More Evidence for Plesiomorphy of the Quadrate in the Eocene Anseriform Avian Genus Presbyornis

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Brief report

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More evidence for plesiomorphy of the quadrate in the Eocene anseriform avian genus *Presbyornis*

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Evidence from the quadrate morphology in the American specimens of *Presbyornis* proved inconsistent with the hypothesis of close relationships of this anseriform genus to modern ducks and geese, but some character states remained uncertain. Here I describe in detail two fairly well preserved *Presbyornis* quadrates from Central Asia, which provide new evidence for the plesiomorphic, galliform-like morphology of this bone among the anseriforms. Most important, and contrary to a recent report, there is no caudomedial foramen that is present in the extant anseriforms. The only pneumatic foramen is in the basiorbital position, which is plesiomorphic for the galloanserines. At least six other plesiomorphic characters of the quadrate consistently suggest that the Presbyornithidae are stem-group anseriforms.

Introduction

The Early Tertiary long-legged anseriforms with duck-like skulls of the genus *Presbyornis* are among the best-known avian fossils and play a pivotal role in reconstructions of anseriform phylogeny. The presbyornithids were once viewed as ancestral anseriforms (Olson and Feduccia 1980) and their close relatives of are now known from Late Cretaceous deposits (Kurochkin et al. 2002; Clarke et al. 2005). Currently, they are widely considered to be closely related to ducks and geese (Anatidae) within crown-group anseriforms (Ericson 1997; Livezey 1997; Clarke et al. 2005; Mayr 2008). However, Mayr (2009: 52) noted apparently plesiomorphic characters in the postcranial skeleton and a detailed study of *Presbyornis* quadrates demonstrated a number of character states that are plesiomorphic for the anseriforms and, in the absence of a detailed study of the *Presbyornis* skull, suggest the presence of other galloanserine plesiomorphies, such as pneumaticity of the pterygoid (Elzanowski and Stidham 2010). The cranial anatomy of *Presbyornis* is in need of a thorough revision, which is likely to result in a more basal placement of this taxon relative to *Anseranas* and Anatidae (Elzanowski and Boles 2012).The preservation and variation of *Presbyornis* quadrates from North American collections left some essential details uncertain (Elzanowski and Stidham 2010). Meanwhile, Kurochkin and Dyke (2010) published four photographs of two *Presbyornis* quadrates from the Early Eocene of the Gobi Desert (Central Asia), but failed to describe them except for some erroneous information (reinforced by a misleading photograph) that “each bears a large pneumatic foramen on its posterior surface”. Here I correct this error, describe in detail the two specimens, and show the significance of characters that they help to define.

Institutional abbreviations.—PIN, The Borissiak Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; USNM , National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Material and methods

Two quadrates, right (PIN 3104-208) and left (PIN 3104-209), both with the orbital process broken off near the base. The left element is slightly damaged at both ends. None of the specimens shows any evidence of unfinished ossification. Both specimens were examined under a stereomicroscope, photographed together in the same positions, and compared to each other and to the American specimens as previously described by Elzanowski and Stidham (2010). The latter study is followed for anatomical terminology.

The two quadrates were recovered by screen-washing and sieving from a single sedimentary lens at the Tsagaan Khushuu locality, Mongolia, among numerous postcranial bones of presbyornithids (Kurochkin and Dyke 2010). While there is no explicit information on whether any other bird bones were found in the same deposits, the prevalence of presbyornithid postcranial bones and a detailed, specific similarity to the American presbyornithid quadrates (Elzanowski and Stidham 2010: fig. 1) do not leave any doubts that the two quadrates represent at least the family Presbyornithidae.

Results

The two Asiatic specimens conform to the reconstruction based on the American specimens (Elzanowski and Stidham 2010). However, they help clarify a few details especially of the rostral view that have not been clearly discernible before. They confirm that the rostral tongue of the squamosal capitulum has a regular, arched outline (Fig. 1B_2) and, in contradistinction to *Anseranas* and Anatidae, does not narrow to a saddle-shaped facet (or secondary tongue). The rostral tongue descends onto the supraorbital crest that is prominent (contra Elzanowski and

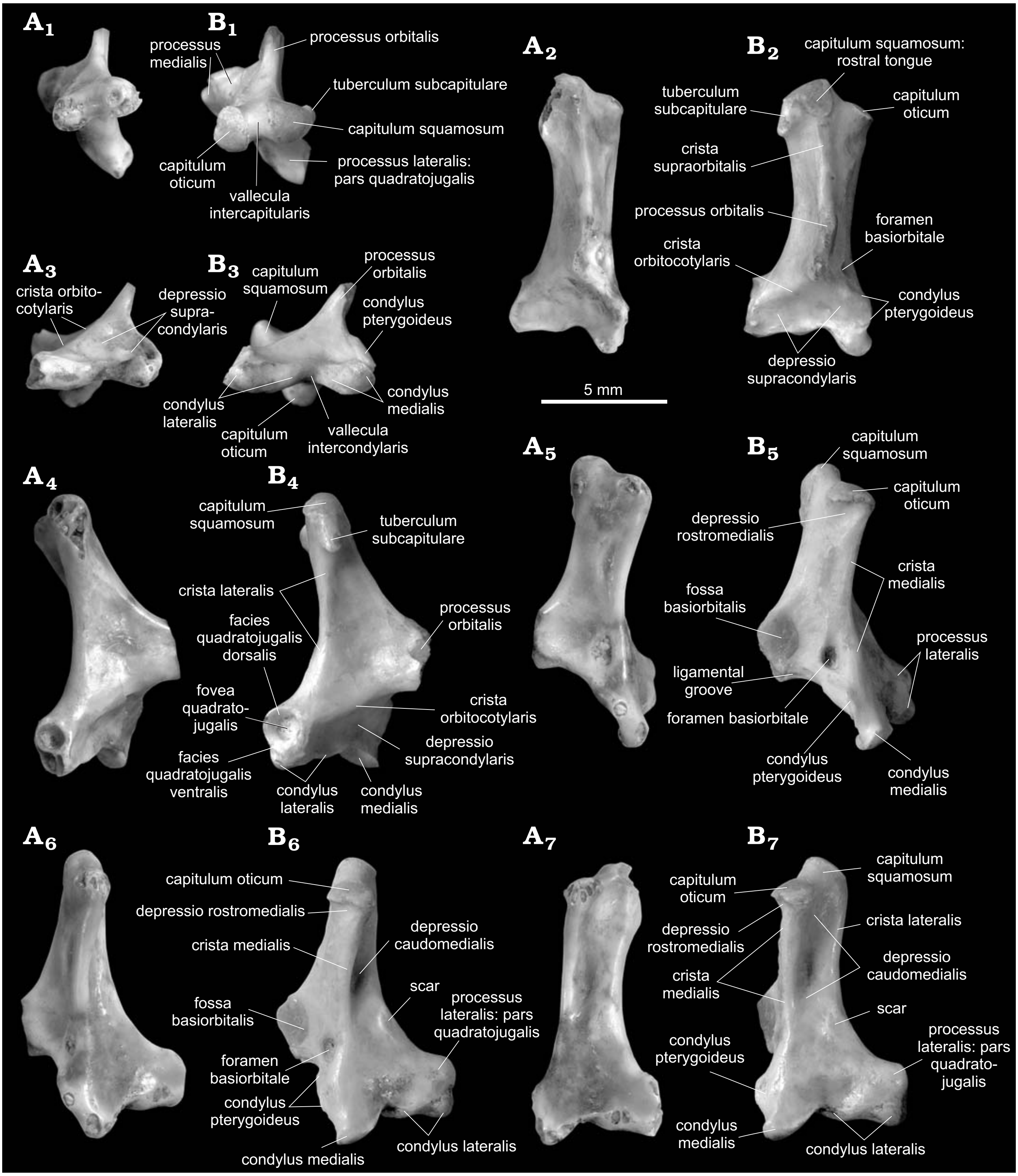

Fig. 1. The quadrates of anseriform bird *Presbyornis* from the Lower Eocene of Tsagaan Khushuu, Mongolia. **A**. PIN 3104-209 (reversed). **B**. PIN 3104-208. In dorsal (A_1, B_1), rostral (A_2, B_2), ventral (A_3, B_3), lateral (A_4, B_4), rostromedial (A_5, B_5), medial (A_6, B_6), and caudal (A_7, B_7) views.

Boles 2012: fig. 3) but rounded or blunt (Fig. 1A_2, B_2). The subcapitular tubercle is prominent distally but poorly defined from or nearly continuous with the squamosal capitulum (Fig. 1B_2, B_3). The orbitocondylar angle (between the axes of mandibular articulation and orbital process) is about 115° (as approximated from Fig. 1A_3, B_3), which is slightly below the range as previ-

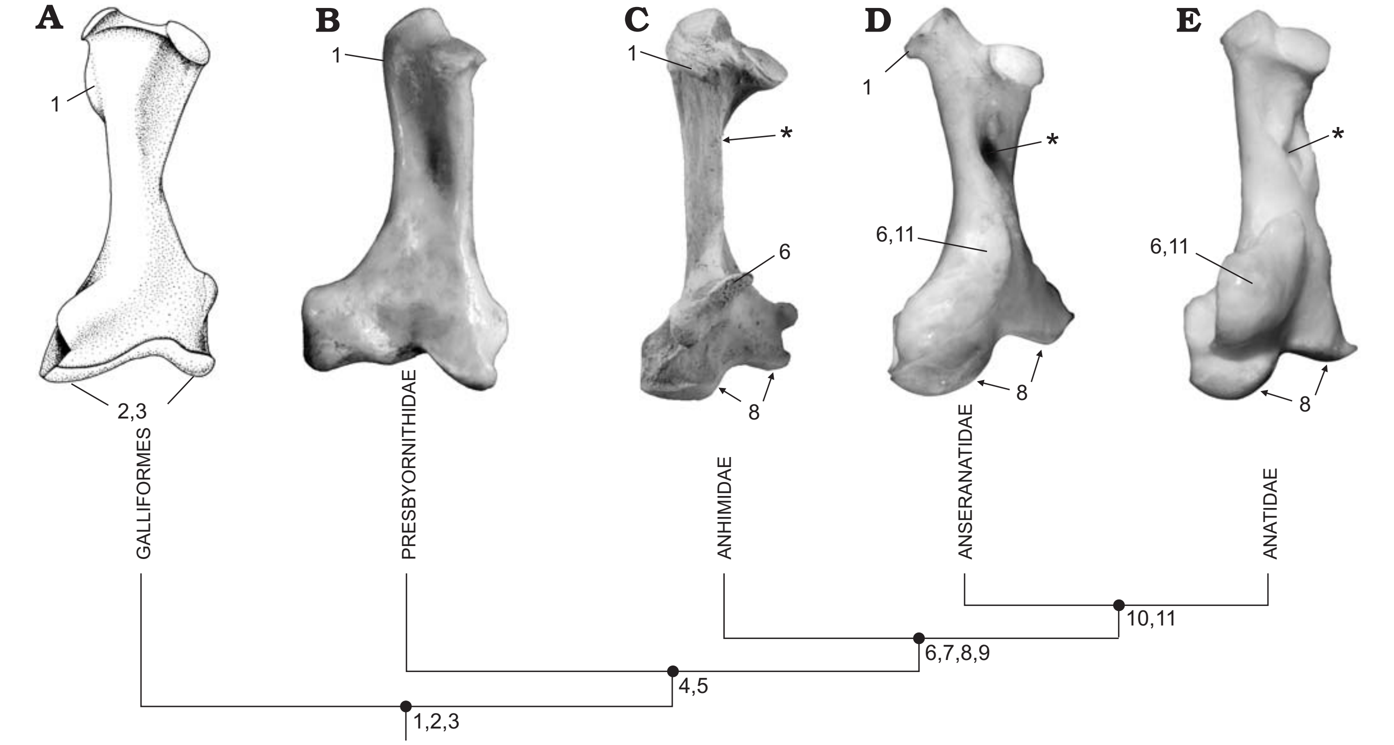

Fig. 2. Most parsimonious distribution of 11 best defined characters of the anseriform quadrate (see also Elzanowski and Stidham 2010), with caudal views of the quadrates. **A**. *Megapodius freycinet* Gaimard, 1823. **B**. *Presbyornis* sp. **C**. *Anhima cornuta* (Linnaeus, 1766). **D**. *Anseranas semipalmata* (Latham, 1798). **E**. *Dendrocygna viduata* (Linnaeus, 1766). Synapomorphies: Galloanseres: 1, subcapitular tubercle present; 2, mandibular articulation bicondylar; 3, mandibular articulation narrower than half the height of the quadrate (which makes it look slender). Anseriformes: 4, supraorbital crest present (see Fig. 1A$_2$, B$_2$); 5, mandibular condyles overlap (interdigitate with their tips) across the intercondylar vallecula (see Fig. 1A$_3$, B$_3$). Crown-group Anseriformes: 6, submeatic prominence or process present; 7, orbitocotylar crest does not extend on the quadrate corpus (as it does in *Presbyornis*; see Fig. 1A$_2$, A$_4$, B$_2$, B$_4$); 8, medial condyle distinctly offset proximad relative to the lateral condyle; 9, no basiorbital foramen (except for a minute opening in some anhimid specimens). Anseranas and Anatidae: 10, the rostral tongue of the squamosal capitulum ending as a saddle-shaped concavity; 11, inflated submeatic prominence. Asterisk marks the presence of the caudomedial foramen (vestigial in the Anhimidae). The presence/absence of this foramen has not been included in the character optimization because its absence in all *Presbyornis* quadrates has yet to be confirmed.

ously estimated for all galloanserines (Elzanowski and Stidham 2010: 310).

The medial view is as reconstructed (Elzanowski and Stidham 2010: fig. 5B) except that the medial crest can be traced further ventrally up to the medial condyle. The basiorbital foramen is separated from the basiorbital fossa by a distinct ridge and the ventral base of the orbital process is excavated by the ligamental groove. The more distal part of the orbital process that probably bore the pterygoid facet is gone.

The right element PIN 3104-208 provides the first complete view of the caudal aspect of the *Presbyornis* quadrate (Fig. 1A$_7$, B$_7$) which shows that, in any realistic orientation of the bone, it is the *medial* condyle that extends further ventrally, whereas in extant anseriforms it is the *lateral* condyle that projects much further ventrally (Fig. 2). A striking feature of the caudal view is the caudomedial depression that is extensive and deep ventrally but, in contradiction to Kurochkin and Dyke (2010), does not contain a foramen (Fig. 1A$_7$, B$_7$). The only pneumatic foramen that is present in either of the two specimens, but has not been mentioned by Kurochkin and Dyke (2010), is in the basiorbital position.

The two Asiatic specimens are nearly identical in size (Table 1) except that the mandibular part tends to be somewhat narrower in PIN 3104-209 (which may or may not be due to damage). However, the two quadrates reveal many detailed differences and even more are probably obscured by damage. Most striking are differences in medial view (Fig. 1A$_6$, B$_6$). The medial crest in the right quadrate PIN 3104-208 has the edge broad and convex (grooved) in cross section whereas in the left quadrate PIN 3104-209 the edge is narrow (sharp) and convex in cross section. In the right but not left quadrate there is a distinct rostromedial depression. The right but not left quadrate bears a distinct scar just medial to the lateral crest, slightly below the mid-height of the bone. Besides, compared to the right quadrate, the left quadrate has the medial condyle descending at steeper angles and thus

Table 1. Measurements (in mm) of the *Presbyornis* quadrates from the early Eocene of Gobi Desert. [1] orthogonal, normal to the line connecting the tips of the medial and lateral condyle; [2] maximum, including the subcapitular tubercle which is damaged in PIN 3104-209; [3] maximum, across the condyles; [4] maximum, between the pterygoid condyle and the rims of the quadratojugal cotyla.

Specimen	Length (height)[1]	Dorsal width[2]	Condylar span[3]	Ventral width[4]
PIN 3104-208	11.0	4.1	5.8	6.0
PIN 3104-209	11.15	3.8+	5.2	5.45

projecting less medially (Fig. 1A_2, B_2, A_7, B_7); the quadratojugal cotyla shallower with dorsal and ventral quadratojugal facets much smaller (Fig. 1A_4, B_4) although this may well result from the wear of the left bone; the lateral condyle less offset caudally relative to the medial condyle (Fig. 1A_4–A_6, B_4–B_6); and the entire lateral process less robust (Fig. 1A_1, B_1, A_3, B_3).

Discussion

In view of the overall duck-like shape of the *Presbyornis* skull, which influenced recent phylogenetic reconstructions (Ericson 1997; Livezey 1997; Clarke et al. 2005; Mayr 2008), the galliform-like morphology of its quadrate has come as a great surprise (Elzanowski and Stidham 2010). If found alone, the quadrate of *Presbyornis* would probably have been identified as galliform (as initially happened to one of the American specimens, the ventral fragment USNM 49771). The galliform similarity is conveyed primarily by the presence of the orbitocotylar crest, basiorbital foramen, and the mandibular condyles ending approximately at the same level (with the medial condyle tending to project slightly more in *Presbyornis*). A complete orbitocotylar crest seems to be a specifically galloanserine symplesiomorphy as it occurs rarely (if ever) in other birds (Table 2). The basiorbital foramen is present in many avian taxa, including *Struthio* (?vestigial), Galliformes, *Phaethon*, *Fregata*, Procellariidae, Diomedeidae, *Pelecanus*, *Balaeniceps*, *Leptoptilus*, Gruidae, *Caprimulgus*, and *Nyctibius.* The mandibular condyles of most birds end approximately at the same level (Table 2) or the medial condyle projects further distally, which makes the condition in the crown-group anseriforms unequivocally derived relative to *Presbyornis* (Fig. 2). Another most probably derived condition of the crown-group anseriforms is the postmeatic prominence or process although a comparable structure is present in the Cracidae (Table 2) and occurs in some taxa outside the galloanserines (e.g., in the Tinamidae) in a close association with the caudal condyle (which is absent in the galloanserines). Outgroup comparisons of the quadrate of *Presbyornis* (Table 2) show that most if not all of its character states that differ from the crown-group anseriforms are in all probability plesiomorphic for the galloanserines.

Table 2. Variable characters of the anseriform quadrate (see Fig. 2) and their states in the palaeognaths, primitive galliforms, and two neoavian neognaths. 0, "absent" or "no"; 1, "present" or "yes"; [1] anseriform submeatic projections are poorly comparable to those of most other birds (palaeognaths and neoavians) that have tricondylar rather than bicondylar mandibular articulation; [2] a depression with small perforations; [3] vestigial.

Character	*Struthio camelus*	*Eudromia elegans*	*Megapodius freycinet*	*Crax elector*	*Presbyornis*	Anhimidae	Anatidae	*Larus marinus.*	*Fulica atra*
Orbitocotylar crest	0	0	1	1	1	0	0	0	0
Submeatic prominence / process[1]	0	1	0	1	0	1	1	0	0
Lateral condyle far beyond medial one	0	0	0	0	0	1	1	0	0
Basiorbital foramen	1[2]	0	1	1	1	0	0	1	0
Caudomedial foramen	1	0	0	0	0–1	1[3]	1	1	0

Galliforms differ from modern anseriforms in the pattern of quadrate pneumatization: galliforms have two foramina, rostromedial and basiorbital, and modern anseriforms have only a single, caudomedial foramen. The presence of the caudomedial foramen would be a likely synapomorphy of *Presbyornis* and modern anseriforms, as assumed by Elzanowski and Boles (2012) who relied on Kurochkin and Dyke's (2010) suggestive and unequivocal report of this foramen in the Asiatic specimens. This stresses the importance of our observation that there is no foramen in the caudomedial depression in either of these specimens (Fig. 1A_7, B_7). The caudomedial foramen is positively absent in two of four American specimens that have been preserved with the otic part, but may be present in the remaining two specimens (Elzanowski and Stidham 2010). This may reflect variability in the presence of this foramen or, possibly, in the depth of the blind recess in the ventral corner of the caudomedial depression which can be easily mistaken for a foramen in some fossil specimens. Whether the caudomedial foramen is always absent or only occasionally present as a result of morphogenetic instability in the growth of pneumatic diverticula as manifested in the Anhimidae (Elzanowski and Stidham 2010), the Presbyornithidae must not be scored with the caudomedial pneumatic foramen for the sake of phylogenetic reconstructions. This makes the quadrate morphology of *Presbyornis* consistently plesiomorphic in lacking at least four robust synapomorphies of the crown-group anseriforms (Fig. 2).

While in size the two Asiatic quadrates are nearly identical (Table 1) and very close to the American specimens (Elzanowski and Stidham 2010: table 3), the qualitative differences between them seem to exceed intraspecies variation, as does the variation of limb bones that has been interpreted in terms of an assemblage of species (Ericson 2000; Kurochkin and Dyke 2010). However, while quantitative skeletal variation has been recorded for a number of avian species, there are very few observations on qualitative intraspecies variation of the osteological details, especially in the skull. It is well known in avian paleontology that closely related species may be osteologically indistinguishable, as is the case of the *Anas* ducks (Ericson 2000). Hence at least some of the marked differences between the two quadrates suggest the presence of at least two species in the Gobi Desert assemblage. This suggestion is compatible with the approach taken by Kurochkin and Dyke (2010), who assigned a large part of the limb bones to a new species, *Presbyornis mongoliensis*, while leaving all other bones, including the quadrates, under the heading of *Presbyornis* sp.

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