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# Systematic revision, skeletal anatomy, and paleoecology of the New World early Tertiary Presbyornithidae (Aves: Anseriformes)

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Since the family Presbyornithidae was first described from the Eocene Green River Fm. of Utah, fossils referred to this genus have been collected from many Paleogene localities around the world. Fossils of this family are extraordinarily abundant and permit detailed studies of all parts of the skeleton. This paper describes the osteology of the Presbyornithidae based upon virtually all the prepared material known from the New World. The family is revised and found to comprise four species placed in the two genera *Presbyornis* (three species) and *Telmabates* (one species). *Presbyornis pervetus* is by far the most common and widespread member of the family. The large size variation in the skeleton of *P. pervetus* is attributed to sexual dimorphism. Phylogenetic analyses of the Presbyornithidae have shown it to be a member of the order Anseriformes (ducks, geese, swans, and their allies). In addition to derived anseriform characters, the presbyornithid skeleton has many features in common with other late Cretaceous and early Tertiary birds. Nearly all presbyornithids have been collected from lacustrine environments. Avian egg-shells associated with the fossils at certain localities suggest *P. pervetus* was a gregarious breeder along the shores of freshwater lakes. At several localities large numbers of presbyornithid fossils form mass-mortality layers in which the skeletons are disarticulated. Although the cause of death is unknown, avian botulism or catastrophic volcanism may have contributed to the mass death of the birds.

## INTRODUCTION

Alexander Wetmore in 1926 described three new fossil species of charadriiform birds from the Early Eocene Green River Fm. of Utah. Two were regarded congeneric, *Nautilornis avus* and *N. proavitus*, and placed in the family Alcidae, whereas the third species, *Presbyornis pervetus*, was made the type of the new family Presbyornithidae. This bird was supposed to be "typical of an ancestral stock, from which existing Avocets and Stilts have descended" (Wetmore 1926).

Nearly thirty years later, Hildegarde Howard (1955) published a description of *Telmabates antiquus*, an early Eocene bird collected in Argentina by George Gaylord Simpson in 1930-1931. Howard regarded *T. antiquus* as a primitive flamingo and placed it in the new family Telmabatidae. A second, smaller species, *Telmabates howardae* Cracraft was later described from the same collection (Cracraft 1970).

In 1970, a field party led by Paul McGrew (University of Wyoming) collected vertebrate fossils at the University of Wyoming Bird Quarry in Wyoming, a large number of which were identified as *Presbyornis*. Description of this new material by Feduccia and McGrew (1974) added considerable knowledge about the anatomy of *Presbyornis*. Feduccia and McGrew (1974) also were the first to draw attention to the similarity between *Presbyornis* and *Telmabates*, leading them to synonymize the two genera. Furthermore, *Telmabates howardae* was regarded conspecific with *P. pervetus*, while it was suggested that *Nautilornis* (the second genus described by Wetmore from the type locality of *P. pervetus*) be synonymized with *Presbyornis*.

Although the postcranial skeleton of the Presbyornithidae was fairly well known in the early 1970s, the cranium was not. A few skull fragments of *Telmabates* were found but given little attention (Howard 1955). Therefore, it was surprising when Feduccia and McGrew (1974) associated the long-legged postcranial skeleton with the duck-like braincases and bills recovered from the University of Wyoming Bird Quarry. However, preservation of the Bird Quarry skulls was poor, and well preserved cranial material was not available until 1977 when Storrs L. Olson and Robert J. Emry (Smithsonian Institution) began collecting *Presbyornis* at Canyon Creek Butte, another Eocene locality in Wyoming. Slabs containing thousands of bones in a thin stratum were collected by Olson, Emry and Arnold Lewis on field trips in 1977 and 1979 (Fig. 1). Subsequently, large quantities of fossils tentatively referred to the Presbyornithidae have been collected at several localities in Utah, Wyoming and Colorado (Fig. 2), as well as in Argentina and Mongolia.

In this study a revision of the Presbyornithidae *sensu* Feduccia and McGrew 1974 is presented, along with a detailed description of presbyornithid skeletal anatomy, which includes several previously undescribed elements of the skeleton, the hyoid apparatus, and syrinx. Comparisons are also made with fossils assigned to the somewhat older "form-family" Graculavidae to which the presbyornithids may be related (Olson and Parris 1987), as well as with other Paleogene birds. Ericson (1997) and Livezey (1997), who independently analyzed the systematic relationships of the Presbyornithidae, both concluded it is the sister to the Anatidae within the order Anseriformes.

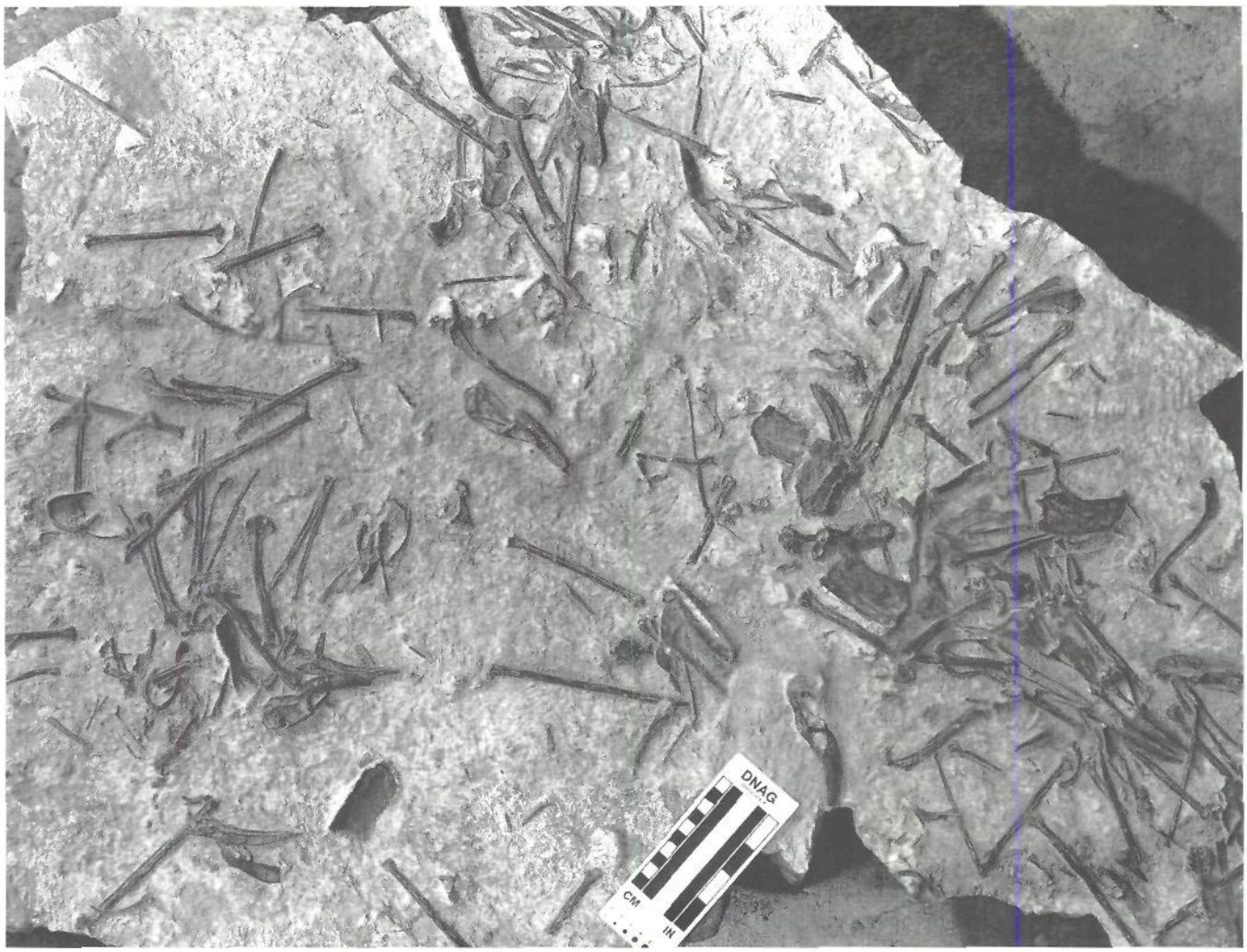


**Fig. 1.** Mass-mortality layer of *Presbyornis pervetus* collected at the Canyon Creek Butte, Sweetwater Co., Wyoming. Photo of slab on exhibit at the National Museum of Natural History, Smithsonian Institution. Photo: Chip Clark, Smithsonian Institution.

## MATERIAL AND METHODS

This revision is based on all known New World fossils of the Presbyornithidae, including North American material from Wyoming, Utah, and Colorado, and Patagonia in Argentina. They all date from Paleocene to Early Eocene.

It was not possible to include the Old World fossils assigned to the Presbyornithidae in this study. Important, but undescribed fossils have been collected from Late Cretaceous and Paleocene deposits in Mongolia that are thought to be referable to the Presbyornithidae (Kurochkin 1988, Evgeny N. Kurochkin, *personal communication*). Other fossils described as new genera of the Presbyornithidae includes *Proherodius oweni* Harrison and Walker 1978 from the Early Eocene London Clay (Ypresian), and *Zhylgaia aestiflua* Nessov 1988 from the Late Paleocene of Kazakhstan in the USSR. Undescribed presbyornithid material has also been recovered from Eocene deposits in Khirgizia (Olga Potapova, *personal communication*). Also, putative presbyornithid remains have been described from Late Cretaceous deposits in Antarctica (Noriega and Tambussi 1995).

Comparisons were made with a wide spectrum of fossil taxa most of which are referred to the "form-family" Graculavidae *sensu* Olson and Parris (1987). *Dakotornis cooperi* Erickson 1975 and *Juncitarsus gracillimus* Olson and Feduccia 1980b were also studied.

The acronyms used herein are **AMNH**—American Museum of Natural History, New York, New York; **BYU**—Brigham Young University Museum, Provo, Utah; **CM**—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; **KUVP**—Museum of Natural History, Vertebrate Paleontology, University of Kansas, Lawrence, Kansas; **LLU**—Loma Linda University, Loma Linda, California; **SMM**—Science Museum of Minnesota, Minnesota; **UCMP**—Museum of Paleontology, University of California, Berkeley, California; **USNM**—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **UW**—Geological Museum, University of Wyoming,

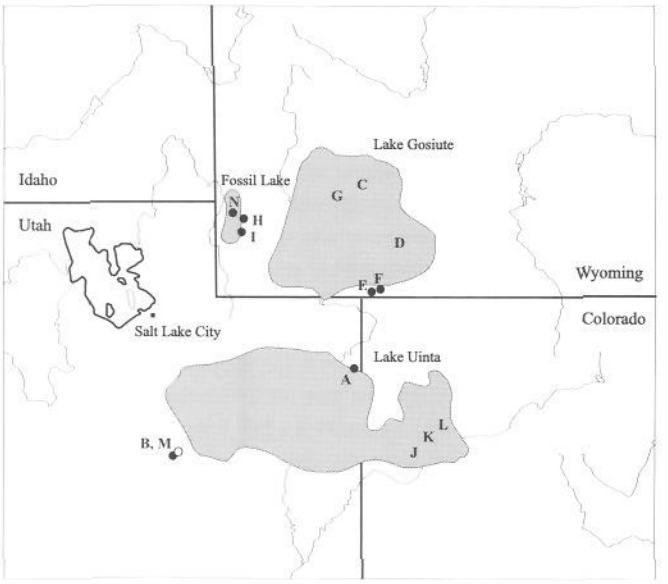


**Fig. 2.** Localities in the western United States where *Presbyornis pervetus* (solid circles) and *P. recurvirostrus* (open circle) have been collected. The distribution of the fossil lakes system in middle or late Early Eocene (Grande 1989) is indicated in grey. **A.** Utah, Uinta Co., White River (type locality). **B.** and **M.** Utah, Sanpete Co., Ephraim Canyon. **C.** Wyoming, Sweetwater Co., University of Wyoming Bird Quarry (UW V58006, USNM 41805). **D.** Wyo., Sweetwater Co., Flamingo Flat (UCMP V78032, USNM 41804). **E.** Wyo., Sweetwater Co., Canyon Creek Butte (USNM 41803). **F.** Wyo., Sweetwater Co., Point Location and Gully Location (UW V75009). **G.** Wyo., Sweetwater Co., Boar's Tusk Bird Locality (UW V75008). **H.** Wyo., Lincoln Co., Powerline Quarry (LLU 1525). **I.** Wyo., Lincoln Co., Warfield Springs Site (USNM 41806). **J.** Colorado, Mesa Co. De Beque Oil Field. **K.** Col., Garfield Co., Grand Valley (Thomas H. Rich locs.), **L.** Col., Garfield Co., Grand Valley (Herman Wilson loc.). **N.** Wyo., Lincoln Co., Bear Divide Quarry (LLU 1530).

Laramie, Wyoming; **YPM**—Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

The anatomical terminology follows Baumel et al. (1993) unless otherwise stated. Descriptive statistics in Tables 1 and 2 refer to measurements defined in Appendix A.

## SYSTEMATIC PALEONTOLOGY

Class: Aves
Order: Anseriformes
Family: Presbyornithidae

**Type genus**—*Presbyornis* Wetmore 1926

**Included genera**—*Presbyornis* Wetmore 1926; *Telmabates* Howard 1955.

**Diagnosis**—The Presbyornithidae are long-legged, wading birds that differ from all other known birds in having heads of a filter-feeding duck.

**Comparisons**—Although very well preserved specimens exist for almost all skeletal elements, no complete, articulated specimen of Presbyornithidae has been found. The anatomy of genus *Telmabates* is less well known than that of *Presbyornis* but the following characteristics of the skeleton seem to be shared by both genera included in the family Presbyornithidae: size and body proportions similar to that of a very large representative of the extant family of thick-knees (Burhinidae: Charadriiformes), although the wings of the Presbyornithidae are relatively longer; head of a filter-feeding duck placed on a long neck; trunk probably small in relation to skull and extremities as indicated by the short sternum, coracoids, and pelvis; notarium absent in the vertebral column; humerus relatively longer than in modern anatids although not extremely long; ulna and radius probably longer than humerus; carpometacarpus about half as long as the humerus; femur slender and relatively longer than in most modern anatids; very long tibiotarsus and tarsometatarsus in relation to the size of the trunk; foot with well developed hind toe.

*Cranium*: In general appearance and in many details, the presbyornithid skull, which is known primarily from the type genus *Presbyornis* and fragments of the braincase and frontal region of *Telmabates*, strongly resembles that of a modern anatid. It is characterized by having two fonticuli occipitalis (Olson and Feduccia 1980a); short distance between orbita and apertura nasi ossea (naris) (Olson and Feduccia 1980a); fossa temporalis aborally deep (Olson and Feduccia 1980a); processus postorbitalis short and blunt (Olson and Feduccia 1980a); processus basipterygoideus well developed; ventral margin of septum interorbitale angled, i.e. the posterior part of the margin is almost parallel to the jugal bar, while the anterior part slopes upward toward the nasal-frontal hinge at an angle of approximately 45 degrees (*contra* Feduccia [1976] who described it as continuously sloping upward toward the nasal-frontal hinge); condylus occipitalis heart-shaped (Feduccia 1976); fossa subcondylaris very deep; anteriormost part of os frontale is concave and has a deep V-shaped appearance (Feduccia and McGrew 1974, Feduccia 1976); supraorbital part of the frontals narrow; sulcus glandulae nasalis supraorbitalis (Feduccia and McGrew 1974, Feduccia 1977) shallow, or lacking; apertura nasi ossea relatively small; septum interorbitalis almost imperforate except for an upper distal opening towards the frontals (Feduccia 1976) and a small hole just below; in lateral view, os palatinum is ventral to jugal bar (Olson and Feduccia 1980a); bill spatulate and upturned (Olson and Feduccia 1980a) with small rostral nail (Olson and Feduccia 1980a); processi maxillopalatinus fused leaving small anterior opening for apertura nasi ossea interna (Olson and Feduccia 1980a).

*Os lacrimale*: The lacrimals in the Presbyornithidae are not fused to the cranium (Olson and Feduccia 1980a); articulate mainly with os frontale; have processus orbitalis long and pointed, and processus supraorbitalis short and blunt.

*Quadratum*: The Presbyornithidae has a quadratum with the posterior region of the processus mandibularis quadrati not inflated (Olson and Feduccia 1980a); dorsal margin of processus orbitalis slightly concave; processus orbitalis long and narrow; a simple cotyla quadratojugalis; condylus caudalis on processus mandibularis lacking; large pneumatic foramina on posterior surface of corpus quadrati.

*Apparatus hyobranchialis* (known only from type genus *Presbyornis*): The hyoid apparatus is known from only one specimen (USNM 299846) which has os basihyale relatively short and triangular in ventral view, with its ventrorostral part pointed; urohyale is a pointed process, twice as long as the basihyale; paraglossum narrow and more than three times as long as basihyale; ceratobranchiale circular in cross-section.

*Syrinx* (known only from type genus *Presbyornis*): Only one specimen is known. The tympanum consists of seven clearly distinguishable, but obviously fused tracheosyringeales. Only the lateral side of the syrinx is exposed in the matrix, but it appears to be laterally compressed as in extant anseriform birds.

*Mandibula*: The mandible of the presbyornithids has a large processus retroarticularis (Olson and Feduccia 1980a); prominent crista intercotylaris directed almost anteroposteriorly dividing the articular fossa into two distinct parts; processus coronoideus well developed and positioned at the lateral side of pars caudalis. Other characteristics of the presbyornithid mandible include slender processus mandibulae medialis projecting from shaft at right angle; caudal margin of processus mandibulae medialis only moderately curved caudally making recessus conicalis very shallow; ramus mandibulae mediolaterally thin, and dorsally curved; deep groove in the ventrolateral surface of the anterior portion of the ramus mandibulae (Olson and Feduccia 1980a).

*Vertebrae thoracicae*: A total of 45 vertebrae thoracicae are known of *Presbyornis pervetus* and *Telmabates antiquus*. The last five vertebrae thoracicae, as well as the synsacrum, are known from one individual of *T. antiquus* (Howard 1955). Because no articulated spine of *Presbyornis* has been found, and the morphology in this region varies considerably between the two genera, it may sometimes be hard to know if elements are comparable. Shared features of the vertebrae thoracicae in the Presbyornithidae include: the last three free vertebrae thoracicae mildly amphicoelous (*contra* Howard 1955 who claimed two of them to be opisthocoelous); relatively massive, slightly hour-glass shaped corpora vertebrae in the caudal thoracic region, with bilateral, deep depressions or pneumatic holes on the dorsolateral part; the most cranial vertebra thoracicae have the processus ventralis well-developed and projecting from the cranial part of the vertebrae.

*Synsacrum*: The presbyornithids have no fusion of the synsacrum to the ossa coxae; corpus of the first synsacro-thoracic vertebra more laterally compressed in ventral view than in the following vertebrae; synsacrum probably not very well pneumatized, although the synsacro-thoracic vertebra has a pneumatic foramen in the area between the zygapophysis cranialis and processus transversus vertebrae; facies articularis cranialis of the synsacro-thoracic vertebra convex and round or slightly heart-shaped; synsacral struts well developed; crista dorsalis well developed (Feduccia and McGrew 1974); sulcus ventralis synsacri deep.

*Os coxae*: The presbyornithid os coxae is not fused to the synsacrum. Furthermore, it is relatively short and shallow (Olson and Feduccia 1980a); crista iliaca dorsalis (and crista iliaca dorsolateralis) well developed (Feduccia and McGrew 1974); antitrochanter well developed (Feduccia and McGrew 1974); craniocaudal length of foramen ilioischiadicum approximately three times greater than the dorsoventral height (Feduccia and McGrew 1974); processus dorsolateralis and processus terminalis ischii pointed with processus terminalis ischii reaching more caudally; has a recessus iliacus in both the cranial and caudal end of fossa renalis, of which the caudal is very deep; pubis straight and narrow; protruding far more caudally than processus terminalis ischii; cranial margin of ala preacetabulis ilii smoothly rounded with medial part protruding slightly more cranially; fenestra ischiopubica broad and more or less continuous with foramen obturatum; caudal margin of foramen ilioischiadicum equals caudal end of synsacrum.

*Sternum*: The presbyornithid sternum is deep and broad (the breadth corresponds approximately to two-thirds of its length) with carina sterni well developed, and having right sulcus articularis coracoideus crossing below left sulcus just past midpoint of rostrum sterni, with a small diagonal ridge dividing the two (Howard 1955); dorsal surface of pila coracoidea flat and shelf-like (Howard 1955); sharp slope caudal of pila coracoidea (Howard 1955), with area below pila coracoidea with, or without, a few, large ridges running down from the pars cardiaca (this area is highly variable), surrounding a large pneumatic foramen placed medially in the cranial part of pars cardiaca (Howard 1955); prominent tuberculum labri ventrale; cranial margin of carina slightly curved anteriorly (Howard 1955, Feduccia and McGrew 1974, Feduccia 1976), with crista laterales well developed; spina externa well developed and blade-like (Howard 1955, Feduccia and McGrew 1974, Feduccia 1976, Olson and Feduccia 1980a); caudal end with four notches (Olson and Feduccia 1980a), of which the incisura lateralis is deeper and slightly narrower than the incisura medialis.

*Furcula*: The furcula has a very small (lacking in some individuals) apophysis furculae; shaft slightly excavated dorsal of apophysis furculae (Feduccia and McGrew 1974); lateral part of shaft ovoid (not round as described by Feduccia and McGrew 1974); extremitas omalis clavicula narrow and pointed with shaft slightly thicker at facies articularis acrocoracoidea.

*Scapula*: The presbyornithid scapula has acromion very elongate and pointed, with outermost part formed as a separate process due to the distinct hollow-shaped facies

articularis clavicularis; glenoid facet ovoid and slightly concave; tuberculum coracoideum large and round; shaft narrow and deflected ventrally (Olson and Feduccia 1980b).

*Coracoid*: The coracoid in Presbyornithidae is typically short and broad, with the sternal end slightly bowed; processus lateralis well developed (Howard 1955); dorsal side of facies articularis sternalis very broad from medial tip laterally to a point at approximately two-thirds of the breadth of the sternal end where the facies ends; facies articularis sternalis curls onto ventral side near medial tip (Howard 1955); linea intermuscularis ventralis extending from neck almost down to sternal margin where it forms a distinct tuberculum situated immediately cranial to the articulation with tuberculum labri ventrale on sternum; small foramen procoracoidei situated just below cotyla scapularis and emerging on medial side of processus procoracoidei (Wetmore 1926, Howard 1955); cotyla scapularis round and very deep (Howard 1955); processus procoracoidei very long and delicate, protruding mediocranially. This delicate process is easily broken and therefore lacking in most of the fossils studied. Howard (1955) claimed that the processus procoracoideus was short and blunt in *Telmabates*, but in these specimens it was actually broken in a way that closely resembles the condition found in most specimens of *Presbyornis*. Therefore, it is most likely that the processus procoracoidei of *Telmabates* resembles that of *Presbyornis*; neck medially excavated below head; cranial margin of neck slightly dorsally curved immediately caudal of facies articularis clavicularis; ventral part of facies articularis clavicularis extends slightly beyond neck.

*Humerus*: The presbyornithid humerus is long in relation to the width of its proximal and distal ends, although not very slender. The proximal end is characterized by having head undercut; dorsal tricipital fossa lacking, while ventral tricipital fossa is deeply excavated but non-pneumatic with a distinct tumescence in the proximoventral portion (Olson and Parris 1987); a large median crest nearly continuous with the central crest of shaft (Howard 1955); large scars for m. scapulohumeralis cranialis and m. scapulohumeralis caudalis, of which the latter is especially long and well pronounced, situated just distal of the median crest immediately medial of the central crest of shaft; distinct impressio m. latissimus dorsi cranialis on the lateral side of the bone, immediately proximal of long scar for m. latissimus dorsi caudalis ending at point of junction of crista deltopectoralis and corpus (Howard 1955); distinct lanceolate scar for m. coracobrachialis cranialis lacking (Olson and Parris 1987); tuberculum dorsale well defined (Olson and Parris 1987), with a large but not depressed, ovoid or triangular attachment for m. supracoracoideus; tuberculum ventrale large and blunt, positioned halfway between margo caudalis and the most medial point of crista bicipitalis; a long, very well developed crista deltopectoralis with a concave surface between margo caudalis and lateral edge of crista deltopectoralis.

The distal end of the humerus has the fossa brachialis deep and a distinct, diagonally-oriented ovoid scar for m. brachialis; processus flexorius pronounced and slightly elevated; sulcus scapulotricipitalis almost obsolete due to a poorly developed epicondylis dorsalis; tuberculum supracondylare ventrale with impressio m. pronator superficialis subdivided into two depressions of equal size; no distinct processus supracondylaris dorsalis (Olson and Feduccia 1980b); impressio m. pronator superficialis pronounced and positioned immediately medial, or somewhat medioproximal, to the attachment of lig. collaterale ventrale; attachment of lig. collaterale ventrale large and ovoid.

*Radius*: The proximal end of the presbyornithid radius is distinctly deflected ventrally in relation to shaft; furthermore, it has facies articularis ulnaris well developed, flat and triangular in shape, with a pronounced tuberculum in the dorsodistal part of facies articularis ulnaris; pronounced ventral tuberculum where lig. collaterale dorsale and meniscus radioulnaris inserts, indicating that these were well developed; impressio lig. craniale cubiti near tuberculum bicipitale very deep (Howard 1955).

The distal end of the radius is moderately flared (Howard 1955); with impressio retinaculum flexorium large and round.

*Ulna*: The ulna in the Presbyornithidae has olecranon moderately developed (Howard 1955), and ventrally curved; depressio m. brachialis very deep; cotyla ventralis ovoid and obliquely placed with respect to olecranon (Howard 1955); large and almost circular depressio m. scapulotricipitis on caudal side of processus cotylaris dorsalis and situated well distal of the cotylar edge; dorsal half of cotyla dorsalis bent distally at its cranial edge, forming a long lip almost at right angles to the cotyla proper (Howard 1955), and ending in a ridge that runs diagonally towards middle of shaft from turned-down lip (Howard 1955); incisura radialis triangular with the above-mentioned ridge making up its dorsal side.

The distal end of the ulna is characterized by having the tuberculum carpale well developed; very deep tendinal pit, but lacks sulcus tendineus with bony ridges.

*Os carpi radiale* (known only from the type genus *Presbyornis*): The radiale has the caudal end mediolaterally compressed, and a deep sulcus on its proximal side, with a pronounced, centrally placed tuberculum immediately cranial of this sulcus. Furthermore, it has a deep and narrow, mediolaterally oriented depression on the distal side, and the incisure at the cranial side is wide and shallow.

*Os carpi ulnare*: The ulnare has a distinct, although not very deep sulcus on the laterodistal side; and a wide incisura metacarpalis.

*Carpometacarpus*: The presbyornithid carpometacarpus is straight with ossa metacarpale majus and minus parallel. In the proximal end, caudal part of dorsal trochlea well developed and connects with dorsal edge of os metacarpale majus (Howard 1955); distal edge of ventral crest approxi-

mately on a line with ventral border of os metacarpale minus (Howard 1955); trochlea well excavated posteriorly (Howard 1955); large scars for insertions of lig. ulnocarpo-metacarpale dorsale and lig. radiocarpo-metacarpale dorsale; small vascular foramen in fossa infratrochlearis.

The distal end of the presbyornithid carpometacarpus has well marked sulcus tendineus on dorsal side of metacarpale majus; sulcus interosseus deep, sometimes with an ossified bridge.

*Alar phalanx proximalis digiti majoris*: In the Presbyornithidae the phalanx proximalis digiti majoris is long and slender, with two deep depressions on dorsal side. It is also characterized by having in proximal view, a blunt, cranioventrally protruding tuberculum; no dorsal tendinal sulcus on pila cranialis and tendinal sulcus along caudal margin present only a short distance at mid-corpus (except for a shallow depression in the proximal end); distal projection of caudal margin lacking (Howard 1955).

*Alar phalanx distalis digiti majoris*: The presbyornithids have proximal facies articularis phalangealis with a prominent cranioventrally protruding process that constitutes the proximoventral part of a canal in which the sulcus tendineus runs; dorsal side of phalanx distalis digiti majoris deeply excavated.

*Femur*: The femur is relatively long and slender. The proximal end has trochanter femoris well developed and non-pneumatic (Howard 1955, Feduccia 1976, Olson and Feduccia 1980a); facies articularis antitrochanter protruding caudally slightly beyond shaft (Howard 1955); a pronounced ridge where cranial margin of facies articularis antitrochanter meets shaft nearly at right angle; depressio m. iliothrochantericus caudalis long and curved, positioned at a point about one-third of the breadth of trochanter measured from the cranial margin; area between impressiones m. ischiofemoralis and m. iliofemoralis narrow and elevated from shaft; impressio mm. obturatorius medialis and lateralis rounded (sometimes heart-shaped) and situated on caudoproximal area of lateral side of trochanter.

The distal end of the presbyornithid femur has impressio m. gastrocnemicus (probably pars intermedia) large and pronounced, with impressio pars medialis of m. gastrocnemicus small and situated immediately medial; linea intermuscularis caudalis marked and reaching from outer edge of condylus medialis to middle of shaft (Howard 1955); cranioproximal end of condylus medialis slightly elevated from shaft; and caudoproximal part of condylus medialis steep although fossa poplitea is not very deep.

*Tibiotarsus*: The proximal end of the tibiotarsus in the Presbyornithidae (known only from *Presbyornis pervetus*) has crista cnemialis cranialis protruding far ventrally, with distal margin smoothly angled and lacking distally projected hook; distal margin of crista cnemialis cranialis meets shaft at an angle of about 150 degrees (not 90 degrees as stated by Feduccia 1976); proximal margin of crista cnemialis cranialis projecting strongly upward; crista cnemialis lateralis has almost no ventral thrust (*contra* Feduccia and McGrew 1974); proximal margins of crista patellaris and crista cnemialis lateralis almost straight, slightly laterodistally directed; almost no hook in lateral end of crista cnemialis lateralis (Feduccia 1976); facies articularis fibularis somewhat triangular with a small hook projecting distally; fossae retrocristales moderately deep and divided into two separate parts by a distinctly elevated, broad ridge; fossa flexoria deep, with several pronounced tuberculi immediately below serving as origins of flexor muscles; two large, clearly separated impressio lig. collateralis medialis of which the proximal is smaller and more rounded than the distal.

The distal end is characterized by being thrust medially; having condylus lateralis rounded and high; condylus medialis long but considerably lower than condylus lateralis (Howard 1955); sulcus extensorius very deep; supratendinal bridge broad and steep in proximodistal direction; well-marked sulcus m. fibularis; presence of a foramen in sulcus m. fibularis just proximolateral to condylus lateralis (*contra* Olson and Parris 1987); epicondylii medialis and lateralis poorly developed; pronounced tuberositas retinaculum extensorium tibiotarsi medialis; very large lateral insertion of retinaculum extensorium tibiotarsi immediately proximal to condylus lateralis; impressio lig. collaterale mediale long and prominent, which reaches from the distal part of epicondylus medialis proximally well up the shaft.

*Fibula*: The caput fibulae has proximal surface slightly concave; no excavation of the lateroproximal margin; large impressio lig. collateralis lateralis near the proximal end.

*Tarsometatarsus*: The tarsometatarsus in the Presbyornithidae is long and slender (Olson and Feduccia 1980a). The proximal end of tarsometatarsus has four-ridged hypotarsus with no closed canals, where crista medialis is large and long, with a hook-shaped distal margin; cristae intermediae and crista lateralis hypotarsi of similar small size and reaching equally, or almost equally as far distally as the medial crest; eminentia intercondylaris pronounced (Wetmore 1926) but not extreme; cotyla lateralis "lower" than cotyla medialis in ventral view; ventral border of cotyla medialis well defined while the corresponding part of the cotyla lateralis curls onto ventral surface of shaft; insertion of lig. collaterale medialis a distinct ridge situated well below mediodorsal margin of cotyla medialis; fossa infracondylaris dorsalis deep with two pronounced parallel scars for m. tibialis cranialis, with the medial scar somewhat larger and located slightly more proximal; ridges for insertions of retinaculum extensorium tarsometatarsi well developed and situated well above scars for m. tibialis anticus; shaft rectangular with longitudinal groove on ventral side.

The distal end of the presbyornithid tarsometatarsus is characterized by having fossa metatarsi I long and not very well developed; foramen vasculare distale large and ovoid (Olson and Parris 1987); pronounced scar for an unknown muscle or ligament situated immediately medioproximal of

foramen vasculare distale; trochleae for digits II and IV shorter than for digit III (trochlea II the shortest) and both are elevated posteriorly and have distinct wings (*contra* Olson and Feduccia 1980b who believed that trochlea digit II lacks wing); trochlea digit III elevated anteriorly from shaft.

*Hallux* (known only from type genus *Presbyornis*): The hallux is long and strongly deflected; articulation with phalanx 1 mediolaterally broad with two distinct condyles.

*Pedal phalanges* (fully known only from type genus *Presbyornis*): The presbyornithid foot has all four digits well developed with a phalangeal formula of 2-3-4-5; phalanx 1 of digits I, II, and III long and slender and all about the same size, whereas phalanx 1 of digit IV is about one-third shorter; proximal end of phalanges 1 with deep sulcus bordered by prominent ligamental insertions on the palmar side; phalanx 1 of the hind toe slightly dorsoventrally curved; phalanx 3 of digit IV slightly larger than phalanx 4; phalanx distalis of all digits approximately the same size, mediolaterally compressed, and slightly curved.

Genus: *Presbyornis*

*Nautilornis* Wetmore 1926:392
*Presbyornis* Wetmore 1926:396
*Coltonia* Hardy 1959:106

**Type species**—*Presbyornis pervetus* Wetmore 1926

**Included species**—*Presbyornis pervetus* Wetmore 1926, *Presbyornis recurvirostrus* (Hardy 1959), *Presbyornis isoni* Olson 1994

**Diagnosis**—Within the Presbyornithidae, the genus *Presbyornis* is diagnosed by the following morphologies (see below for a full comparison with *Telmabates*): *Presbyornis* lacks an impressio frontalis immediately caudal to the supraorbital region of the cranium (present in *Telmabates*); has most caudal vertebra thoracicae weakly amphicoelous (heterocoelous in *Telmabates);* possesses a synsacrum incorporating three lumbar vertebrae (four in *Telmabates*); has the insertion for m. sternocoracoidei on facies dorsalis of coracoid shallow (deeply excavated in *Telmabates*); has the impressio m. pronator superficialis on distal humerus reaching farther proximally than that for the lig. collaterale ventrale (in *Telmabates* the scars reach about equally far proximally); lacks a distinct, large papilla centrally placed on cranial surface immediately proximal to facies articularis radiocarpalis of radius (present in *Telmabates*); has a femur with linea intermuscularis hardly distinguishable from crista trochanteris (linea intermuscularis cranialis very prominent and clearly separated from lateral margin of crista trochanteris in *Telmabates*).

Species: *Presbyornis pervetus* Wetmore 1926

*Nautilornis avus* Wetmore 1926:392
*Nautilornis proavitus* Wetmore 1926:394
*Presbyornis pervetus* Wetmore 1926:396

**Holotype**—CM 11360, left tarsometatarsus collected by E. Douglass and L. R. Kay in 1923.

**Type locality**—Utah, Uinta Co., Bird Hollow, 2 mi. east of Powder Springs, formation unknown, age unknown.

**Distribution**—late early (Lostcabinian) to early middle Eocene (Gardnerbuttean to Bridgerian), Sweetwater Co., Wyoming; ?Paleocene, Sanpete Co., Utah; Eocene, Uinta Co., Utah; late early to middle Eocene, Lincoln Co., Wyoming; ?early Eocene, Mesa Co. And Garfield Co., Colorado.

**Previously referred specimens**—CM 11358, 11359, 11360a, 12032, 12033, 12035-12038 (White River, "2 miles from Colorado state line," formation unknown, age unknown, Uinta Co., Utah); UW 20593-20600, 20651-20653, 20655-20666 (UW V58006, Sweetwater Co., Wyoming); USNM 299845-299847, 492550-492551 (Canyon Creek Butte, formation unknown, age unknown, Sweetwater Co., Wyoming).

**Newly referred specimens**—CM 12038; almost complete bill, complete vertebrae thoracale, two complete synsacra, manubrial and costal parts of two sterna, incomplete furcula, caudal left coracoid, incomplete left coracoid, cranial left scapula, proximal right radius, incomplete left tarsometatarsus (White River, "2 miles from Colorado state line," formation unknown, age unknown, Uinta Co., Utah). UCMP 119394-119401, 126173-126257, USNM 492552, USNM 498771; (UCMP V78032 = USNM loc. 41804, Cathedral Bluffs Tongue of Wasatch FM., late early or middle Eocene, Sweetwater Co., Wyo.). USNM 8551; a slab containing partly articulated cranial and postcranial elements from one individual (near old tunnel, 3 miles southeast of Ephraim, Sanpete Co., Utah). USNM 498770, 510082; many slabs and many disarticulated elements (USNM loc. 41803. Canyon Creek Butte, formation unknown, age unknown, Sweetwater Co., Wyoming). UW 7833, 27463, 27487-27489; slabs with disarticulated elements (UW loc. V75009, Wilkins Peak Mbr. of Green River Fm., early middle Eocene, Sweetwater Co., Wyoming). UW 6946, 7834; slabs containing disarticulated postcranial elements (UW loc. V75008, New Fork Mbr. of Wasatch Fm., late early Eocene or middle Eocene, Sweetwater Co., Wyoming). USNM 7629 ("De Beque Oilfield," formation unknown, ?Eocene, Mesa Co., Colorado).

**Additional material examined**—many postcranial and cranial elements from: UCMP V78032, (Cathedral Bluffs Tongue of Wasatch Fm., late early or middle Eocene, Sweetwater Co., Wyo.); USNM loc. 41805 (=UW V58006, Sweetwater Co., Wyoming); LLU 1525 (LLU Powerline Quarry, Angelo Mbr. of Green River Fm., ?early middle Eocene); USNM loc. 41806 (12 miles SW of Kemmerer, Fossil Butte Mbr., Green River Fm., late early Eocene, Lincoln Co., Wyoming); USNM uncataloged specimens from Thomas H. Rich localities (THR 2, THR 3, THR 1975-57, 1975-58, Grand Valley, Shire Mbr.,

**Table 1.** Descriptive statistics for the New World species included in *Presbyornis* and *Telmabates*. Measurements in mm.

| | *Presbyornis pervetus* | | | | *Presbyornis recurvirostra* | *Presbyornis isoni* | | | | *Telmabates antiquus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | n | mean | min | max | | n | mean | min | max | n | mean | min | max |
| **Cranium** | | | | | | | | | | | | | |
| 1. greatest length | 18 | 87.99 | 81.0 | 101.5 | | | | | | | | | |
| 2. length of incisivum | 35 | 51.69 | 45.0 | 68.0 | | | | | | | | | |
| **Mandibula** | | | | | | | | | | | | | |
| 1. greatest length | 49 | 79.22 | 64.0 | 88.0 | | | | | | | | | |
| **Synsaccrum** | | | | | | | | | | | | | |
| 1. length of vertebral column | 56 | 48.93 | 38.0 | 63.0 | | | | | | 1 | | 73.0 | |
| 2. breadth of vertebral column | 5 | 7.02 | 6.6 | 7.6 | | | | | | 1 | | 7.4 | |
| **Coxae** | | | | | | | | | | | | | |
| 1. greatest length | 6 | 71.25 | 64.5 | 75.6 | | | | | | | | | |
| **Sternum** | | | | | | | | | | | | | |
| 1. greatest length | 31 | 59.80 | 45.0 | 65.0 | | | | | | | | | |
| 2. apex carinae - caudal end | 2 | | 23.0 | 24.7 | | | | | | | | | |
| **Coracoid** | | | | | | | | | | | | | |
| 1. greatest length | 46 | 37.84 | 35.0 | 48.0 | | | | | | | | | |
| 2. medial length | 24 | 33.08 | 28.9 | 38.4 | | | | | | 2 | | 43.0 | 44.5 |
| 3. breadth of proc. acrocoracoideus | 142 | 7.06 | 6.0 | 8.5 | | | | | | 5 | 10.20 | 9.3 | 11.6 |
| 4. depth of neck | 186 | 6.68 | 5.9 | 8.0 | | | | | | 3 | 9.27 | 9.0 | 9.8 |
| 5. breadth of facies art. hum. | 252 | 5.16 | 4.1 | 7.1 | | | | | | 5 | 6.98 | 6.6 | 7.5 |
| 6. breadth of facies dorsalis | 164 | 4.81 | 3.9 | 5.6 | | | | | | 4 | 6.00 | 5.8 | 6.3 |
| 7. breadth of sternal end | 22 | 17.59 | 14.2 | 19.6 | | | | | | 1 | | 27.3 | |
| 8. length of proc. lateralis | 20 | 7.38 | 5.9 | 9.7 | | | | | | 1 | | 8.1 | |
| **Scapula** | | | | | | | | | | | | | |
| 1. greatest length | 19 | 59.10 | 45.0 | 66.0 | | | | | | | | | |
| 2. length of acromion | 105 | 7.87 | 6.9 | 9.1 | | | | | | 3 | 9.50 | 9.1 | 9.8 |
| 3. breadth of shaft | 208 | 6.93 | 5.9 | 8.3 | | | | | | 5 | 8.96 | 8.6 | 9.4 |
| **Humerus** | | | | | | | | | | | | | |
| 1. greatest length | 87 | 95.64 | 56.0 | 104.0 | | | | 195.0 | | 1 | | 141.0 | |
| 2. proximal breadth | 17 | 20.56 | 17.5 | 22.1 | | | | | | 2 | | 26.7 | 27.0 |
| 3. depth of caput humeri | 80 | 5.73 | 5.0 | 6.4 | | | | | | 10 | 7.60 | 6.6 | 8.0 |
| 4. smallest breadth of shaft | 13 | 6.26 | 5.9 | 6.9 | | | | 8.2 | | 3 | 8.10 | 7.6 | 8.5 |
| 5. greatest breadth of distal end | 80 | 13.43 | 11.2 | 15.0 | | 2 | | 23.3 | ca 27 | 7 | 16.97 | 15.8 | 18.4 |
| **Radius** | | | | | | | | | | | | | |
| 1. greatest length | 70 | 95.51 | 85.0 | 105.0 | 131.5 | | | | | | | | |
| 2. proximal breadth | 83 | 4.10 | 3.6 | 4.6 | | | | | | 4 | 5.88 | 5.7 | 6.0 |
| 3. proximal depth | 83 | 5.00 | 4.0 | 5.6 | | | | | | 3 | 6.43 | 6.3 | 6.5 |
| 4. distal breadth | 66 | 6.66 | 5.5 | 7.8 | 7.3 | | | | | 5 | 9.36 | 9.0 | 9.7 |
| **Ulna** | | | | | | | | | | | | | |
| 1. greatest length | 54 | 100.70 | 90.4 | 112.0 | 136.5 | | | | | | | | |
| 2. proximal breadth | 19 | 9.00 | 8.3 | 10.0 | 10.9 | | | | | | | | |
| 3. length of cond. dorsalis | 42 | 7.59 | 6.7 | 8.4 | | | | | | 2 | | 9.5 | 10.2 |
| **Radiale** | | | | | | | | | | | | | |
| 1. length facies artic. cran. | 2 | 7.50 | 7.3 | 7.7 | 9.0 | | | | | 2 | | 7.7 | 8.0 |
| 2. length of caudal end | 2 | | 5.3 | 5.9 | 6.0 | | | | | 1 | | 5.8 | |
| **Ulnare** | | | | | | | | | | | | | |
| 1. width of incisura | 14 | 6.58 | 6.0 | 7.8 | | | | | | | | | |

**Table 1 (cont.).** Descriptive statistics for the New World species included in *Presbyornis* and *Telmabates*. Measurements in mm.

| | *Presbyornis pervetus* | | | | *Presbyornis recurvirostra* | *Presbyornis isoni* | *Telmabates antiquus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | n | mean | min | max | | | n | mean | min | max |
| **Carpometacarpus** | | | | | | | | | | |
| 1. greatest length | 82 | 45.67 | 40.0 | 54.0 | | | 1 | | 63.0 | |
| 2. proximal breadth | 49 | 10.67 | 9.7 | 11.9 | 13.0 | | 2 | | 15.8 | 16.6 |
| 3. depth of trochlea carpalis | 88 | 4.90 | 4.1 | 5.3 | | | 6 | 6.28 | 5.3 | 6.8 |
| 4. length of proc. extensorius | 53 | 6.45 | 5.4 | 7.5 | 7.8 | | 3 | 9.50 | 9.4 | 9.7 |
| 5. smallest breadth | 46 | 5.31 | 4.6 | 6.2 | | | 3 | 7.37 | 7.0 | 7.7 |
| 6. depth of shaft | 40 | 3.88 | 3.4 | 4.4 | | | 3 | 5.53 | 5.4 | 5.7 |
| 7. diagonal depth of distal end | 52 | 6.14 | 5.1 | 7.1 | | | 2 | | 7.1 | 7.4 |
| **Phalanx I, digit 2** | | | | | | | | | | |
| 1. greatest length | 18 | 22.92 | 19.8 | 27.6 | | 40.6 | 2 | | 29.7 | 30.7 |
| 2. breadth of facies art. metacarp. | 35 | 4.97 | 4.3 | 5.8 | | 9.5 | | | | |
| 3. greatest height | 12 | 6.28 | 5.9 | 6.8 | | | 1 | | 8.5 | |
| **Femur** | | | | | | | | | | |
| 1. greatest length | 60 | 50.49 | 45.0 | 58.5 | | | | | | |
| 2. medial length | 7 | 49.31 | 45.2 | 54.5 | | | | | | |
| 3. proximal depth | 10 | 7.12 | 4.6 | 7.9 | | | 1 | | 9.6 | |
| 4. diameter of caput femoris | 41 | 4.93 | 4.3 | 5.9 | | | 2 | | 5.7 | 5.8 |
| 5. breadth of shaft | 14 | 5.19 | 4.5 | 7.6 | | | 1 | | 6.1 | |
| 6. distal breadth | 20 | 8.73 | 7.6 | 9.7 | | | 2 | | 8.7 | 9.3 |
| 7. depth of cond. medialis | 22 | 10.60 | 9.3 | 11.2 | | | 1 | | 10.8 | |
| 8. depth of cond. lateralis | 33 | 11.81 | 11.0 | 13.3 | | | 1 | | 12.8 | |
| **Tibiotarsus** | | | | | | | | | | |
| 1. greatest length | 77 | 124.46 | 107.0 | 139.0 | | | | | | |
| 2. length from area intertrochl. | 7 | 124.49 | 114.4 | 134.7 | | | | | | |
| 5. breadth of shaft | 4 | 4.98 | 4.8 | 5.3 | | | 1 | | 5.9 | |
| 6. length of pons supratendineus | 64 | 2.25 | 2.1 | 4.4 | | | 4 | 3.78 | 3.1 | 4.2 |
| 7. breadth of distal end | 30 | 10.68 | 9.1 | 12.1 | | | 3 | 12.43 | 11.4 | 13.5 |
| 8. depth of distal end | 20 | 10.33 | 9.5 | 11.1 | | | 2 | | 10.9 | 11.0 |
| 9. depth inc.intertr.-sulc.cart.tib. | 31 | 7.11 | 5.7 | 8.0 | | | 3 | 6.67 | 5.8 | 7.2 |
| 10. length of cond. medialis | 20 | 10.54 | 9.7 | 11.4 | | | 1 | | 11.0 | |
| **Tarsometatarsus** | | | | | | | | | | |
| 1. greatest length | 94 | 102.40 | 85.0 | 120.0 | | | | | | |
| 2. proximal breadth | 45 | 11.34 | 8.4 | 13.6 | | | 1 | | 15.7 | |
| 3. breadth of trochlea mt III | 136 | 4.45 | 3.4 | 5.3 | | | 1 | | 4.5 | |
| **Hallux** | | | | | | | | | | |
| 1. greatest length | 3 | 12.27 | 11.5 | 12.7 | | | | | | |

Wasatch Fm., Eocene, Garfield Co., Colorado); and USNM uncataloged, a complete right radius (Grand Valley, Wasatch Fm., Eocene, Garfield Co., Colorado). The LLU locality is probably identical with that from which one slab containing an uncataloged right tarsometatarsus at the USNM has been collected.

**Diagnosis**—*Presbyornis pervetus* differs from all other known members of the genus by its smaller size (Table 1). Although a considerable variation in both morphology and size occurs in the material referred to *P. pervetus*, its magnitude is not larger than that found within extant species of Phoenicopteridae, Anhimidae, or Anatidae, for example (Ericson, *personal observation*). Thus, since the variation may be due to individual and/or sexual variability, all specimens are assumed to belong to only one species, albeit highly variable.

**Measurements**—see Table 1.

Species: *Presbyornis recurvirostrus* (Hardy 1959), new combination Ericson

*Coltonia recurvirostra* Hardy 1959:106

**Holotype**—KUVP 10105, distal humerus, radius, ulna, radiale, ulnare and proximal carpometacarpus collected by K.E. Boker.

**Type locality**—Utah, Sanpete Co., mouth of Ephraim Canyon, Wasatch Plateau.

**Distribution**—late Paleocene to early Eocene (Colton Fm.), Sanpete Co., Utah.

**Diagnosis**—Morphologically, *Presbyornis recurvirostrus* n. comb. fully agrees with *P. pervetus*, but the larger size of KUVP 10105 (Table 1) precludes it from being incorporated in that species. Due to the lack of corresponding elements no direct comparison of morphology has been possible with *P. isoni*, but *P. recurvirostrus* is distinctly smaller than that species.

**Comparisons**—The only remains known of *Presbyornis recurvirostrus* are a few partially articulated wing elements belonging to a single individual. Although the bones are poorly preserved, the characters observed agree with the family Presbyornithidae:

*Humerus*: The distal end of the humerus has the processus flexorius pronounced and slightly elevated; impressio m. pronator superficialis pronounced and positioned immediately medial, or somewhat medioproximal, to the attachment of the lig. collaterale ventrale; the attachment of the lig. collaterale ventrale is large and ovoid.

*Radius*: The distal end is moderately flared.

*Ulna*: Proximally, the depressio m. brachialis is very deep; cotyla ventralis is ovoid and the dorsal half of cotyla dorsalis is bent distally at its cranial edge, forming a long lip almost at right angles to the cotyla proper. This lip ends in a ridge that runs diagonally towards the middle of the shaft; incisura radialis is triangular with the above-mentioned ridge making up its dorsal side. In the distal end, the tuberculum carpale is well developed.

*Os carpi radiale*: Radiale is mediolaterally compressed with a deep sulcus on its proximal side, and a pronounced, centrally-placed tuberculum immediately cranial of this sulcus, and the incisure at the proximal side is wide and not very deep.

*Os carpi ulnare*: Ulnare has a wide incisura metacarpalis.

*Carpometacarpus*: The proximal carpometacarpus has a small vascular foramen in fossa infratrochlearis.

In the following characters, KUVP 10105 agrees with the genus *Presbyornis* but differs from *Telmabates*:

*Humerus*: Distal humerus has impressio the m. pronator superficialis reaching farther proximally than the scar for the lig. collaterale ventrale (*Telmabates*: the scars reach about equally far proximally).

*Radius*: In distal radius, shaft is only slightly convex immediately proximal to the distal end (*Telmabates*: shaft sharply convex). Furthermore, the cranial surface immediately proximal to facies articularis radiocarpalis is flat (*Telmabates*: a distinct and large, centrally-placed papilla).

*Ulna*: Distally, the tuberculum carpale is proximodistally short and has ventral margin straight (*Telmabates*: tuberculum carpale is very long with a slightly convex ventral margin).

*Carpometacarpus*: In the proximal end of carpometacarpus os metacarpale alulare is relatively short and projects slightly proximocranially (*Telmabates*: metacarpale alulare long and directed almost straight cranially); the area immediately cranial of processus pisiformis is deeply excavated (*Telmabates*: area shallow); fossa infratrochlearis has several pronounced muscle scars and excavations (*Telmabates*: fossa infratrochlearis nearly flat and shallow).

Given the generic allocation of this individual, its large size precludes an assignment to *P. pervetus*, although being distinctly smaller than *P. isoni* (Table 1).

**Measurements**—see Table 1.

Species: *Presbyornis isoni* Olson 1994

**Holotype**—USNM 294116, left humerus, distal two-thirds, collected in March 1993 by Ronald M.A. Ison.

**Type locality**—Maryland, Charles Co., east bank of the Potomac River, from the area designated as Bluebanks, south of Liverpool Point and north of Douglas Point, Aquia Fm., Piscataway Mbr., upper Paleocene (Landenian).

**Distribution**—upper Paleocene (Landenian), Charles Co., Maryland; late Paleocene, Billings Co., North Dakota.

**Paratype**—USNM 294117; left phalanx proximalis digiti majoris, collected in June 1984 by Eugene Hartstein at the same locality as the holotype.

**Referred specimen**—SMM P96.9.2, complete right humerus, (Wannagan Creek Quarry, Tiffanian 4, Bullion Creek (Tounge River) Fm., late Paleocene, ca 16 km NW of Meodora, Billings Co., North Dakota).

**Diagnosis**—Although no morphological characters separate USNM 294116 from humeri of other members of the genus, the very large size of *Presbyornis isoni* justifies its recognition as a separate species (Table 1).

**Comparisons**—The humerus USNM 294117 agrees with the Presyornithidae in having the fossa brachialis deep and a distinct, diagonally oriented ovoid impressio m. brachialis; processus flexorius pronounced and slightly elevated; sulcus scapulotricipitalis almost non-existant due to a poorly developed epicondylis dorsalis; tuberculum supracondylare ventrale with impressio m. pronator superficialis subdivided into two depressions of equal size; no distinct processus supracondylaris dorsalis (Olson and Feduccia 1980b); impressio m. pronator superficialis pronounced and positioned immediately medial, or somewhat medioproximal to the attachment of the lig. collaterale ventrale; attachment of lig. collaterale ventrale large and ovoid.

The specimen further agrees with *Presbyornis*, and differs from *Telmabates*, in having impressio m. pronator superficialis reaching farther proximally than that for the lig. collaterale ventrale (*Telmabates*: the scars reach about equally far proximally).

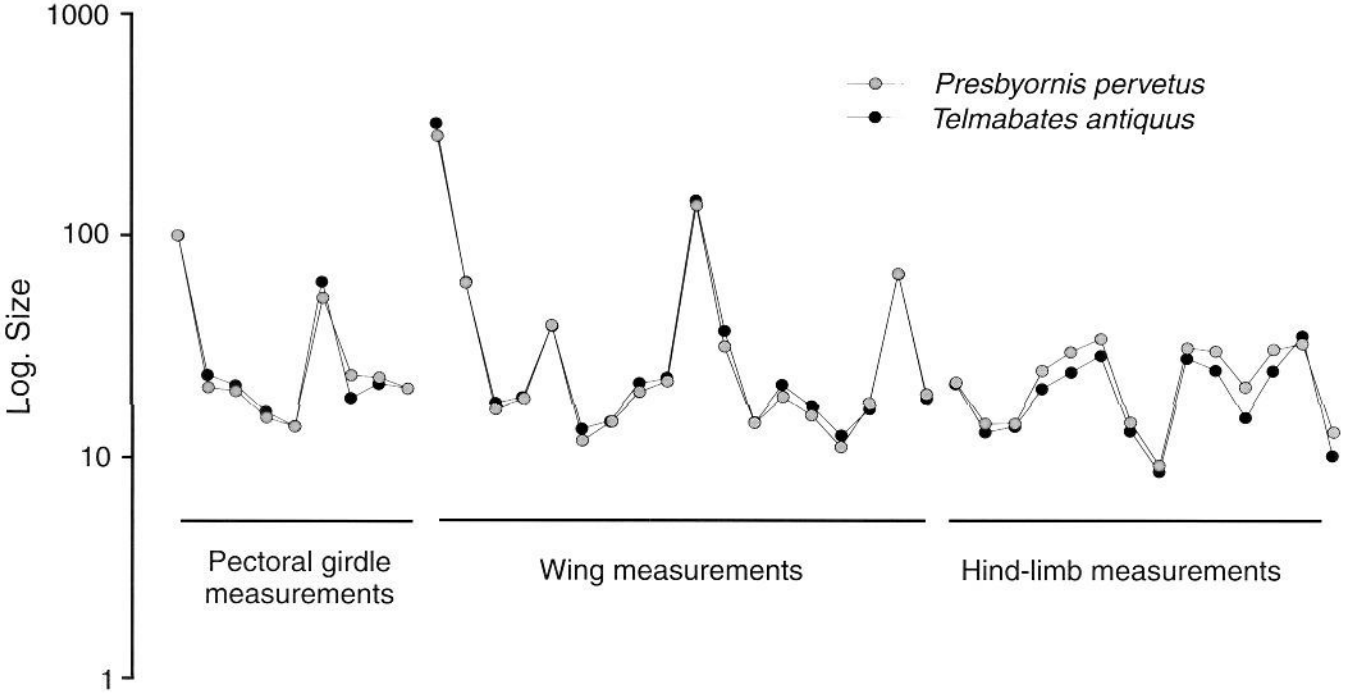


**Fig. 3.** Comparison of skeletal proportions in *Presbyornis pervetus* and *Telmabates antiquus*. The individual measurements are expressed as percentage of the humerus length. The overall resemblance between the curves shows the similarity of the two genera. The only notable differences are in the measurements of the hindlimb where *T. antiquus* is relatively larger than *P. pervetus*.

**Measurements**—see Table 1.

Genus: *Telmabates*

**Type species**—*Telmabates antiquus* Howard 1955, the only known species of the genus.

**Included species**—Type species only.

**Diagnosis**—A differential diagnosis between *Telmabates* and *Presbyornis* was given above. Some of the skeletal variation found between the genera *Telmabates* and *Presbyornis* is related to the large difference in size between the only two representatives for each genus that can effectively be compared, *T. antiquus* and *P. pervetus*. Unfortunately, too few elements are known of *P. recurvirostrus*, which equals *T. antiquus* in size, to make meaningful comparisons. The morphology of the two genera consistently differ in many aspects (see Comparisons below), which justifies the recognition of two genera within the Presbyornithidae. Furthermore, the material of *Presbyornis* and *Telmabates* exhibits different body proportions, with the hind limb bones of *Telmabates* being relatively longer and more robust than in *Presbyornis* (Fig. 3).

**Comparisons**—In details of morphology, *Telmabates* compares with *Presbyornis* as follows.

*Cranium*: The only skull element known for *Telmabates* are the occipital condyle, a part of the temporal region including the quadratal articulation, and the frontals. These skull bones were included among the associated elements referred to *T. antiquus* by Howard (1955). *Telmabates* differs from *Presbyornis* in having a small condylus occipitalis as compared with the estimated overall size of the cranium (*Presbyornis*: condylus occipitalis relatively large); supraorbital region of the frontals long and narrow relative to the size of orbita (*Presbyornis*: supraorbital region shorter and broader); and impressio frontalis present immediately caudal to the supraorbital region (*Presbyornis*: lacks impressio frontalis).

*Os lacrimale, quadratum* and *apparatus hyoideus*: None of these elements are known for *Telmabates*.

*Mandibula*: The mandible of *Telmabates* is known only from a few fragments and differs from *Presbyornis* in having the cotyla lateralis of the fossa articularis quadratica longer and relatively broader; and the processus lateralis with relatively less lateral protrusion.

*Vertebrae thoracicae*: *Telmabates* most caudal vertebra thoracicae with a well-developed processus ventralis, clearly heterocoelous (*Presbyornis*: weakly amphicoelous); corpus vertebrae with distinct bilateral, pneumatic foramen on the dorsolateral part (*Presbyornis*: very deep, but non-pneumatic, depression in this part of corpus); dorsolateral depression (pneumatic foramen) largest in the middle of the series of vertebrae thoracicae (number four counted from the synsacrum), decreasing in size cranially and caudally (*Presbyornis*: although no complete series of thoracic vertebrae are available for comparison, and there is no sign of variation in size of the dorsolateral depression among the vertebrae present); area between processus transversus and facies articularis caudalis broad and flat (*Presbyornis*: this area narrow and bridge-like); area between fovea costalis

and processus transversus broad and flat (*Presbyornis*: large round or slightly ovoid foramen in this area); fovea costalis for capitulum costae relatively large, not situated very close to cranial margin of arcus vertebrae (*Presbyornis*: fovea costalis relatively small and very close to cranial margin of the arcus vertebrae).

*Synsacrum*: *Telmabates* has one synsacro-thoracic, four lumbar, four sacral and at least four synsacro-caudal vertebrae (*Presbyornis*: one synsacro-thoracic, three lumbar, four sacral and five synsacro-caudal vertebrae); *Telmabates* has evenly deep sulcus ventralis synsacri that reaches cranially to the first lumbar vertebra (*Presbyornis*: sulcus reaches cranially only to the third lumbar vertebra).

*Sternum*: The sternum of *Telmabates* is poorly known, especially the caudal part. In *Telmabates* the cranial margin of the carina is less curved than in *Presbyornis*.

*Furcula*: Furcula of *Telmabates* are not sufficiently known to permit comparison with *Presbyornis*.

*Scapula*: Although still elongate, the acromion is shorter and blunter (*Presbyornis*: acromion longer and pointed); *Telmabates* has a round, moderately deep depression on the lateral side between tuberculum coracoideum and acromion (*Presbyornis*: depression is shallow or lacking).

*Coracoid*: Processus lateralis not very deep craniocaudally in relation to the total length (*Presbyornis*: processus lateralis deep); insertion for m. sternocoracoidei on facies dorsalis deeply excavated (*Presbyornis*: insertion for m. sternocoracoidei is shallow); and the bicipital attachment is pronounced forming a deep scar (Feduccia and McGrew 1974) (*Presbyornis*: bicipital attachment is less pronounced).

*Humerus*: Median crest much more delicate (*Presbyornis*: median crest more robust); incisura capitis undercuts not only caput humeri but also tuberculum ventrale (*Presbyornis*: only the caput humeri is undercut by the incisura capitis); size of m. pronator superficialis attachment only slightly smaller than that of the lig. collaterale ventrale (*Presbyornis*: attachment of the m. pronator superficialis significantly smaller than that for the lig. collaterale ventrale).

With additional material of *Presbyornis* available, the observation of a relatively less excavated olecranal fossa in *Telmabates antiquus* (Feduccia and McGrew 1974) is not sustained.

*Radius*: Ventral tuberculum not distinctly bipartite (*Presbyornis*: bipartite); shaft sharply convex immediately above distal end (Howard 1955) (*Presbyornis*: shaft weakly convex); distinct, large papilla centrally placed on cranial surface immediately proximal to facies articularis radiocarpalis (Howard 1955) (*Presbyornis*: the cranial surface flat); distinct ridge at the cranial end of facies articularis radiocarpalis (*Presbyornis*: no ridge present).

*Ulna*: Impressio lig. collaterale ventrale long and somewhat triangular (*Presbyornis*: typically long and kidney-shaped); condylus dorsalis sloping gradually to join shaft on caudal side of shaft (Howard 1955) with its dorsal contour somewhat ovoid (*contra* Howard who described the contour as rounded) (*Presbyornis*: trochlea is set off from shaft abruptly and has contour rounded); no distinct scar for a muscle where condylis dorsalis is set off from caudal side of shaft (*Presbyornis*: depression circular); tuberculum carpale very long in proximodistal direction (Howard 1955) and slightly convex in cranial view (*Presbyornis*: tuberculum short in proximodistal direction with ventral margin straight).

*Carpometacarpus*: Dorsal trochlea extending as far or slightly farther caudally as ventral trochlea (*Presbyornis*: dorsal trochlea extends well caudally of ventral trochlea); os metacarpale alulare projecting almost straight cranially (Howard 1955) (*Presbyornis*: processus extensorius relatively shorter and directed more proximocranially); area cranial of processus pisiformis shallow (*Presbyornis*: deeply excavated); fossa infratrochlearis flat and shallow (*Presbyornis*: with several pronounced muscle scars and excavations); facies articularis digitalis minor considerably smaller than ventral part of facies articularis digitalis major in distal view (*Presbyornis*: slightly smaller than ventral part of facies articularis digitalis major); area distal of sulcus tendineus on dorsal side of os metacarpale majus only a shallow depression (*Presbyornis*: deeply excavated); dorsocranial contour of facies articularis digitalis major angled in distal view (*Presbyornis*: a smooth curve); distal end of cranial side flat or with a shallow depression immediately proximal to margin of facies articularis digitalis major (*Presbyornis*: round, deep excavation in this area).

Howard (1955) mentions the presence of a wide, definite groove that marks the junction of ossa metacarpale majus and minus on internal side of proximal symphysis in *Telmabates*. Although this groove is deep in most specimens of *Telmabates* (shallow in AMNH 3169 and 3171) and is absent or very shallow in most *Presbyornis*, it seems to be too variable to be characteristic of the genus.

*Alar phalanx proximalis digiti alulae*: This element is not known for *Telmabates*.

*Alar phalanx proximalis digiti majoris*: No morphological differences have been found between the elements compared.

*Os coxae*: Five fragments of os coxae are known for *Telmabates*. These fragments, mainly parts of the acetabular region, are morphologically identical to *Presbyornis*, although much larger.

*Femur*: The trochanter femoris is significantly elevated (*Presbyornis*: less elevated); impressio m. obturatorius medialis very deep (*Presbyornis*: less deep); impressio m. obturatorius lateralis a distinct, round and shallow depression (*Presbyornis*: a rough ovoid surface with almost no depression); linea intermuscularis cranialis very prominent and clearly separated from lateral margin of crista trochanteris but connects with trochanter before junction of trochanter with iliac facet (Howard 1955) (*Presbyornis*: linea intermuscularis hardly distinguishable from crista trochanteris); impressio m. iliofibularis is a round and relatively small papilla with a distinct pit in it (Howard 1955) (*Presbyornis*: large and kidney-shaped, but no pa-

pilla); trochlea fibularis large in relation to the size of the crista tibiofibularis *(Presbyornis:* trochlea fibularis relatively smaller).

*libiotarsus:* Only the distal end is known for *'Iclmabatcs.* Sulcus m. fibularis continues distally toward the most distal part the of tuberositas retinaculum extensorium tibiotarsi lateralis *(Presbyornis:* distal end of sulcus m. fibularis becomes obsolete proximal to, or at level with, the proximal pan of the tuberositas); epicondylis medialis pronounced with a proximodistally oriented, ridge-shaped impressio lig. collaterale medialis *(Presbyornis:* epicondylis medialis less pronounced and lacks ridge-shaped scar).

*Fibula:* No morphological differences have been found between the elements compared.

*Tarsometatarsur.* Only a few, poorly preserved remains ot the tarsometatarsus in *Telmabates*are available for study. The only morphological characteristic of *Telmabates* observed is a moderately deep fossa metatarsi I *(Presbyornis:* fossa metatarsi I shallow).

*Hallux:* This element is not known for *Telmabates* although the large size of fossa metatarsalis I on the tarsometatarsus indicates it is well developed.

*Pedal phalanges:* No morphological differences have been found between *Presbyornis* and *Telmabates* although it has not been possible to locate the pedal phalanges of the holotype of *T. antiquus* (AMNH 3170).

Species: *Telmabates antiquus* Howard 1955

*Telmabates antiquus* Howard 1955:3

Holotype—AMNH 3170, associated remains of a single individual collected by G. G. Simpson in 1930-1931.

Type locality—Argentina, southern Chubut Territory, south of Rio Chico del Chubut in Canadon Hondo near Paso Niemann,

Distribution—lower Eocene, Chubut Territory, Argentina.

Previously referred specimens—Elements belonging to catalogue numbers AMNH 3166-3169, 3171-3187^ as listed by Howard (1955:3, 4), (south of Rio Chico del Chubut in Canadon Hondo near Paso Niemann, Casamayor Fm., lower Eocene, southern Chubut Territory, Argentina).

Newly referred specimens—AMNH 3169; phalanx pedis (distal part), AMNH 3170; fragments of left and right ossa ilii (postacetabular region), left os ischium (including acetabulum), four fragments of costae vertebralis and costae sternalis, two right first phalanges of digit II mantis (proximal ends), AMNH 3171; right femur (distal end), AMNH 3175; right radius (distal end), AMNH 3180; cervical vertebrae (complete), AMNH 3181; os frontale, condylus occipitalis, left os squamosum (including facics anicularis quadratica), left os pterygoideum, left tibiotarsus (proximal shaft), AMNH 3183; right humerus (distal end), AMNH 3185; sternum (costal margin), right fibula, AMNH 3186; left os carpi ulnare (complete), left tarsometatarsus (condvlus lateralis), pedal claw phalanx (complete), AMNH 3225; left coracoid (proximal part); AMNH 3226; rib fragment, right os coxae (acetabular part), synsacrum (midpait), AMNH 3227; left scapula (almost complete). All from south of Rio Chico del Chubut in Canadon Hondo near Paso Niemann, Casamayor Fm., lower Eocene, southern Chubut Territory, Argentina.

Diagnosis—As for the genus.

Measurements- see fable 1.

## CHARACTERIZATION OE THE PRESBYORNITHI DAE

### Species delimitations

flic family Presbyornithidae, as defined here, consists of four species in two genera. Two species, *Telmabates antiquus* and *Presbyornis rccurvirostrus* are each known from a single collecting locality, while *P. isoni* is known from two localities. The species constitute the only presbyornithid represented at each of these sites. In contrast, the fourth species, *P. pcrvetus,* is known from several localities in Colorado, Utah, and Wyoming (Fig. 2), spanning a considerable amount of geological time, and exhibiting significant morphometric variation. Although the size variation in the material from these sites is considerable (Tabic 1), it does not exceed that found in extant anscriform species (e.g., Woelfle 1967, Ericson 1987). Nevertheless, it is possible that the material assigned here to *P. pervetus*may well include more than one species. The extant anscriform genus *Anas* (dabbling-ducks) consists of many closely related species that differ mainly in plumage characters and size. These species seldom can be separated based solely on skeletal morphology (Woelfle 1967). They are sexually dimorphic in size and often sympatric, either at breeding grounds or during migration. In winter, several species of *Anas* forage together. If these birds were to die and subsequently become fossilized, it would be almost impossible to assign individual bones to the correct species. Only the smallest and largest bones could be singled out as representing different ta.xa.

The aggregations of numerous individuals *of Presbyornis* that obviously fed in limited areas, might be an early Tertiary analog to the modern example for dabbling-ducks. The difference between the smallest and the largest individuals of *Presbyornis* in the sample from the Flamingo Flat locality, for example, is very large (Fig. 4) and more than one species could be involved. It would be pointless to assign them to different species, however, because that would result in thousands of *Presbyornis-specimens* unassignable to either species. Furthermore, in the case of the humeri the two bones constitute the extremes in a series of specimens (Fig. 5) among which no morphological traits co-vary with size. The smallest specimen in Figure 5 is mensurally an outlier, but not morphologically. The descriptive statistics also show that the variation in the distal breadth of the humerus (coefficient of variation=4.5, n=53) is only slightly larger than in a sexually dimorphic modern