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A gigantic bird from the Upper Cretaceous of Central Asia

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We describe an enormous Late Cretaceous fossil bird from Kazakhstan, known from a pair of edentulous mandibular rami (greater than 275 mm long), which adds significantly to our knowledge of Mesozoic avian morphological and ecological diversity. A suite of autapomorphies lead us to recognize the specimen as a new taxon. Phylogenetic analysis resolves this giant bird deep within Aves as a basal member of Ornithuromorpha. This Kazakh fossil demonstrates that large body size evolved at least once outside modern birds (Neornithes) and reveals hitherto unexpected trophic diversity within Cretaceous Aves.

Keywords: Kazakhstan; Aves; phylogeny; Neornithes; anatomy

1. INTRODUCTION

The successful and diverse dinosaurian clade Aves (*ca* 10 000 extant species) [1,2] predominantly consists of small species (median average mass = 37.6 g): only a handful of lineages (e.g. Ratitae, Gastornithidae, Dromornithidae, Sphenisciformes, Teratornithidae) include taxa whose mass exceeds 30 kg [2]. Small size predominated during the first 70 Ma or so of avian history [3]: of the more than 100 Mesozoic bird taxa currently known, only one (*Gargantuavis philoinos*) [4] appears to have been large-bodied, and the avian identity of this taxon has recently been debated [5,6].

In this paper, we augment the Mesozoic fossil record of birds significantly by describing the remains of a huge avian from the Cretaceous of Kazakhstan, an undisputed giant.

2. SYSTEMATIC PALAEOLOGY

Theropoda Marsh 1881

Aves Linnaeus 1758

Ornithuromorpha Chiappe *et al.* 1999

Samrukia nessovi gen. et sp. nov.

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(a) Etymology

Samruk, the mythological Kazakh Phoenix, and *nessovi* for Lev Nessov (1947–1995).

(b) Holotype

WDC (Wyoming Dinosaur Center, Thermopolis, USA) Kz-001 (figure 1; see the electronic supplementary material for additional information).

(c) Locality and horizon

Santonian–Campanian Bostobynskaya Formation (Bostobe Svita), Akkurgan (Kyzylorda District), southern Kazakhstan (figure 2). This is the type locality for the non-diagnostic hadrosaurid *Arstansaurus akkurganensis* Suslov & Shilin 1982; a continental vertebrate assemblage is known from these sediments [7,8].

(d) Diagnosis

Large size (mandibular length >275 mm) and presence of a deep mediodorsal sulcus in the post-dentary region are autapomorphies of *Samrukia nessovi*. An additional potential autapomorphy revealed by our phylogenetic analysis is the presence of a prominent and raised anterior margin of the mandibular cotyla.

3. DESCRIPTION

The more complete mandibular ramus of this giant bird measures 275 mm (figure 1). Both rami are edentulous, with alveoli absent, and are shallowest posteriorly; the ventral margins of both rami are straight in lateral view. Sutures cannot be discerned: extensive fusion of mandibular bones is characteristic of Aves [9,10]; it is present in some oviraptorosaurs but is otherwise not typical for non-avian theropods. Mandibular fenestrae are absent in *Samrukia* (figure 1) and the shallow concavities on the lateral and medial surfaces represent breakage. Elsewhere within Theropoda, mandibular fenestrae are absent in compsognathids but are otherwise ubiquitous in non-avian theropods and only absent in certain avian lineages [9–11] (see the electronic supplementary material).

A deep mediodorsal sulcus extends from just anterior to the mandibular cotyle to a quarter of the way along the mandible (figure 1). Posteriorly, the floor of the sulcus forms a lamina that extends to the medial cotyle. As no similar structure has been reported within Theropoda, this is an autapomorphy. A more anteriorly positioned Meckel's groove is present ventrally: its dorsal and ventral margins are parallel. The splenial is not preserved and the ventral margins of both rami are straight in lateral view.

A transversely narrow ridge extends along the dorsal margin of each ramus to the start of the mediodorsal sulcus. Posteriorly, the ridges merge into each ramus to form wider, convex edges to the jaws. These terminate posteriorly at flattened vertical faces that form the anterior borders of the complex mandibular cotyle. Two obliquely oriented cotyla are present. The medial cotyle is positioned more posteriorly than the lateral cotyle and an anteromedially oriented ridge separates the two. A dorsally flattened flange projects medially from the medial cotyle. Immediately posterior to the medial cotyle, a large oval pneumatic foramen

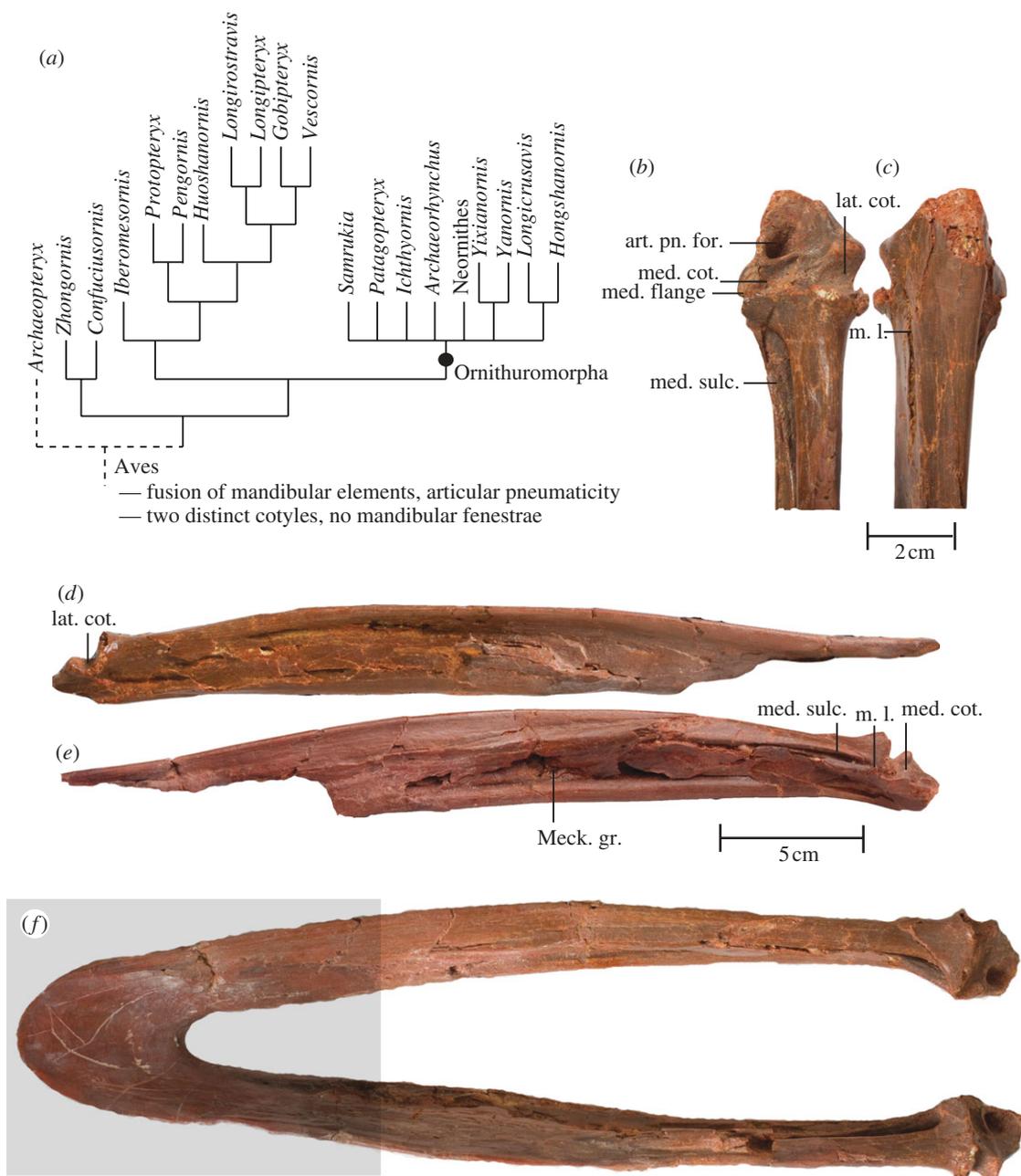


Figure 1. *Samrukia nessovi*, gen. et sp. nov. (a) Summary phylogenetic topology (based on the strict consensus tree, of 24 shortest trees). Our global analysis is one of the first to hypothesize *Archaeopteryx* as a basal member of Paraves, although these inter-relationships are condensed here for brevity using a dotted line (see the electronic supplementary material for complete tree, names of nodes and details of analysis). MPT length, 3888 steps; consistency index (CI) excluding uninformative characters, 0.3187; retention index (RI), 0.5810. (b–f), Holotype Wyoming Dinosaur Centre, Thermopolis, USA (WDC Kz-001), posterior portion of left mandibular ramus, in (b) dorsal and (c) ventral views, and right ramus in (d) lateral and (e) medial views. (f) Dorsal view of both rami, with area of specimen originally reconstructed in plaster and painted (photographed before preparation) inset in grey. Area of specimen originally reconstructed in plaster and painted (photographed before preparation) is inset in grey. Abbreviations: art. pn. for., articular pneumatic foramen; lat. cot., lateral cotyle; Meck. gr., Meckel's groove; med. cot., medial cotyle; med. flange, medial flange; med. sulc., medial sulcus; m. l., medial lamina.

(6 mm wide and 5 mm long) invades the articular region, as in *Ichthyornis* and *Neornithes* [9,10].

It is likely (although not certain) that dentary teeth were entirely absent in *Samrukia*. However, teeth are retained only in the symphyseal regions of some other Mesozoic birds (such as *Jeholornis prima*), so it remains possible that *Samrukia* possessed a small number of teeth at least at the tip of the lower jaw. The new Kazakh bird differs substantially from other clades with edentulous jaws (Testudines, Pterosauria,

Ceratosauria, Ornithomimosauria and Oviraptorosauria), lacking the derived characters present in their mandibular rami. Furthermore, it possesses a suite of characters unique to Aves.

4. PHYLOGENETIC ANALYSIS

We coded WDC Kz-001 into a phylogenetic analysis that encompasses the whole of Theropoda (see figure 1 and the electronic supplementary material [11–20]);



Figure 2. Map of the Republic of Kazakhstan showing the location of Akkurgan (star). Sites in southern Kazakhstan well known for yielding Cretaceous terrestrial vertebrates include the nearby Shakh-Shakh (*ca* 200 km from Akkurgan) and the more southerly Kyrk-Kuduk and Syuk-Syuk. See Malakhov *et al.* [7] for more details.

the results indicate that *Samrukia* is nested deeply within Aves at the base of Ornithuromorpha (*sensu* Chiappe & Witmer [9]), unresolved alongside *Patagopteryx*, *Ichthyornis*, *Archaeorhynchus*, the *Yixianornis* + *Yanornis* clade, Hongshanornithidae and Neornithes (figure 1). A series of derived characters, revealed by our analysis (i.e. two distinct mandibular cotyles, fusion of mandibular elements and absence of mandibular fenestrae) place *Samrukia* deep within Aves (figure 1) [9,10] and suggest that this taxon is not closely related to any of the modern bird lineages that evolved large size during the Cenozoic. All other known taxa within this region of the tree are relatively small (body size <2 kg and with mandibles *ca* 100 mm long or less) [3,9,21].

5. DISCUSSION

The discovery of *Samrukia* expands our extremely limited knowledge of Cretaceous Central Asian birds: only the hesperornithine *Asiahesperornis bashanovi* (Kazakhstan) and indeterminate avian fragments (Uzbekistan) have otherwise been described [22,23]. Despite this paucity of fossil evidence, it is now clear that at least three major avian lineages [7,8,22,23] were present in Central Asia at this time. These lineages, all well removed from Neornithes, reveal a pattern in Central Asia common to numerous contemporaneous sites worldwide, supporting the contention that neornithines were extremely rare and/or restricted in their distributions during the Late Cretaceous [24,25].

The enormous size of *Samrukia* is also highly significant: we suggest that this giant bird was at least similarly sized to a large albatross if flighted, or to a large ratite (e.g. *Struthio*) if flightless. Clearly, we are unable to provide a reliable mass estimate for *Samrukia*, but assume that any bird of this size would weigh 12 kg at absolute minimum and almost certainly much more (greater than 50 kg) if flightless (based on

the masses of the flighted *Diomedea exulans* and the flightless *Struthio camelus* where mandible length in both is *ca* 260 mm) [2]. Only one other comparably sized, putative, Mesozoic bird has been reported: *Gargantuavis philoinos* from the Campanian or Maastrichtian of France, known from a synsacrum and referred femur [4]. Because cranial material is unknown for *Gargantuavis*, we are unable to test the possibility that *Gargantuavis* and *Samrukia* might be close relatives. This is conceivable, but the restriction of *Gargantuavis* to a younger, western European fauna with no close biogeographic ties to the Santonian–Campanian of Central Asia renders it unlikely that *Gargantuavis* and *Samrukia* are congeneric. We also note that the avian status of *Gargantuavis* has been debated [5,6], making *Samrukia* the only certain giant Mesozoic avian. *Samrukia* therefore confirms that body size evolution was more diverse within Mesozoic birds than has long been assumed [3,26]. Furthermore, *Samrukia* is a reminder that there was ‘ecospace’ in the Mesozoic for large terrestrial animals in addition to non-avian dinosaurs.

Furthermore, gigantism in birds well removed from modern lineages demonstrates that neornithines were not unique in evolving large body size and, potentially, large wingspans. This is significant as it weakens the argument that survivorship of neornithines across the K–Pg boundary (and the concomitant extinction of contemporary enantiornithine and basal lineages) somehow reflects the greater morphological diversity and ecological adaptability of this lineage. *Samrukia* shows that large body size was not unique to Neornithes, and in fact evolved far earlier in the Mesozoic than previously recognized.

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