The changing face of birds from the Age of Dinosaurs

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The origin of the modern bird skull from dinosaurian ancestors can be traced in the fossil record. The discovery of a bizarre new fossil bird reveals a surprising diversion during this transformation.

As living dinosaurs, birds are the product of a long and complex evolutionary history that has given rise to over 11,000 living species[1]. Recent years have witnessed a surge of interest in the evolution of the avian skull—a structure that is hugely variable across living bird diversity[2]. However, without incorporating fossils into evolutionary models, we are limited in our ability to test hypotheses of how, and when, key transformations in the history of the avian skull have taken place. On page XX[3], by revealing a stunning new fossil bird discovery from the Age of Dinosaurs, O'Connor et al. remind us of the critical value of fossils for casting light on unforeseeable complexities in the evolutionary history of the avian skull.

This bizarre new addition to the Mesozoic aviary comes from the Late Cretaceous of Madagascar, and is named *Falcatakely forsterae*, translating roughly to 'Forster's small scythebeak.' The name references the distinctive morphology of the fossil's bill, and honours Prof. Catherine Forster's numerous contributions to vertebrate palaeontology in Madagascar. The specimen is small and delicate, yet the stunning preservation of the bones allow us a spectacular look at the anatomy of this roughly-70-million-year-old beast.

Although the new fossil is only represented by the front half of a skull, it's clear that *Falcatakely* is more than just a pretty face. The skull is utterly bizarre, characterized by a very deep and elongate snout unlike those seen in any other Mesozoic birds. The skull's architecture gets even weirder: it preserves three small teeth at the very tip of the snout, but teeth are found nowhere else along its jaws. By contrast, the closest relatives of modern birds from the Age of Dinosaurs show the opposite pattern, with teeth found throughout the jaws *except* at the very tip of the bill[4]. These features give the skull of *Falcatakely* an almost comical profile—imagine a creature resembling a tiny, buck-toothed toucan flitting from branch to branch, occasionally glancing down at Madagascar's formidable Late Cretaceous inhabitants, which included equally bizarre mammals[5] and giant predatory dinosaurs[6]. Despite the present-day recognition of approximately 200 Mesozoic bird species from around the world[7], none have a skull resembling anything like that of *Falcatakely*—its discovery probes morphological space previously unbroached by any known bird from the Age of Dinosaurs.

In addition to the unusual proportions of its snout, the exceptional degree of preservation of *Falcatakely* reveals more surprises. O'Connor et al.[3] gathered high-resolution microCT scans of the specimen in order to digitally 'extract' the fragile skull bones from the surrounding rock matrix. This allowed the team to reassemble the delicate components of the bill, including rarely-preserved elements like the paper-thin palate bones, into a compelling 3D model (see their video illustrating this process **here**). Studying the palate, the authors recognised the presence of a surprising ossification, called the 'ectopterygoid'. This bone has been lost in living birds, but is a component of the palate of non-avian dinosaurs and early bird-like forms, such as *Archaeopteryx* and *Sapeornis*[8]. However, on the basis of several detailed analyses, O'Connor et al.[3] have inferred that *Falcatakely* belongs to a group of Mesozoic 'pre-modern' birds called Enantiornithes (hereafter 'Opposite Birds' for simplicity), which occupy a branch of the dinosaur family tree much closer to modern birds than do either *Archaeopteryx* or *Sapeornis*. While the presence of an ectopterygoid in Opposite Birds has been previously suggested[9], this identification have been questioned in recent years[10]. Thus, the recognition of an ectopterygoid in *Falcatakely* either shows that this ancestral component of the palate was retained in Opposite Birds—and thus at a surprisingly late stage in avian evolutionary history—or it may challenge the identification of *Falcatakely* as an Opposite Bird, suggesting instead that it belongs on an earlier-diverging branch of the Mesozoic bird family tree.

Although it is impossible to definitively delineate between these two options without the discovery of additional fossil material, O'Connor et al.[3] grapple with this uncertainty to an impressively thorough degree, illustrating that *Falcatakely* 'nests' with Opposite Birds under a range of alternative analytical approaches. In addition, the identification of *Falcatakely* as an Opposite Bird jibes with the previous recognition of fragmentary Opposite Bird bones from the same Madagascan fossil locality[11]. Nonetheless, recent work has emphasized that family tree reconstructions of dinosaurs may return conflicting results when skulls, instead of complete skeletons, are analysed[12]. This lack of certainty will provide all the more reason for the field team to continue their productive work in future years in hopes of discovering more complete material.

Over the last several years it has become increasingly apparent that the end of the Cretaceous was a pivotal interval in avian evolutionary history, with the earliest events in the evolution of modern birds taking place[13]. The discovery of *Falcatakely* shows us that the importance of this interval for bird evolution extends well beyond the origin of modern birds, with 'pre-modern' bird lineages such as Opposite Birds experimenting with bold new morphologies—and possibly novel ecologies—well into the terminal stages of the Cretaceous, immediately preceding their global demise along with all other dinosaurs outside of modern birds themselves[14]. Considering the impressive diversity and global distribution of Opposite Birds in the Late Cretaceous, determining why they disappeared in the end-Cretaceous mass extinction, while the earliest modern bird lineages survived, remains one of the greatest mysteries in avian palaeobiology. The answers to such questions, much like the unforeseeable anatomy of creatures like *Falcatakely*, can only be revealed by evidence from the fossil record. So, let's get digging.

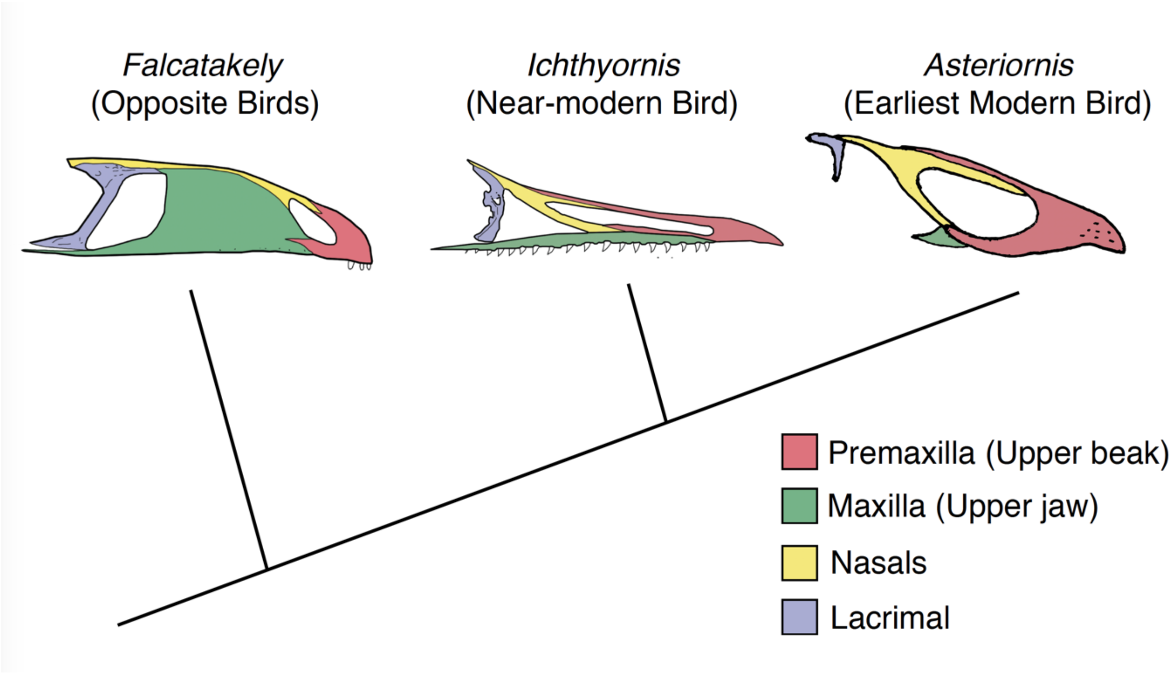

Figure 1 | The changing face of Mesozoic birds. Recent discoveries of bird skulls from the Age of Dinosaurs have illustrated both the surprising variability of ancient bird skulls, as well as how the skull of modern birds arose. O'Connor et al.[3] describe the skull of *Falcatakely*, which shows an unusually deep and elongate snout, with teeth positioned only at the very tip of the upper jaw. Like other distant relatives of modern birds, the upper jaw of *Falcatakely* is composed mainly of the maxilla (green). Closer relatives of modern birds like *Ichthyornis*[4] exhibit teeth throughout the jaws, except at the tip, while retaining the ancestrally large maxilla. Modern birds, like the recently discovered *Asteriornis*[13], have completely lost their teeth, and have upper jaws dominated by the premaxilla (red). (Adapted from Fig. 2 of ref. 3, Fig. 3 of ref. 4, and Fig. 1 of ref. 14).

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1 *All the Birds of the World*. (Lynx Edicions, 2020).

2 Felice, R. N. & Goswami, A. Developmental origins of mosaic evolution in the avian cranium. *Proceedings of the National Academy of Sciences* **115**, 555-560, doi:10.1073/pnas.1716437115 (2018).

3 O’Connor, P. M. *et al.* Late Cretaceous bird from Madagascar reveals novel development of beaks. *Nature* (2020).
4 Field, D. J. *et al.* Complete *Ichthyornis* skull illuminates mosaic assembly of the avian head. *Nature* **557**, 96-100, doi:10.1038/s41586-018-0053-y (2018).
5 Krause, D. W. *et al.* First cranial remains of a gondwanatherian mammal reveal remarkable mosaicism. *Nature* **515**, 512-517 (2014).
6 Lavocat, R. Sur une portion de mandibule de Théropode provenant du Crétacé supérieur de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle* **27**, 256-259 (1955).
7 Pittman, M. *et al.* in *Pennaraptoran theropod dinosaurs: past progress and new frontiers* Vol. 440 (eds M. Pittman & X. Xing) 37-95 (Bulletin of the American Museum of Natural History, 2020).
8 Hu, H. *et al.* Evolution of the vomer and its implications for cranial kinesis in Paraves. *Proceedings of the National Academy of Sciences* **116**, 19571-19578 (2019).
9 Elzanowski, A. Cretaceous birds and avian phylogeny. *Courier Forschungsinstitut Senckenberg* **181**, 37-53 (1995).
10 Mayr, G. *Avian evolution: the fossil record of birds and its paleobiological significance*. (John Wiley & Sons, 2016).
11 O’Connor, P. M. & Forster, C. A. A Late Cretaceous (Maastrichtian) avifauna from the Maevarano Formation, Madagascar. *Journal of Vertebrate Paleontology* **30**, 1178-1201 (2010).
12 Li, Y., Ruta, M. & Wills, M. A. Craniodental and postcranial characters of non-avian Dinosauria often imply different trees. *Systematic biology* **69**, 638-659 (2020).
13 Field, D. J., Benito, J., Chen, A., Jagt, J. W. M. & Ksepka, D. T. Late Cretaceous neornithine from Europe illuminates the origins of crown birds. *Nature* **579**, 397-401, doi:10.1038/s41586-020-2096-0 (2020).
14 Longrich, N. R., Tokaryk, T. & Field, D. J. Mass extinction of birds at the Cretaceous-Paleogene (K-Pg) boundary. *Proceedings of the National Academy of Sciences* **108**, 15253-15257 (2011).