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A New Presbyornithid Bird (Aves, Anseriformes) from the Late Cretaceous of Southern Mongolia

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ABSTRACT

We describe a new large representative of the important fossil anseriform taxon Presbyornithidae from the latest Cretaceous (Maastrichtian) Nemegt Formation of southern Mongolia. This new taxon, *Teviornis gobiensis*, n. gen. et n. sp., is known from the associated manual portion of a right wing and the distal end of a right humerus, but is clearly diagnosable with respect to all other known representatives of the fossil Presbyornithidae. It is placed within the clades Anseriformes and Presbyornithidae, respectively, on the basis of a number of derived characters of the carpometacarpus and digits. Importantly, description of *Teviornis* confirms the presence of members of the neornithine clade Anseriformes (“waterfowl”) in the Late Cretaceous, as has been suggested previously on the basis of much less diagnostic fossil material as well as from clade divergence estimates founded on molecular sequence data. The extinct Presbyornithidae thus has a worldwide distribution and ranged in age from at least the Maastrichtian through to the uppermost Eocene.

INTRODUCTION

The fossil remains of modern birds (= Neornithes sensu Cracraft, 1988) are abundant and well represented in early Tertiary deposits from all over the world, but particularly in Asia, Europe, and North America

(Olson, 1985; Unwin, 1993). A great deal of controversy, however, surrounds the question of the timing and extent of the diversification of these so called “modern” clades by the time of the Cretaceous-Tertiary (K-T) boundary. Although some interpretations of the fossil record have led to the proposal that the

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bulk of the neornithine diversification occurred in the aftermath of the K-T event (Feduccia, 1999), recent “molecular clock” hypotheses have estimated some divergences to have been deep in the Cretaceous (e.g., Cooper and Penny, 1997; Rodionov, 1997; Van Tuinen et al., 2000; Paton et al., 2002). As a result, recent debates have focused on the question of just how deep the extant lineages of birds can be traced prior to the K-T boundary (Kurochkin, 1995; Cracraft, 2001) in the absence of well-dated and even partially complete fossil material from the Mesozoic (Dyke and Mayr, 1999; Dyke, 2001a).

In spite of the known diversity of birds from the Paleocene and Eocene (e.g., Brodkorb, 1964; Olson, 1985; Unwin, 1993; Mlíkovsky, 2002), thus far the well-known fossil anseriform *Presbyornis* Wetmore remains the most abundant described taxon of this age simply in terms of the sheer numbers of specimens that have been recorded (Olson and Feduccia, 1980; Olson, 1985; Ericson, 2000). *Presbyornis*, along with the other members of the clade Presbyornithidae, has been described from Tertiary localities in both northern and southern hemispheres (Wetmore, 1926; Howard, 1955; Harrison and Walker, 1978; Olson, 1985; Ericson, 1997, 2000; Dyke, 2001b) as well as putatively from the latest stages of the Mesozoic (Noriega and Tambussi, 1995; Ericson, 2000; Hope, 2002; Hope and Stidham, 2001). However, many Cretaceous specimens thus far considered are poorly constrained temporally and preserve too few anatomical characters to be informative within a phylogenetic context (Clarke and Chiappe, 2001; Chiappe and Dyke, 2002). The recognition of well-dated Cretaceous fossil material that can be demonstrated to have certain affinities within Neornithes is imperative to further address questions relating to both the timing and extent of the evolutionary radiation of modern birds before, and after, the K-T boundary (Dyke, 2001a; Kurochkin, 2001).

We describe a fossil presbyornithid bird that was collected in 1987 from the Late Cretaceous of southern Mongolia by an expeditionary team of the Joint Russian-Mongolian

Paleontological Expedition⁴. This new taxon is similar in size to both the known specimens of *Presbyornis isoni* Olson (from the Upper Paleocene of Maryland, USA; Olson, 1994) and to the less well-known *Headonornis hantoniensis* Harrison and Walker (from the Upper Eocene of England; see also Dyke, 2001b). However, comparisons with both these larger taxa as well as the smaller *Presbyornis pervetus* Wetmore, *Telmabates antiquus* Howard, and large numbers of additional bones referred to Presbyornithidae from the Mongolian Lower Eocene locality of Tsagaan Khushuu⁵ present a number of osteological features that allow us to diagnose an additional taxon.

The new specimen (PIN 4499-1) is from the locality of Gurilyn Tsav in the central part of the Umnogobi Aimak, east of the Altan Ula Ridge, but close to the well-known fossil site of Bugeen Tsav (fig. 1). Sediments at Gurilyn Tsav form the lower portions of the Nemegt Horizon, at the base of the the Nemegt Formation, and have been dated Campanian to Early Maastrichtian in age (Martinson, 1982; Barsbold, 1983; Shuvalov, 2000; Khand et al., 2000). Fossil vertebrates are relatively common from Gurilyn Tsav; taxa that have been collected (some of which remain undescribed) include a variety of theropods and hadrosaurian dinosaurs, as well as varanid lizards, turtles, fish, and the large enantiornithine bird *Gurilynia* (see Kurochkin, 1999).

For many years, *Presbyornis* and its kin were considered intermediate in their morphology, apparently combining characters

⁴ Although PIN 4499-1 was collected in 1987, its identification as presbyornithid was not seriously considered at first because of both its Cretaceous age and the fact that all other records for these birds were from the Paleocene and Eocene. However, at a round table discussion at the Fourth Meeting of the Society of Avian Paleontology and Evolution in Washington, D.C., in June 1996 (Olson et al., 1999), data were presented that documented the presence of presbyornithids from the Cretaceous(?) of Antarctica (Noriega and Tambussi, 1995). Notes from members of the original 1987 PIN field team indicated that more remains of this single specimen were initially collected from this locality. This material was subsequently damaged and lost.

⁵ Olson (1985: 171) and Ericson (2000: 2) have referred to our data regarding the presence of *Presbyornis* sp. in the Paleocene of Mongolia (Tsagaan Khushuu locality).

seen in both extant ducks and flamingos. Thus members of Presbyornithidae were widely cited as providing evidence for an evolutionary link between a number of the traditional avian orders by the time of the earliest Eocene (Olson and Feduccia, 1980; Feduccia, 1995, 1999). However, the recent inclusion of *Presbyornis* within numerical analyses of Recent waterfowl have demonstrated that this taxon can be placed well within order Anseriformes (commonly referred to as “waterfowl”; also comprising the extant screamers, ducks, and geese), closely related to the true ducks (Anatidae; see Ericson, 1997, 2000; Livezey, 1997, 1998; see also Paton et al., 2002).

MATERIALS AND METHODS

Our use of anatomical terminology follows Baumel and Witmer (1993), with some modifications to English after Howard (1929). For discussion of diagnosis and character distributions within Anseriformes we follow Livezey (1997, 1998) and Ericson (1997); within fossil Presbyornithidae we follow Ericson (2000). Institutional abbreviations are as follows: **AMNH**, American Museum of Natural History, New York; **BMNH PAL**, The Natural History Museum, London (Palaeontology Department Collections); **MLP**, Department of Vertebrate Paleontology, Museo de la Plata; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow; **USNM**, United States National Museum, Washington D.C.

SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758
 ANSERIFORMES (“WATERFOWL”)
 WAGLER, 1831
 ANATOIDEA (“TRUE WATERFOWL”) SENSU
 LIVEZEY, 1997
 PRESBYORNITHIDAE WETMORE, 1926

TYPE GENUS: *Presbyornis* Wetmore, 1926.

CURRENTLY INCLUDED GENERA: *Presbyornis* Wetmore, 1926; *Telmabates* Howard, 1955; *Headonornis* Harrison and Walker, 1976 (Harrison and Walker, 1979); *Teviornis*, n. gen. (this paper).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION: Members of Presbyornithidae are known from the Upper Cretaceous of Mon-



Fig. 1. Map showing the Mongolian Late Cretaceous localities of Gurilyn Tsav (1), where PIN 4499-1 was found, and Bugeen Tsav (2). Both have been dated Campanian to Early Maastrichtian in age (see text for details).

golia (this paper) as well as putatively from Antarctica and North America (Noriega and Tambussi, 1995; Hope and Stidham, 2001; see Discussion), the Upper Paleocene–Lower Eocene of North America (Wetmore, 1926; Olson and Feduccia, 1980; see also Ericson, 2000), Argentina (Howard, 1955), and Mongolia (Kurochkin, 1988), as well as the Middle–Upper Eocene of England (Harrison and Walker, 1978; see also Dyke, 2001b). Isolated elements that may also be presbyornithid have been reported from the Late Paleocene of Kazakhstan (Nessov, 1988), and the Eocene of Khirghizia (personal commun. cited in Ericson, 2000).

Teviornis gobiensis, new genus and species

Figures 2, 3, table 1

ETYMOLOGY: For Victor Tereschenko, paleontologist at the PIN, who found the specimen; *ornis* (Greek), bird (masculine); *Gobi*, a severe desert in Central Asia.

HOLOTYPE: PIN 44991-1, partially crushed associated remains of a right forelimb, including a fragment of the distal humerus, both the radiale and ulnare, the complete carpometaarpus, phalanx 1 of digiti majoris, and the phalanx of digiti minoris (figs. 2, 3).

TYPE LOCALITY AND HORIZON: Gurilyn Tsav, Nemegt Basin (fig. 1); 15 km north of the Altan Ula ridge and 7 km east of Bugeen Tsav; north west corner of Umnogobi Aimak, Mongolia; Nemegt Formation, lower Nemegt Horizon, Upper Cretaceous (Maastrichtian).

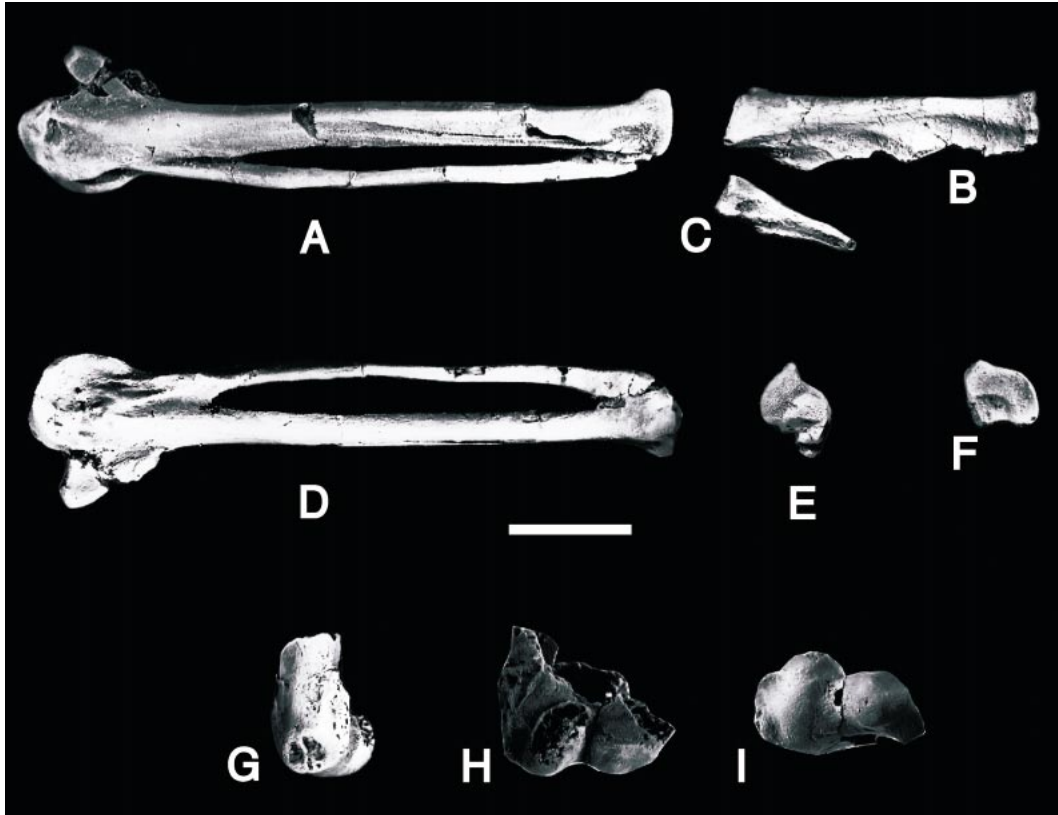


Fig. 2. *Teviornis gobiensis*, new genus and species, holotype PIN 4499-1. **A**, Right carpometacarpus in dorsal view; **B**, Right phalanx 1 of digiti majoris in dorsal view; **C**, Right phalanx of digiti minoris in dorsocaudal view; **D**, Right carpometacarpus in ventral view; **E**, Distal end of the right carpometacarpus in distal view; **F**, Proximal end of right phalanx 1 of digiti majoris in proximal view; **G**, Fragment of the right humerus in dorsal view; **H**, in cranial view; and **I**, distal view. Specimens have been coated with ammonium chloride to enhance contrast. Scale bar is 1 cm.

KNOWN DISTRIBUTION: Upper Cretaceous (Maastrichtian) of southern Mongolia.

DIAGNOSIS: Our referral of *Teviornis* to Anseriformes is based, in the first place, on clear similarity with the other known members of Presbyornithidae. In addition, the preserved carpometacarpus of this new taxon exhibits the following character listed by Livezey (1997) as diagnostic for Anseriformes (based on cladistic analysis to the exclusion of Tinamidae and Galliformes; Livezey, 1998): absence of craniocaudal curvature of corpus of carpometacarpus (os metacarpale minus) relative to os metacarpale majus. *Teviornis* is placed within Presbyornithidae on the basis of the following character conditions as listed by Ericson (2000): dorsal ridge

of trochlea carpalis well developed and connected to the dorsal emargination of os metacarpale majus (see also Howard, 1955); presence of well-developed scars for lig. ulnocarpometacarpale dorsale and lig. radiocarpometacarpale dorsale; presence of a small canalis interosseus distalis in fossa infratrochlearis.

DIFFERENTIAL DIAGNOSIS: *Teviornis* is distinguished from the other known members of Presbyornithidae on the basis of the following character conditions: tuberculum supracondylare dorsale of humerus extended far proximally; fossa infratrochlearis of carpometacarpus stretched markedly craniocaudally; proximal portion of the branch of os metacarpale minus widened both dorsoventrally

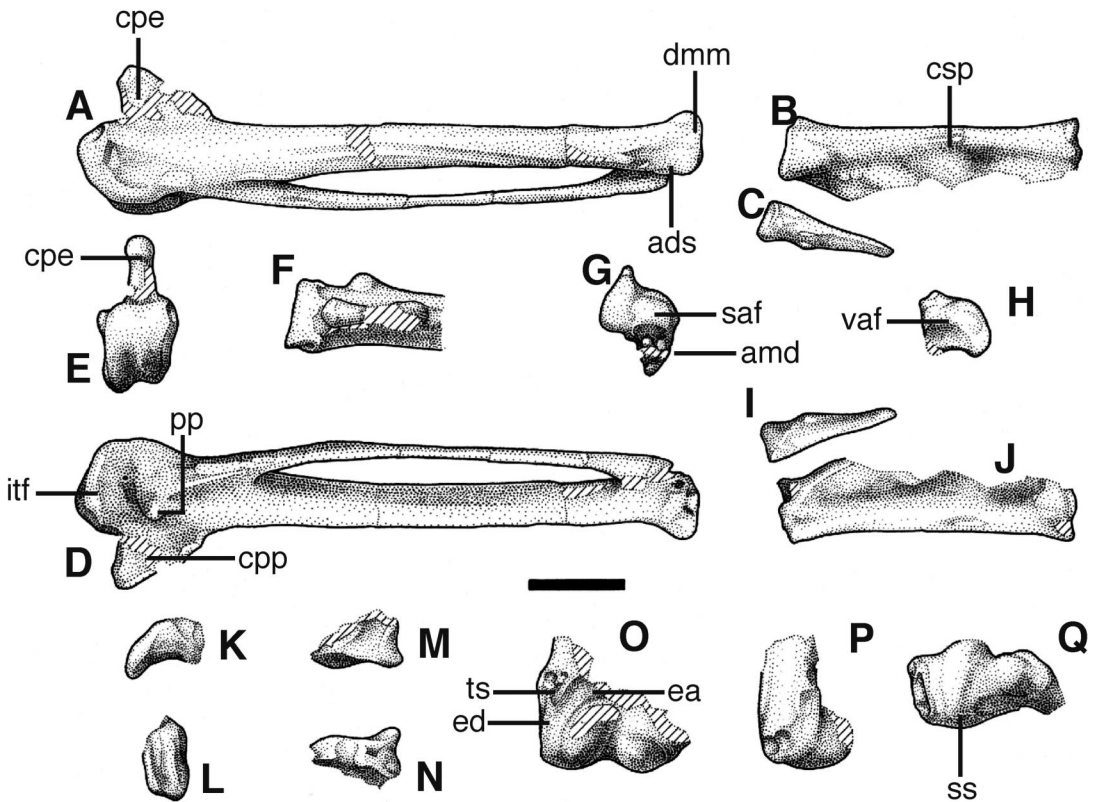


Fig. 3. Drawings of the preserved elements of the right wing of *Teviornis gobiensis*, new genus and species, holotype PIN 4499-1. Carpometacarpus in dorsal (A), ventral (D), proximal (E), cranial (F), and distal (G) views. Phalanx 1 of digiti majoris in dorsal (B), ventral (J), and proximal (H) views. Phalanx of digiti minoris in dorsocaudal view (C) and in ventrocranial view (I). Ulnare in dorsal (K) and caudal (L) views. Radiale in cranial (M) and caudal (N) views. Fragment of distal end of the humerus in cranial (O), dorsal (P), and distal (Q) views. Abbreviations: ads, area distal of sulcus tendineus; adm, facies articularis digiti minoris; dmm, distal branch of os metacarpale majus; cpe, cranial end of processus extensorius; cpp, area cranial of proc. pisiformis; csp, cranial side of the phalanx 1; ea, excavated area between condylus dorsalis and tuberculum supracondylare dorsale; ed, epicondylus dorsalis; fit, fossa infratrochlearis; pp, processus pisiformis; prm, proximal area of os metacarpale minus; saf, smaller portion of facies articularis digiti majoris; ss, sulcus scapulotricipitalis; ts, tuberculum supracondylare dorsale; vaf, ventral metacarpal articular facet. Scale bar is 1 cm.

and craniocaudally with respect to its distal continuation; facies articularis digitis minoris on os metacarpale minus divided by a cranio-caudal groove into two distinct facets; distal extension of facies articularis digitalis major widened distally; ventral portion of facies articularis digitalis major elevated in the direction of the tubercle for the insertion of m. abductor digiti majoris. It should be noted, however, that although portions of the humerus are known for *Presbyornis isoni* (Olson, 1994), Dyke (2001b) only tentatively referred this element to the Eocene genus *Hea-*

donornis; hence, further differentiation with respect to this taxon must await the recovery of additional fossil material. On the basis of the carpometacarpus (as far as this element is known in the genera of Presbyornithidae), we consider *Teviornis* to be a distinct taxon (see below).

TYPE SPECIES: *Teviornis gobiensis*; only currently recognized species.

MEASUREMENTS (in mm): Craniocaudal width of condylus ventralis of the humerus, 5.3; length of carpometacarpus, 65; dorso-ventral height of proximal end of carpome-

TABLE 1
Selected Measurements of Preserved Wing Elements for Members of Presbyornithidae
(from various sources)

	<i>V. gobiensis</i>	<i>P. pervetus</i>	<i>P. recurvirostris</i>	<i>P. isoni</i>	<i>T. antiquus</i>
Carpometacarpus					
Greatest length	65	44–54			63
Proximal width	15.2	9.7–11.9	13		15.8–16.6
Distal width	7.7	5.1–7.1			7.1–7.4
Phalanx 1 of major digit					
Greatest length	30.8	19.8–27.6		40.6	29.7–30.7
Proximal width	8.3	4.3–5.8		9.5	

tacarpus, 7.2; craniocaudal width of proximal end of carpometacarpus across the processus extensorius, 15.2; dorsoventral height of distal end of carpometacarpus, 7.7; length of phalanx 1 digiti majoris, 30.8; ventral proximal width of phalanx digiti majoris, 8.3; length of phalanx digiti minoris, 13.9; proximal width of phalanx digiti minoris, 4.2 (for comparative measurements, see table 1).

DESCRIPTION AND COMPARISONS

HUMERUS (figs. 2G–I, 3O–Q): The portion of the distal right humerus that is preserved as part of PIN 4499-1 is broken ventral to the condylus ventralis and across the remainder of the fossa m. brachialis. However, the shapes of both the dorsal and ventral condyles are discernible; notably, a well-excavated depression is present between the tuberculum supracondylare dorsale and the condylus dorsalis that is not evident in specimens referred to either *Presbyornis* or *Telmabates* (Olson, 1994; Ericson, 2000). Since a depression of similar depth and width is also seen in BMNH PAL A 5105, a distal end of a left humerus referred to the large *Headonornis* by Harrison and Walker (1979; also figured by Dyke, 2001b), but it is not evident on the holotype humerus of the similarly sized *Presbyornis isoni* (USNM 294116; Olson, 1994), this feature does not seem to be related to overall size (see Discussion). *Teviornis* is also distinguished from *Presbyornis* and *Telmabates* because the tuberculum supracondylare dorsale is remarkably far extended proximally in the former. Because of the poor preservation of this element, most of the morphological features

listed by Ericson (2000) as characteristic for Presbyornithidae are lacking in PIN 4499-1, with the exception of a weakly developed sulcus scapulotricipitalis (resulting from the small epicondylus dorsalis in this specimen).

ULNARE: The small but remarkably well-preserved ulnare of *Teviornis* (fig. 3K, L) exhibits two characters listed by Ericson (2000) as distinctive to Presbyornithidae, a distinct but shallow sulcus on its lateral side as well as a wide incisura metacarpalis. These characters, however, are based entirely on the known material of *Presbyornis pervetus*, the only presbyornithid other than *Teviornis* for which this element is known.

RADIALE: The radiale is also represented as part of PIN 4499-1 (fig. 3M, N). As noted by Ericson (2000) again for *Presbyornis pervetus*, this element has a mediolaterally compressed caudal end, a deep sulcus on its proximal side with a pronounced and centrally located tuberculum cranial to it. The incisura on the cranial edge of the radiale in *Teviornis* is also wide and shallow.

CARPOMETACARPUS: The best preserved and most anatomically informative element of PIN 4499-1 is an almost complete right carpometacarpus (figs. 2A–D, 3A–H). Because this element is well known in the other presbyornithids with the exception of *Presbyornis isoni* (Olson, 1994) and *Headonornis* (Dyke, 2001b), it forms the basis of our diagnosis for *Teviornis*. As is the case in the known presbyornithids (Ericson, 2000), the Lower Eocene *Anatalavis oxfordi* Olson (Olson, 1999), and the basal Anseriformes *Anhima*, *Chauna* (Anhimidae), and *Anseranas*, the distal end of the carpometacarpus bears

a well-developed and deep sulcus tendineus on its dorsal surface that extends at least one-third of its length. Although only the proximal and distal ends of the right carpometacarpus and the distal end of the left are preserved as part of the holotype of *Telmabates* (AMNH 3170), this conformation of the sulcus is seen in a number of the additional specimens referred to this taxon (Howard, 1955).

On the proximal end of the carpometacarpus, the fossa infratrochlearis of PIN 4499-1 is stretched craniocaudally to a greater extent than it is in either *Presbyornis pervetus* or *Telmabates*, which both have a much more circular contour of this fossa. The angle between the processus extensorius and the trochlea carpalis is almost perpendicular, as opposed to being distinctly curved, as is the case in the other presbyornithids. In this respect, this element of *Teviornis* closely resembles another large and as yet undescribed presbyornithid carpometacarpus from the Lower Eocene London Clay Formation of England (BMNH PAL A 6241).

The proximal portion of the os metacarpale minus in *Teviornis* is distinctly widened dorsoventrally when viewed in dorsal view as opposed to being equal in width, as is the case in both *Presbyornis pervetus* and *Telmabates*. Just as in *Telmabates*, the dorsal part of the trochlea carpalis in PIN 4499-1 extends as far caudally as does the ventral part of the trochlea carpalis; in *Presbyornis pervetus*, the dorsal ridge of the trochlea carpalis extends far caudally with respect to the ventral ridge of the trochlea carpalis. In both *Teviornis* and *Presbyornis* the processus pisiformis lies on the same level as os metacarpale majus, but in *Telmabates* this process follows the line of extension of os metacarpale minus. Variation in the relative degree of excavation of the area cranial to the processus pisiformis is seen between the three genera: in *Victornis* this area is somewhat excavated, whereas it is shallow in *Telmabates* and very deep in *Presbyornis pervetus*. Further, the fossa infratrochlearis in PIN 4499-1 bears several pronounced muscle scars and excavations (as is seen in *Presbyornis*)—in *Telmabates* this fossa is almost flat (Howard, 1955).

The distal end of the carpometacarpus of

PIN 4499-1 is stretched dorsoventrally whereas it is much shorter in both *Telmabates* and *Presbyornis pervetus* (perhaps as a result of the much larger size of *Teviornis*). The articular facet for phalanx digiti minoris is undivided in the two smaller taxa but is grooved craniocaudally in *Teviornis*, and the area distal to the sulcus tendineus (in dorsal view) bears no depression (in both *Telmabates* and *Presbyornis pervetus* this area is excavated to varying degrees).

Ericson (2000) listed a number of characters of the carpometacarpus as diagnostic for Presbyornithidae, the majority of which are seen clearly in PIN 4499-1. Of these features, the following are preserved in the holotype of *Teviornis*: carpometacarpus straight with major and minor metacarpals parallel; caudal portion of dorsal part of trochlea carpalis well developed and connected to the edge of the major metacarpal; presence of large scars for the insertions of lig. ulnocarpometacarpale dorsale and lig. radiocarpometacarpale dorsale; small vascular foramen present in the fossa infratrochlearis; marked and deep sulcus tendineus; sulcus interosseus deep, having an ossified bridge.

PHALANX 1 DIGITI MAJORIS: The proximal phalanx of the major digit (figs. 2B, 3B, J) in *Teviornis* is long and slender and bears two deep depressions on its dorsal side. On the proximal side of this element there is a blunt and cranioventrally protruding tuberculum, no dorsal tendinal sulcus on the pila cranialis, and no distal projection on the caudal margin. All three of these characters are seen in members of Presbyornithidae; this element is known for both *Presbyornis* (Olson, 1994; Ericson, 2000) and *Telmabates* (AMNH 3180; Howard, 1955). The preserved phalanx 1 of *Teviornis* exhibits a further two characters that allow taxonomic differentiation from other taxa: a straight cranial margin (in dorsal view) and an elevated ventral portion of the metacarpal articular facet (in the direction of the tubercle for the insertion of *m. abductor digiti majoris*). In other presbyornithids, this phalanx is not raised ventrally and has a curved cranial margin when viewed dorsally (e.g., AMNH 3180 [*Telmabates*], USNM 294117 [*P. isoni*], USNM 483164 [*P. pervetus*]).

PHALANX DIGITI MINORIS: The small, well-

preserved phalanx of the minor digit of *Tevionis* (fig. 2C, I) is flattened dorsoventrally and has a sharp and projected pila caudalis and a well-developed tuberculum located distally with respect to the pila caudalis. These features were described for *Presbyornis pervetus* by Ericson (2000).

DISCUSSION

Previous studies have demonstrated that the Presbyornithidae were an extremely widespread group of birds during early Tertiary times. Members of this clade have been recovered from the Paleocene–Eocene of Europe (Harrison and Walker, 1978, 1979; Dyke, 2001b), South America (Howard, 1955; Cracraft, 1970), and Asia. Indeed, these birds are probably the most abundantly known taxa from throughout the Tertiary of North America (see, for example, McGrew and Feduccia, 1974; Olson and Feduccia, 1980; Olson, 1994; Leggitt and Buchheim, 1997; Benson, 1999; Feduccia, 1999; Ericson, 2000). Recent phylogenetic studies have placed *Presbyornis* within Anseriformes, close to the divergence of the Anatidae, the true ducks, geese, and swans (Ericson, 1997; Livezey, 1997, 1998), indicating that the divergence of this large extant taxon must have occurred earlier than the oldest known member of Presbyornithidae. Our description of *Tevionis* serves to confirm previous suggestions that Anseriformes did indeed occur prior to the K-T boundary—existing proposals that this was the case have been based either on more incomplete fossil material (i.e., single and isolated elements presenting few characters for comparisons; e.g., Hope and Stidham, 2001; Hope, 2002) or on records collected from rocks that are of uncertain Cretaceous age (e.g., Olson and Parris, 1987; Noriega and Tambussi, 1995; see contrary citations in Olson, 1994; Clarke and Chiappe, 2001). Comparisons between PIN 4499-1 and other putative records of Presbyornithidae from the ?Cretaceous are not possible here, either because of the fragmentary preservation of the available material (see illustrations in Hope, 2002) or because of the lack of corresponding skeletal elements (as is the case in MLP 93-I-3-1 described by Noriega and Tambussi [1995] from the ?Cretaceous

of Antarctica). It is however of note that records of “*Presbyornis*-like” birds from the Mongolian Cretaceous have been listed previously by some authors (Olson, 1985; Kurochkin, 1995) on the basis of a small, damaged, and isolated tarsometatarsus figured as Presbyornithidae(?) by Kurochkin (1995). This single specimen, from the Udan Sayr locality within the Baruungoyot Formation, is considered Aves incertae sedis here as it preserves no anatomical features that can be considered diagnostic of either Presbyornithidae or Anseriformes (Ericson, 2000).

The internal composition of Presbyornithidae remains controversial and complex. For more than 100 years the remains of fossil birds bearing varying degrees of resemblance to living Anseriformes have been described from the earliest Tertiary (e.g., Owen, 1846; Milne-Edwards, 1867–1871; Lydekker, 1891; Kurochkin, 1976), but only recently have clear character diagnoses for this group been presented (Livezey, 1997, 1998; Ericson, 1999, 2000). The genus *Telmabates*, for example, originally described by Howard (1955) from the Eocene of Patagonia has variously been considered to be synonymous with *Presbyornis*, especially following the description of the giant *Presbyornis isoni* by Olson (1994). Olson (1985, 1994), for example, has considered that Presbyornithidae comprises simply a number of differently sized species within the single genus *Presbyornis*. Recently, Ericson (2000: 7, 11) has shown that not only do the two genera vary significantly in the relative sizes of their hindlimb bones (those of *Telmabates* are also somewhat more robust; cf. AMNH 25552, 28505 [slabs containing *Presbyornis pervetus* remains] and AMNH 3167, 3169, 3180, 3171 [referred specimens of *Telmabates*]), but that there are clear osteological differences between them (e.g., linea muscularis cranialis of coracoid obsolete in *Presbyornis* [welldeveloped in *Telmabates*].) More problematical with respect to these diagnoses are the less completely known taxa *Headonornis hantoniensis* Harrison and Walker and *Presbyornis isoni* Olson. Although the holotype of *Headonornis* is an isolated coracoid (BMNH PAL A 30325), Dyke (2001b) showed that incomplete portions of humeri (BMNH PAL A 3686, A 5105) referred to

this taxon by Harrison and Walker (1976, 1979) are in fact referrable to *P. isoni* (on the basis of a more recently collected and more complete humerus, BMNH PAL A 6240). It remains entirely possible that these two large presbyornithids, *P. isoni* and *Headonornis*, are actually the same taxon, but the discovery of additional material will be required to confirm this (Dyke, 2001b). Because *Presbyornis isoni* is currently known largely on the basis of the humerus (Olson, 1994; Benson, 1999), only a few of the differential characters listed by Ericson (2000) (with respect to *Telmabates*) apply (i.e., impressio m. pronator superficialis on distal humerus extends much farther than lig. collaterale ventrale in *Presbyornis*). An additional specimen, BMNH PAL A 43164, an incomplete portion of sternum described by Lydekker (1891) as the holotype of *Proherodius oweni*, is very similar in its size and overall morphology (e.g., in the shape of the coracoidal sulci) to this element in *P. pervetus* (Dyke, 2001b); although tantalizingly incomplete, it remains possible that this specimen is in fact the earliest described presbyornithid (as suggested by Harrison and Walker, 1978).

Whatever the final outcome of these niggling taxonomic problems, it is clear that Presbyornithidae was one of the most abundant groups of Late Cretaceous–Tertiary neornithine birds. The abundance of these birds in deposits of this age is probably a result of their aquatic or semiaquatic ecology, resulting in their differential preservation across the K–T boundary (when compared to other groups of largely terrestrial taxa). Since a similar bias is seen in the fossil record of non-neornithine birds throughout the Cretaceous (Padian and Chiappe, 1998; Chiappe and Dyke, 2002), it seems logical to infer that members of other clades of modern birds were also present prior to the terminal Cretaceous extinction event; these have either yet to be found or have not so far been recognized convincingly on the basis of phylogenetically informative fossil material.

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