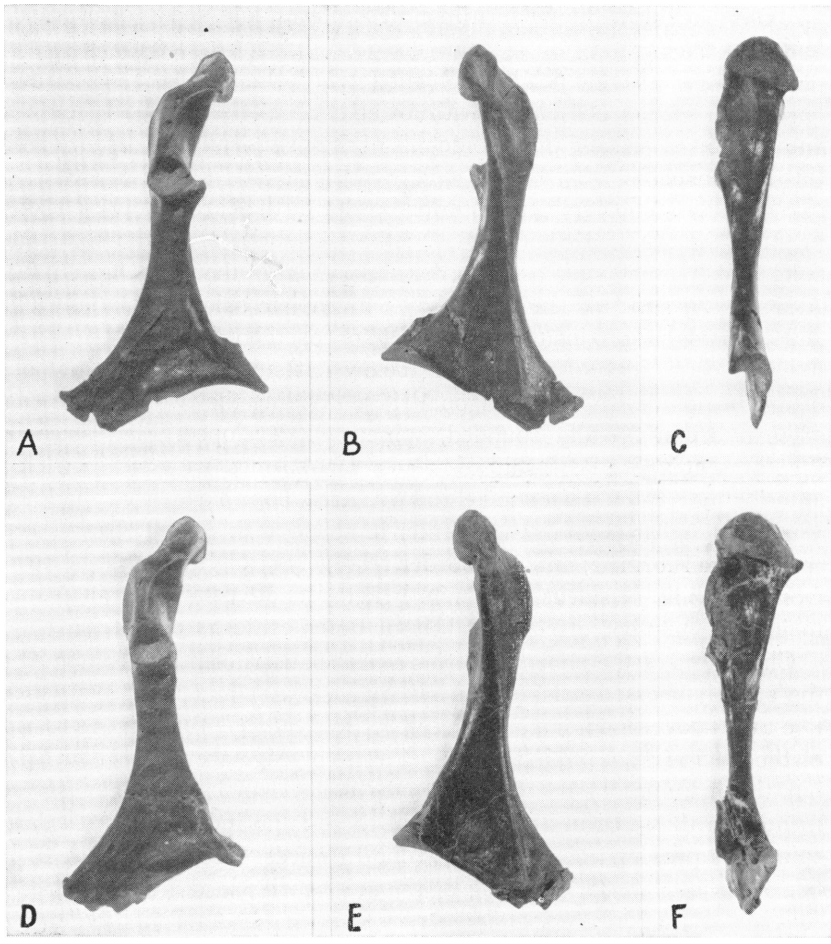

FIG. 2. *Telmabates antiquus*, new species. Left coracoids. A, B, C. Dorsal, ventral, and internal views, A.M.N.H. No. 3183. D, E, F. Dorsal, ventral, and internal views, A.M.N.H. No. 3181. Natural size.

markedly flared laterally, tapering up to slender body. Sternocoracoidal process well developed. Dorsal surface above sternal end excavated in triangular space. Sternal facet extending broadly on dorsal edge, though widest part stops short of external tip; near medial edge, facet curls onto ventral surface as well. Head symmetrically placed on neck (internal view), although furcular facet extends slightly beyond neck, ventrally; ventral edge of head broad, its external border clearly demarcated; bicipital attachment a marked gash through center of ventral edge, nearly

parallel with slope of neck. Internally, head convex, with undercut below furcular facet. Neck excavated below head; a diagonal rise tends to separate ventral and dorsal aspects of this region. Scapular facet a round, deep cup; foramen present close to lower margin of facet, proceeding diagonally to emerge in internal aspect near margin of procoracoid and slightly nearer sternal end. Procoracoid only moderately developed. Measurements are given in table 1.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF CORACOIDS OF *Telmabates antiquus*

	A.M.N.H. No. 3181	A.M.N.H. No. 3183	A.M.N.H. No. 3172	A.M.N.H. No. 3175	A.M.N.H. No. 3186
Length from center of sternal end to head	43.8	42.3	—	—	—
Length from scapular facet to tip of head	19.3	19.7	18.9	—	—
Greatest breadth of sternal end	—	27.3	—	—	—
Dorsoventral depth of head	11.2	10.2	9.3	10.0	10.0
Dorsoventral depth of neck	9.8	9.1	8.9	—	—
Breadth through head at widest point	5.9	5.8	5.3	5.9	5.1
Least breadth below scapular facet	6.0	5.8	5.7	—	—

In its short body and flaring sternal end, the coracoid of *Telmabates* resembles that of *Phoenicopterus, Paloelodus,* and *Apatornis,* but the body is relatively more slender than in the first two genera. In shape of head and position of the head on the neck, the ibises and geese are also similar, but *Apatornis* differs. In the undercut below the furcular facet, and adjacent excavation of the neck, the geese and ibises may be satisfactorily, though not exactly, compared, but *Phoenicopterus* and *Apatornis* cannot be considered. The description of *Paloelodus* (Milne-Edwards, 1867–1871, vol. 2, p. 68) suggests similarity to *Telmabates* in this area. The exact combination of roundness and depth of scapular facet is not certainly duplicated in any of the genera compared. The facet is deep but oval in shorebirds, round but less deep in the anseriforms; *Phoenicopterus* approaches the condition, but does not match it precisely; the closest approximation is suggested in *Apatornis,* though

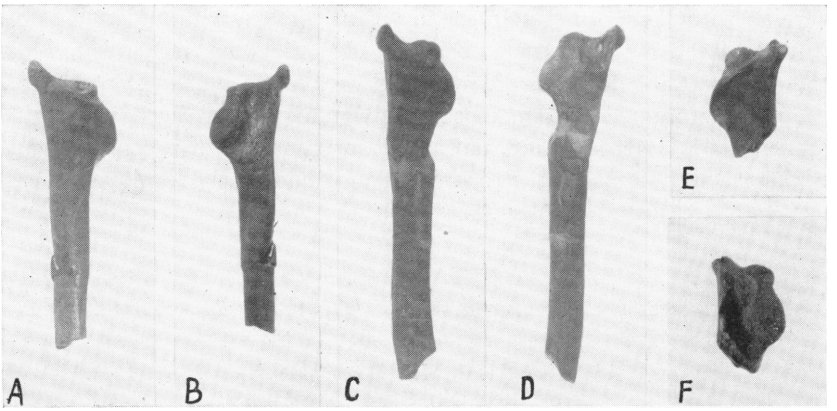

FIG. 3. *Telmabates antiquus*, new species. Scapulae. A, B. Ventral and dorsal views, left, type, A.M.N.H. No. 3170. C, D. Ventral and dorsal views, left, A.M.N.H. No. 3181. E, F. Ventral and dorsal views, articular end, right, A.M.N.H. No. 3181. Natural size.

unfortunately the facet is chipped away on one edge. The position of the foramen appears similar to that of *Apatornis*. The moderately developed procoracoid is best compared with the condition in the geese; this region is broken in the specimen of *Apatornis*.

SCAPULA (FIG. 3): The scapula is represented in the type and A.M.N.H. Nos. 3181 and 3178. It is a stout bone, measuring roughly 9 mm. across the expanded proximal region. Acromion a strong, extended process. Coracoidal articulation a large, rounded ball (coinciding with deep, cup-shaped socket on the coracoid). Glenoid facet heavy, elongate, and upward protruding at its distal border. No foramina.

The scapula of *Telmabates* resembles that of *Apatornis,* although the acromion is less extended than in the Cretaceous bird. Characters of acromion and coracoidal articulation are similar, also, to those found in *Phœnicopterus, Paloelodus,* and in the anseriforms, especially the geese. Characters of the glenoid facet are also goose-like.

HUMERUS (FIG. 4): At least 10 individuals are represented by the 18 available specimens of humerus. Although the complete length of the element can be taken only on the type, all parts are duplicated among the other, more fragmentary specimens. The humeri of A.M.N.H. No. 3181 are badly crushed.

Relatively long, slender element: length, 140.8 mm.; breadth proximal end, 25–26 mm.; breadth distal end, 17–18 mm.; breadth shaft at middle, 7–7.8 mm. Deltoid crest about one-third of length of bone (48.5 mm. in type). Bicipital crest approximately half of the length of the deltoid

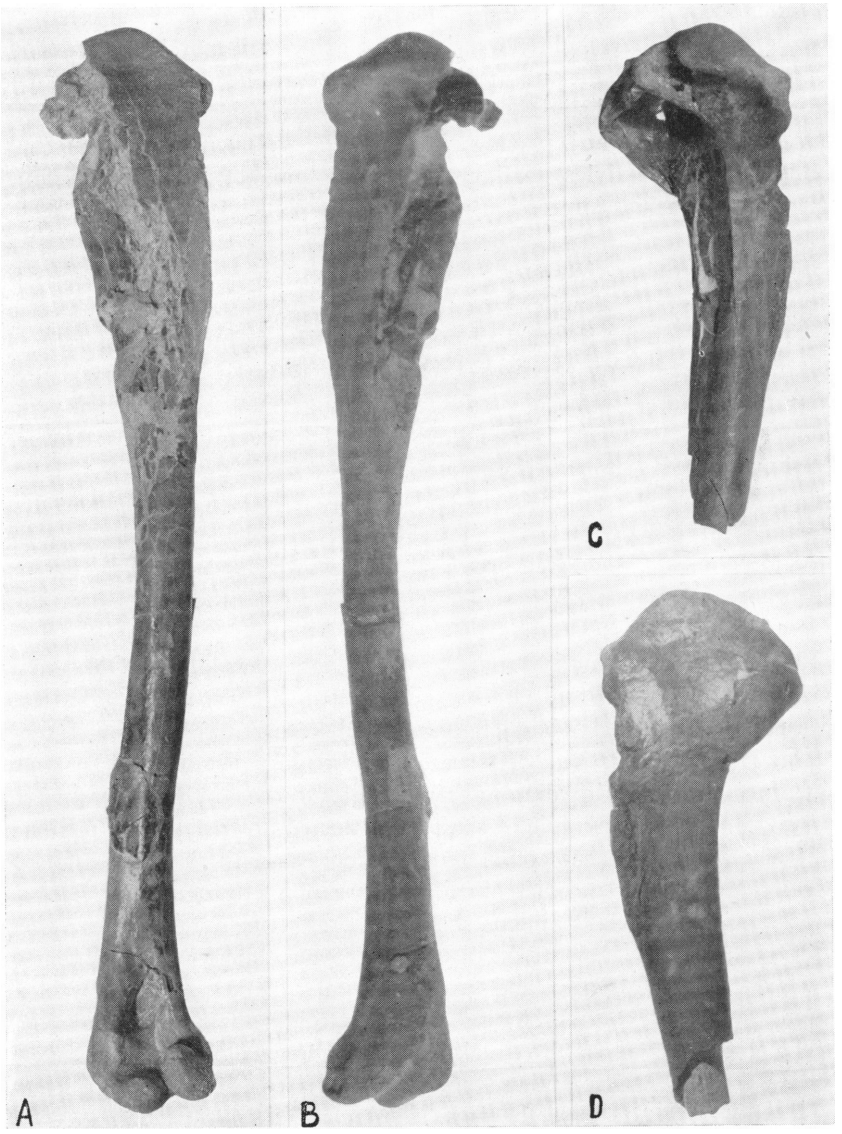

FIG. 4. *Telmabates antiquus*, new species. Humeri. A, B. Palmar and anconal views, left, type, A.M.N.H. No. 3170. C, D. Anconal and palmar views, right proximal end, A.M.N.H. No. 3179. Natural size.

crest. Subtrochanteric fossa deeply but simply excavated, devoid of complex laminations or foramina; median edge of fossa nearly continuous with central crest of shaft. Intermuscular line on deltoid crest slightly external to central crest of shaft, and running diagonally to end at point

of junction of deltoid crest and shaft. Lower border of head (anconally) nearly straight and slightly overhanging, with well-marked depression beneath, and between it and median crest. Apex of head pointing slightly externally. Distal end slightly thrust towards external side. Internal distal margin sloping upward, placing entepicondyle well proximal to internal condyle. Distal condyles small, entepicondyle thin, ectepicondylar prominence low. Brachial impression narrow and obliquely placed; deep at its distal margin.

Two outstanding characters distinguish the humerus of *Telmabates:* (1) the shape and simplicity of the subtrochanteric fossa and (2) the upward slope of the internal distal margin. The former character finds no counterpart in any species compared. The latter is closely paralleled in *Phoenicopterus* and *Paleolodus* and is suggested in the swans; the entepicondyle, however, is less developed than in any of these forms. The humerus of *Apatornis* is not known.

ULNA: A right proximal end and left distal end of this element are present in the type material (fig. 5C–F); the element is lacking in A.M.N.H. No. 3181; three proximal and two distal ends occur among the other assigned specimens. These, together with the type, show the following characters:

Length not less than 140 mm., probably not much longer. Olecranon moderately developed and curving slightly palmad. Internal cotyla oval with edges well raised; obliquely placed with respect to olecranon. Intercotylar ridge well marked. External cotyla bending distally at its palmar edge, forming a long lip almost at right angles to the cotyla proper; ridge running obliquely to middle of shaft from turned-down lip. Two papillae obliquely below internal cotyla tend to connect with above-mentioned ridge, completing boundaries of radial depression (triangular in shape). Impression of brachialis anticus sharply depressed below prominence for anterior articular ligament. At distal end, carpal tuberosity prominently developed both laterally and proximodistally. Contours of trochlea rounded; external condyle sloping gradually to join shaft on anconal side.

The characters of the proximal end of the ulna are not unlike those of *Phoenicopterus,* and to judge from Milne-Edwards' description (1867–1871, vol. 2, pp. 69–70), they are even more closely approximated in *Paloelodus.* The bending of the external cotyla and arrangement of the papillae beneath are paralleled also in some of the shorebirds. The distal end is distinguished from that in the flamingos both by the large carpal process and the gradual slope from external condyle to shaft. In these characters, *Telmabates* bears close resemblance to *Anser albifrons* and to the swans. No ulna of *Apatornis* is available for comparison.

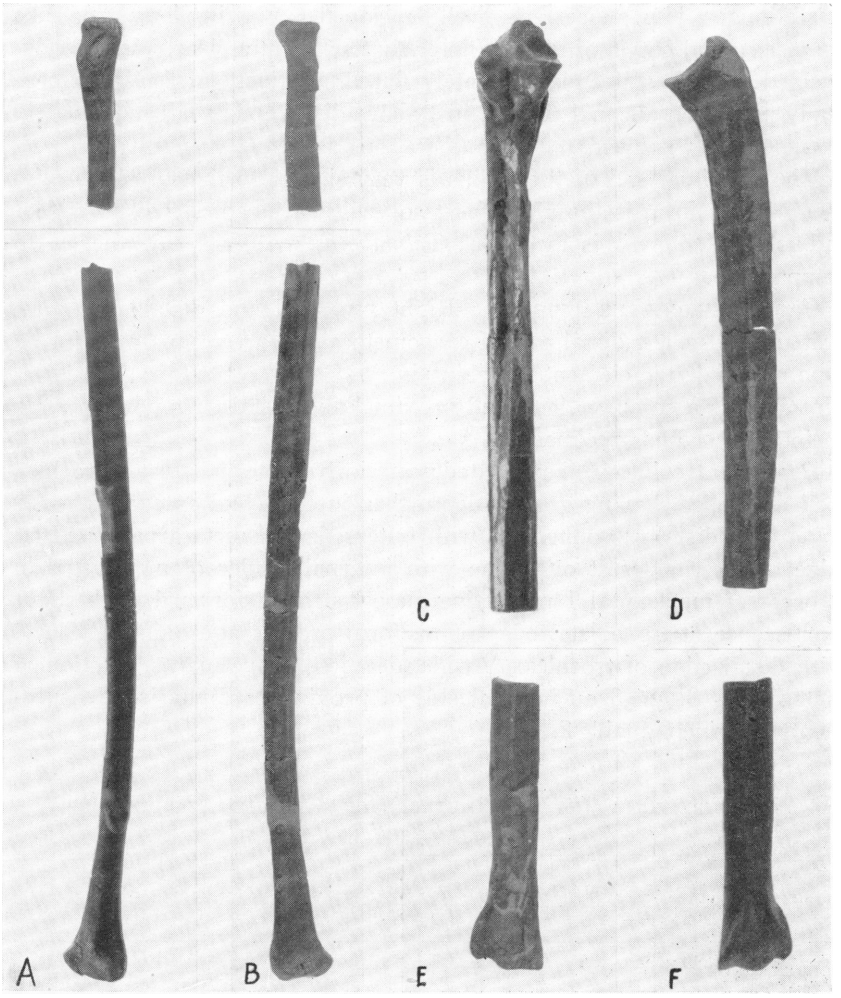

FIG. 5. *Telmabates antiquus*, new species. Radii and ulnae of type, A.M.N.H. No. 3170. A. Anconal view, left radius (section of shaft missing between proximal and distal portions). B. Palmar view of distal portion and external view of proximal portion of left radius. C, D. Palmar and internal views, right ulna (proximal end). E, F. Palmar and anconal views, left ulna (distal end). Natural size.

RADIUS: A nearly complete left radius (in two pieces, with no contact) is present in the type (fig. 5A, B), a right distal end in A.M.N.H. No. 3181. Three other distal ends and three proximal ends occur among the assigned specimens. Length not less than 130 mm.; probably not

much longer. Ulnar facet very well developed (reflecting long, facet-like lip of external cotyla of ulna). Bicipital attachment a clearly defined, depressed scar. Distal end moderately flared. Distinct, large papilla centrally placed on anconal surface just above distal end; shaft immediately above, sharply convex.

The proximal end of the radius is very similar to that of *Apatornis;* in no living form is the ulnar facet so well developed. No distal end of radius of *Apatornis* is available; *Telmabates* resembles no other form compared.

CARPOMETACARPUS (FIG. 6): Right proximal and distal ends (not united) and a left distal end of carpometacarpus are represented in the type material; the element is lacking in A.M.N.H. No. 3181; A.M.N.H. No. 3166 is a complete left; and proximal and distal ends occur among the other assigned specimens.

Proximal trochlea well excavated posteriorly. External crest of trochlea well developed, having greater depth than internal and extending as far or farther distally; connecting with outer edge of metacarpal 3; distal edge of internal crest on a line with internal border of metacarpal 3. Process of metacarpal 1 projecting almost straight forward, with slight excrescence at tip. Distal edge of pisiform process approximately level with distal edge of trochlea. A wide, definite groove marks junction of metacarpals 2 and 3 on internal side of proximal symphysis. Measurements are given in table 2.

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF CARPOMETACARPUS OF *Telmabates antiquus*

	A.M.N.H. No. 3170	A.M.N.H. No. 3166	A.M.N.H. No. 3169
Length (externally)	—	63.1	—
Depth proximal end			
Internal	15.7	—	16.6
External	15.9	—	16.7
Height metacarpal 1	9.6	9.5	9.7

In the most outstanding character of the carpometacarpus (the great development of the external crest of the trochlea) *Telmabates* is approached only by *Apatornis*. In distal extent of the crest and connection to metacarpal 3, *Apatornis* and *Telmabates* are alike; in posterior development, however, the external crest in *Apatornis* lacks a fraction of a millimeter of equaling the internal. In all other species compared, the external crest is markedly smaller than the internal. The internal edge

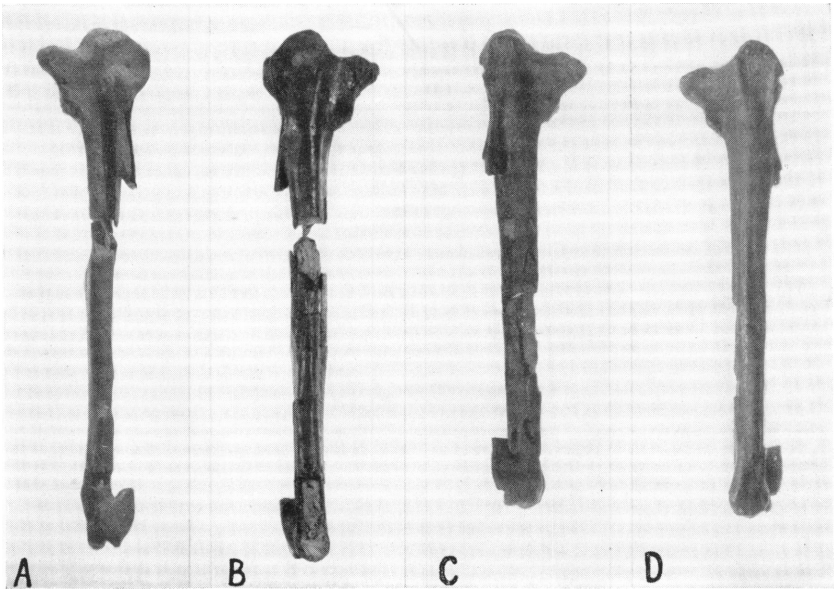

FIG. 6. *Telmabates antiquus*, new species. Carpometacarpi. A, B. Internal and external views, right, type, A.M.N.H. No. 3170. C, D. Internal and external views, left, A.M.N.H. No. 3166. Natural size.

of metacarpal 3 is not on a line with the internal crest of the trochlea in either *Apatornis* or *Paloelodus,* but is considerably internal to it. In the position and shape of the process of metacarpal 1 and the presence of an excrescence at the tip of the process, the geese are similar to *Telmabates. Apatornis* is similar in shape of the process, but the excrescence is lacking.

WING PHALANX: The two available specimens of wing phalanx (the type and A.M.N.H. No. 3180) represent phalanx 1 of digit 2 (fig. 1D, E). No. 3180 is practically complete; the type is incomplete but resembles No. 3180 in all visible respects. The complete specimen is similar to the corresponding element of the Roseate Spoonbill, *Ajaia ajaja,* and of the ibises. It also resembles that of *Paloelodus ambiguus,* though it is slightly shorter and lacks the strong distal projection (Milne-Edwards, 1867–1871, vol. 1, pl. 85, figs. 10–11). Differences exist, however, between species within the genus *Paloelodus.*

	LENGTH	GREATEST DEPTH
A.M.N.H. No. 3170	29.6 mm.	—
A.M.N.H. No. 3180	30.4	8.5 mm.

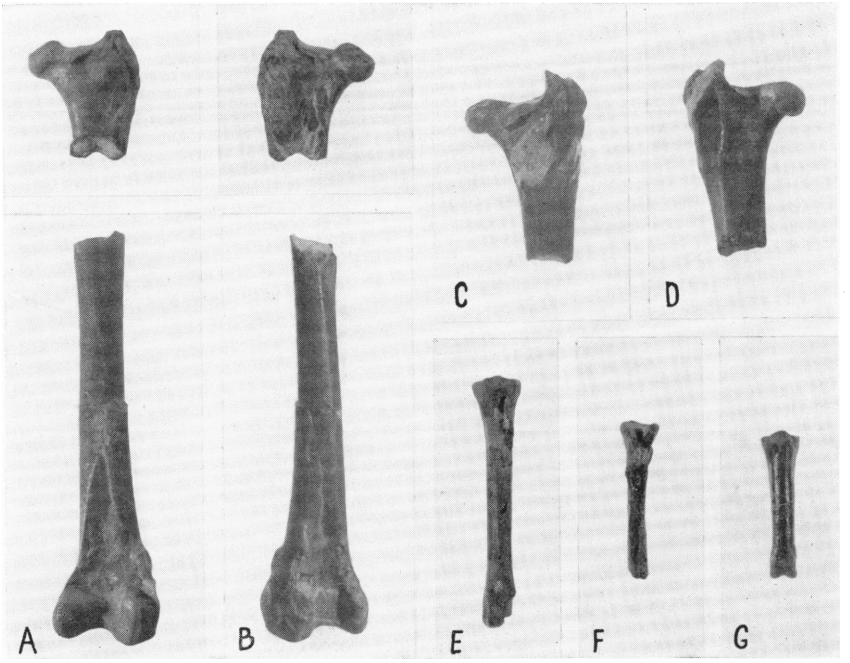

FIG. 7. *Telmabates antiquus*, new species. Femora and phalanges. A, B. Posterior and anterior views, right femur (minute portion of shaft between proximal and distal portions lacking), type, A.M.N.H. No. 3170. C, D. Posterior and anterior views, proximal end, right femur, A.M.N.H. No. 3169. E. Posterior view, phalanx 1, digit 3, A.M.N.H. No. 3176. F. Posterior view, phalanx 1, digit 2, A.M.N.H. No. 3181. G. Anterior view, phalanx 2, digit 3, A.M.N.H. No. 3181. Natural size.

FEMUR (FIG. 7A–D) : No complete specimen of femur is available, but proximal and distal ends are represented in the type and in two assigned specimens ; the element is lacking in A.M.N.H. No. 3181.

From the type the length is estimated at between 69 mm. and 72 mm. Trochanter high, well above iliac facet, and tending to bend over this facet (this area incomplete in type, but shows clearly in A.M.N.H. No. 3169) ; iliac facet jutting out posteriorly beyond shaft. Anterior intermuscular line connecting with trochanter near proximal end, but before junction of trochanter with iliac facet. No pneumatic openings along trochanter. Large papilla, with distinct pit in it, above fibular condyle. Strong intermuscular line rising from outer edge of internal condyle, proceeding obliquely to middle of shaft (about 20 mm. above condylar area).

The femur of *Apatornis* is badly crushed but appears generally similar to that of *Telmabates* except for smaller size. The trochanter is raised above the iliac facet, but its full extent is limited by breakage. The femur of *Paloelodus* is a somewhat stouter element with lower trochanter. It resembles that of *Telmabates,* however, in absence of pneumatic openings. In *Phoenicopterus* the intermuscular lines are somewhat similar in position to those of *Telmabates,* and the trochanter is high. The *Phoenicopterus* femur, however, exhibits much greater pneumaticity. None of the anseriforms resembles *Telmabates* in this element.

TIBIOTARSUS (FIG. 8E–J): Only the distal end is represented in the four available specimens of this element (type, left; A.M.N.H. No. 3181, right and left; and A.M.N.H. No. 3180, left). Groove for peroneus profundus bounded anteriorly by strong ridge or tubercle which is pointed proximally, wider distally; small swelling just distal to this ridge, at external-distal edge of bridge (this area abraded in type, but swelling evident in Nos. 3180 and 3181). Supratendinal bridge well formed and long (3 mm. to 5 mm. proximodistally). Anteroposterior depth of condyles moderate; slight thrust of distal end internally[1]; condyles unequally developed, with internal condyle longer, but lower than external. Breadth condyles (A.M.N.H. No. 3180), 12.1 mm., depth condyles (same specimen), 11.3 mm.

This element combines characters found in *Paloelodus,* the geese, and certain shorebirds, but does not resemble that of the highly specialized *Phoenicopterus.* The general shape of the distal end (its moderate depth and tendency to be thrust towards the internal side) is suggestive of the geese. The long supratendinal bridge and the character of the adjacent ridges distinguish the fossil from the geese. The position of the ridges above the external condyle is somewhat similar to the condition found in the curlews, although the separation between the larger ridge and the smaller swelling adjacent to the distal edge of the bridge is greater in the shorebirds. The illustration (Milne-Edwards, 1867-1871, vol. 1, pl. 83, fig. 5) and description (*op. cit.,* vol. 2, p. 64) of *Paloelodus ambiguus* suggest similarity of *Paloelodus* and *Telmabates* in this area. The character of the supratendinal bridge is also closest to *Paloelodus.* The two depressed areas which occur on the distal surface of the distal end of the tibiotarsus in *Phoenicopterus* and *Paloelodus* are absent in *Telmabates.* The right tibiotarsus of *Apatornis celer* has been used in the composite mount of *Ichthyornis victor* in the Peabody Museum of Natural History at Yale. The specimen is mounted in plaster and there appears

[1] The apparent lack of thrust in the figured type (fig. 8J) is due to the angle of the photograph and the abrasion of the internal border.

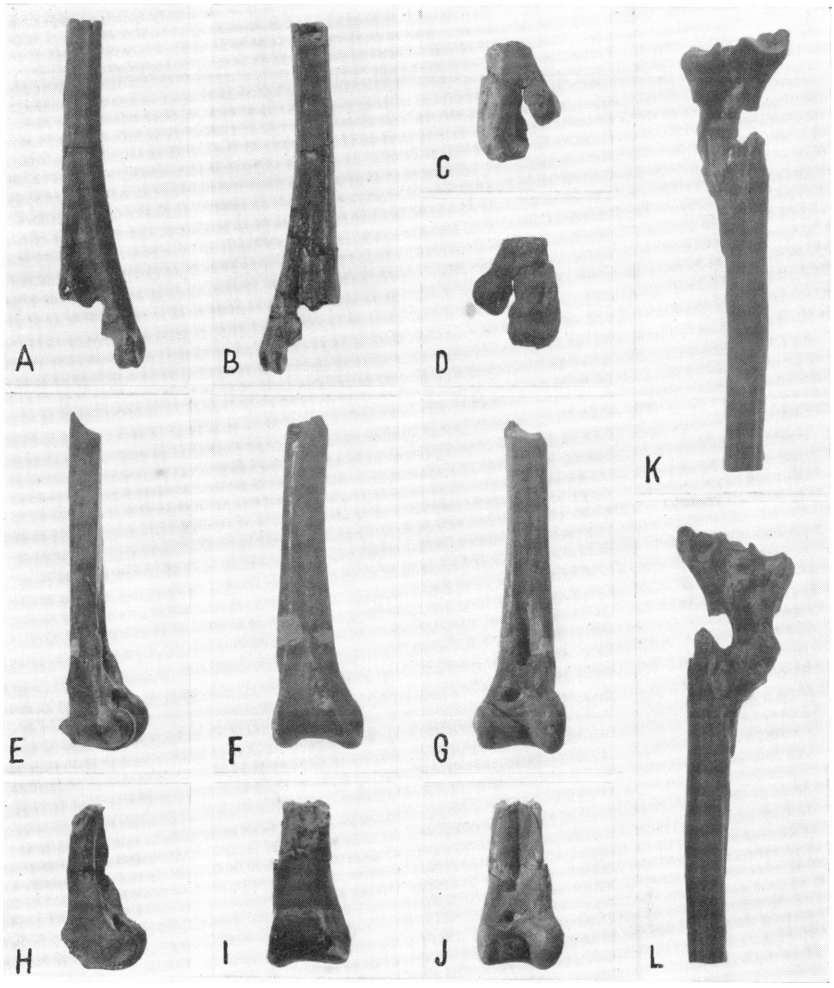

FIG. 8. *Telmabates antiquus*, new species. Tarsometatarsi and tibiotarsi. A, B. Posterior and anterior views, right tarsometatarsus (distal end), A.M.N.H. No. 3171. C, D. Anterior and posterior views, fragment of right tarsometatarsus (middle and inner distal trochleae), type, A.M.N.H. No. 3170. E, F, G. Internal, posterior, and anterior views, left tibiotarsus (distal end), A.M.N.H. No. 3180. H, I, J. Internal, posterior, and anterior views, left tibiotarsus (distal end), type, A.M.N.H. No. 3170. K, L. Anterior and posterior views, right tarsometatarsus (proximal portion badly crushed and distorted), A.M.N.H. No. 3181. Natural size.

to be matrix adhering to it. From what can be seen of the element, it appears that there are no characters which can be compared with *Telmabates;* there is no evidence of a supratendinal bridge.

TARSOMETATARSUS (FIG. 8A–D, K, L): Only three specimens of tarsometatarsus are available: (1) type, fragment of left distal end with internal and median trochleae; (2) A.M.N.H. No. 3181, a right proximal end badly crushed and offset from a portion of shaft; (3) A.M.N.H. No. 3171, a portion of shaft (right) with external trochlea attached, and other trochleae present, but detached. From these fragments the following meager information has been obtained.

By overlapping specimens Nos. 3181 and 3171, a possible length of the element is suggested, at 105 mm. Measurements of breadth are:

	SHAFT	PROXIMAL END	DISTAL END
A.M.N.H. No. 3181	5.3 mm.	14.7 mm.	—
A.M.N.H. No. 3171	5.3	—	13.3 mm.

At distal end, external and internal trochleae shorter than median trochlea, with internal shortest and sloping diagonally in towards posterior face of bone. Depressed area above internal trochlea in specimen A.M.N.H. No. 3171 suggests presence of hind toe. Distal foramen (seen anteriorly) set in deep groove. External side of shaft flat with angular borders anteriorly and posteriorly.

At proximal end, two longitudinal ridges, forming groove between, occur on anterior face 4.6 mm. below internal cotyla. Attachment of external ligament large and clear on external surface of proximal part of shaft. Internally, shaft at proximal end set off from hypotarsus by ridge which may be continuous with internal border of shaft (intervening area destroyed). Internal calcaneal ridge approximately 11 mm. long. The hypotarsus is badly crushed and reconstruction is impossible; however, it appears that at least four ridges were present.

Proportions of the tarsometatarsus indicate a longer, more slender element than in the anseriforms, but much shorter than in *Phoenicopterus*. Closer comparison of proportions may be drawn with *Paloelodus,* the ibises, and certain shorebirds. 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* the slope is less marked. The area for attachment of the hind toe is more marked than in *Phoenicopterus* or the geese, but lacks the distinct facet found in the ibises. The hypotarsus differs from that of *Phoenicopterus* and is suggestive of that of *Paloelodus* in multiplicity of ridges. This element is not known in *Apatornis.*

PEDAL PHALANGES (FIG. 7E–G) : A single badly eroded pedal phalanx in the type material represents phalanx 2, digit 2. A.M.N.H. No. 3181 includes proximal fragments of the first phalanx of digits 2 and 3 and a second phalanx of the latter; a fourth phalanx of A.M.N.H. No. 3181 cannot be readily placed; it is only slightly shorter in length than phalanx 2, digit 3, with a flattened distal end suggesting articulation with the ungual. A.M.N.H. No. 3176 is a nearly complete phalanx 1 of digit 3.

These fossil phalanges are all very similar to the corresponding elements in *Phoenicopterus,* except for the fourth specimen of A.M.N.H. No. 3181, the placing of which is uncertain. Milne-Edwards (1867–1871, vol. 2, p. 63) states that in *Paloelodus ambiguus* the phalanges show the characteristics of the flamingos except that they are more strongly compressed, and his illustration (*op. cit.,* vol. 1, pl. 83, fig. 1) shows that the first phalanges of all digits are relatively longer. Strong lateral compression is not noted in *Telmabates;* phalanx 1 of digit 3 is shorter than in *Paloelodus,* and in proportion to breadth is similar to that of *Phoenicopterus;* phalanx 1 of digit 2 is incomplete; phalanx 2 of digit 2 is equal in length to the corresponding element in *Phoenicopterus* and slightly longer than in *Paloelodus ambiguus.*

SUMMARY OF CHARACTERS OF *Telmabates antiquus*

From the preceding details, the following outstanding characteristics of *Telmabates antiquus* may be noted:

1. Posteriormost thoracic vertebrae amphicoelous or opisthocoelous.
2. Synsacrum narrow, apparently lacking broad plate of transverse processes; not fused to pelvis.
3. Sulci of sternum crossed.
4. Humerus lacking pneumatic foramina in subtrochanteric fossa, and entepicondyle of distal end receding proximally and anconally from ulnar condyle.
5. Carpometacarpus with external crest of the trochlea better developed than the internal crest.
6. Tibiotarsus with unevenly developed distal condyles, and internal condyle thrust slightly towards internal side. Very faintly developed tubercle at lower lip of well-developed supratendinal bridge.
7. Hypotarsus of tarsometatarsus with more than two calcaneal ridges.

Although the measurements taken on *Telmabates antiquus* were not all obtained from one individual bird, a general conformity in size in all individuals studied was evident. It is therefore considered feasible to present the following generalities regarding proportions: coracoid 30 per cent of length of humerus (coracoid A.M.N.H. No. 3181, humerus of type); humerus and ulna of about equal length (humerus and ulna both

of type, but ulnar length only estimated); tarsometatarsus shorter than humerus and approximately one and one-half times the length of the femur (length of tarsometatarsus estimated from two fragments representing two individuals; length of femur estimated on type; humerus of type).

SYSTEMATIC POSITION OF *TELMABATES*

Order

In a determination of the proper ordinal allocation of *Telmabates,* three possibilities merit consideration: (1) assignment to a new order; (2) allocation with *Apatornis* in the Ichthyornithiformes; and (3) allocation with the flamingos.

Evidence favoring the first possibility lies in several characteristics which distinguish the genus from any other birds compared, namely: the amphicoelous and opisthocoelous posterior thoracic vertebrae, the absence of foramina in the subtrochanteric fossa of the humerus, and the large external crest of the carpometacarpus. Unfortunately the characters of the humerus and vertebrae could not be checked with *Apatornis.*

In contrast with these few distinctive characters are a great many others which are shared with *Apatornis* or with the flamingos (particularly the fossil genus, *Paloelodus*) or with the geese and swans. Of the few available bones of *Apatornis,* all except the tibiotarsus have characters which compare favorably with *Telmabates,* although in no instance are the elements identical in the two genera. Similar correlations are possible as well between *Telmabates* and the fossil flamingoid form *Paloelodus,* and in lesser degree similarities to the living *Phoenicopterus* are noted, with certain suggested relationship evidenced also with the geese or swans.

Apatornis was originally allocated to the genus *Ichthyornis.* Although later reassigned and given generic and family distinction, it is still retained in the Order Ichthyornithiformes. In contrast to the abundant material (representing several species) of *Ichthyornis,* very little is known of *Apatornis.* A single species (*A. celer* Marsh) is represented by incomplete skeletal parts. There are no humeri, ulnae, tarsometatarsi, skull parts, or vertebrae (other than sacral). It is not surprising, therefore, that the entity of this little bird has been overshadowed by the better known *Ichthyornis.* As a matter of fact, however, the available elements of *Apatornis* are so different from those of its famous contemporary that it is entirely possible that the two are members of distinct orders. Certainly *Telmabates* shows no relationship to *Ichthyornis,* and allocation to

the order which bears its name would not be justified on the basis of the similarities noted to the incomplete skeleton of *Apatornis*.

Of the three possibilities, the third (allocation with the flamingos) seems most suitable. The taxonomic position of the flamingos has long been under discussion, and the allocation to the Order Ciconiiformes is subject to considerable question. Mayr and Amadon (1951, p. 7) have formally recommended the placing of this group in a distinct order. This recommendation is based on the fact that the group bears certain resemblances to the anserines on the one hand and the storks and ibises on the other. They state: "In view of this conflicting evidence, it seems best to place the flamingos as a separate order between the Anseres and the Gressores [Ciconiiformes]. They may be related to both." On the basis of the present study, I am in full accord with this recommendation. As the fossil forms related to *Phoenicopterus* are studied, the flamingo group assumes an important role. In past times its relatives were the dominant forms of wading birds, and several families were represented. In this large group of ancient lineage, *Telmabates* properly takes its place, and in so doing serves to emphasize the relationship of the flamingos to the Anseriformes.

In recommending allocation of *Telmabates* to the flamingo group, I should emphasize that this assignment is ordinal and not subordinal. *Telmabates* is no more a ciconiiform bird than it is an ichthyornithiform bird. The name Phoenicopteri proposed for the flamingo order by Mayr and Amadon may become modified to Phoenicopteriformes, in order to conform with present American usage, but in the light of the present study, its ordinal distinction from the Ciconiiformes should unquestionably be recognized.

Consideration should be given to the possibility that *Apatornis,* too, should be referred to this group, and that it may represent an ancestral form of wading bird leading to *Telmabates*. However, until such time as a thorough comparative study of the Cretaceous birds can be undertaken, it would be unwise to recommend reallocation of *Apatornis*.

Family

Paloelodus has been classified with the Phoenicopteridae, although it differs from *Phoenicopterus* in several important respects. Related to the flamingos, its relatively short tarsometatarsus with complex hypotarsus nevertheless strongly suggests family separation. With the recognition of ordinal status for the flamingo group, such family separation of *Paloelodus* from the true phoenicopterids now seems even more justifiable.

Although *Telmabates* resembles the Paloelodidae more closely than

the Phoenicopteridae, it is even less specialized than *Paloelodus* and differs sufficiently in several characters to warrant separate family status.

It is here proposed that the families Paloelodidae and Telmabatidae be recognized as distinct from the Phoenicopteridae.

FAMILY PALOELODIDAE

DIAGNOSTIC CHARACTERS: (Selected from Milne-Edwards, 1867–1871, vol. 1, pls. 82–89 and vol. 2, pp. 58–82.) Distinguished from the Phoenicopteridae by (1) tarsometatarsus relatively short with shaft deeper than broad and with hypotarsus made up of more than two crests; (2) distal end of tibiotarsus more asymmetrical with less extent of condyles posteriorly and with less complicated development of tubercles adjacent to supratendinal bridge; (3) femur lacking pneumatic foramina, and trochanter relatively low; and (4) furcula with large fossa in symphysis, perforated with pneumatic openings.

FAMILY TELMABATIDAE

DIAGNOSTIC CHARACTERS: Similar to the Paloelodidae as distinct from the Phoenicopteridae in (1) shortness of tarsometatarsus and multiplicity of crests of hypotarsus; (2) characters of distal end of tibiotarsus; (3) lack of pneumatic foramina in the femur. Distinguished from both the Paloelodidae and the Phoenicopteridae as follows: (4) posterior thoracic vertebrae not heterocoelous; (5) synsacrum not fused with pelvis, but articulating (at least anteriorly) by means of broad facets; (6) subtrochanteric fossa of humerus devoid of complex laminations or foramina; and (7) external crest of trochlea of carpometacarpus better developed than internal crest.

SUMMARY AND CONCLUSIONS

Four species of birds are represented by 93 bones from a fossil pocket of the Casamayor formation in Chubut Territory, Argentina. Three species are represented by a single fragment each, none of which is assigned. The fourth, and most abundant, species is herein described as *Telmabates antiquus*. This species, represented by 90 bones, is a primitive wader similar in many respects to the flamingo-like *Paloelodus* of the European Tertiary, but even more primitive. It is here allocated to the Phoenicopteriformes, recognized as a separate order by Mayr and Amadon (1951, p. 7), whose opinions are substantiated by evidence derived from the present study. Similarities to *Apatornis* (Order Ichthyornithiformes) of the North American Cretaceous are also noted. The family Telmabatidae is set up to contain the new species. It is also recommended that *Paloelodus* be given family designation, separate from

the Phoenicopteridae, but within the order Phoenicopteriformes. The family Paloelodidae is therefore delineated.

The position of *Telmabates* with respect to degree of specialization is between *Apatornis* on the one hand and *Paloelodus* on the other. *Paloelodus* in a measure bridges the gap between *Telmabates* and *Phoenicopterus*. However, it is not suggested that a direct line of evolution can be traced through *Telmabates* and *Paloelodus* to *Phoenicopterus*. On the contrary, a recognizable and well-advanced *Phoenicopterus* (*P. croizeti*) occurred contemporaneously with *Paloelodus* in Europe. The derivation of *Telmabates* from a line stemming from *Apatornis* in the Cretaceous is a possibility worthy of consideration. As pointed out by Simpson (1950, p. 373), late Cretaceous reptiles of South America show closest affinity with those of North America, and the earliest South American mammals also suggest North American origin. Owing to greater freedom of movement of birds, avian distribution does not necessarily agree with that of reptiles or mammals, but the resemblance of *Telmabates* to *Apatornis* bears significance in this regard.

Table 3 lists the fossil members of the Order Phoenicopteriformes as

TABLE 3

FOSSIL MEMBERS OF THE ORDER PHOENICOPTERIFORMES

Geologic Age	Species	Family	Locality
Pleistocene	*Phoenicopterus copei*	Phoenicopteridae	North America
	Phoenicopterus minutus	Phoenicopteridae	North America
Pliocene	*Phoenicopterus stocki*	Phoenicopteridae	North America
Miocene	*Paloelodus steinheimensis*	Paloelodidae	Europe
	Megapaloelodus connectens	Paloelodidae	North America
Oligocene	*Paloelodus goliath*	Paloelodidae	Europe
	Paloelodus crassipes	Paloelodidae	Europe
	Paloelodus ambiguus	Paloelodidae	Europe
	Phoenicopterus croizeti	Phoenicopteridae	Europe
	Elornis littoralis	Phoenicopteridae	Europe
	Elornis grandis	Phoenicopteridae	Europe
Eocene	*?Elornis anglicus*	Phoenicopteridae	British Isles
	Agnopterus laurillardi	Agnopteridae	Europe
	Agnopterus hantoniensis	Agnopteridae	Europe
	Telmabates antiquus	Telmabatidae	South America
Cretaceous	*Scaniornis lundgreni*	Scaniornithidae	Europe
	Parascaniornis stensioi	Scaniornithidae	Europe

now recognized. A possible exception should be noted in the case of the two Cretaceous species of the family Scaniornithidae, the remains of which are very fragmentary and subject to some question. In any consideration of this list, the possibility of collateral relationship of *Apatornis celer* of the North American Cretaceous should be borne in mind.

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