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Research Highlight

Mosaic evolution in birds: Brain vs. feeding apparatus

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Tracing the evolutionary sequence of major characteristics among various groups of organisms, and deciphering the interaction between the pattern of development and function of major biological structures are among the primary tasks in evolutionary biology. In this regard, recent significant advances have been made in bird evolution, but controversial issues and an incomplete understanding of avian evolution still remain [1,2]. In the May 3, 2018 issue of *Nature*, Field and colleagues present novel observations of a historically significant species, *Ichthyornis dispar* [3], and some of their data are unexpected and promise to change the story of the evolution of the bird head (Fig. 1).

Ichthyornis was the first bird known to have had teeth [4], providing straightforward evidence linking toothed reptiles and beaked birds, and its evolutionary significance was quickly recognized by Charles Darwin a few years after the publication of *On the Origin of Species* [5]. For nearly 100 years, the volant *Ichthyornis* along with the flightless diving *Hesperornis* were the major sources of information about early avian evolution. It has only been in the last few decades when a burst of discoveries of new Mesozoic bird fossils and localities around the world (particularly in China) [6], which seem to diminish the significance and role of *Ichthyornis* and other iconic historically known species in the study of avian evolution. However, *Ichthyornis* remains a pivotal player in the study of avian evolution for several reasons, including some related to its phylogenetic position and fossil preservation.

Some of the current significant problems pertaining to early bird evolution relate to the relatively poor sampling of extinct close relatives of crown-group birds and the two-dimensional preservation of many Mesozoic bird fossils [3]. Those factors hinder our understanding of some key evolutionary stages and of the evolutionary origin of some major structures. As a taxon that is among the closest relatives of modern birds and represented by three-dimensionally preserved fossils, *Ichthyornis* has the potential to help resolve some major issues. Utilizing both historical museum collections and newly discovered material of *Ichthyornis*, Field and colleagues have composed the most complete reconstruction of any Mesozoic bird skull using high-resolution computed tomography, that provides important new data and insight into the saga of the evolution of the bird head [3].

Two major avian cranial innovations are the edentulous feeding apparatus (i.e., the beak or bill that is used for feeding, preening, and other functions), and the enlarged brain that is key to aerial (and aquatic) locomotion and the diversity of song, behavior, and cognitive function we see among living birds. The new reconstruction demonstrates that *Ichthyornis* has an essentially modern avian brain, as indicated by the enlarged and posteroventrally rotated forebrain, and inflated and laterally shifted optic lobes [3]. Similarly, the feeding apparatus of *Ichthyornis* has many derived features. The new data from *Ichthyornis*, in combination with the results from morphological analysis of the cranial rostrum of selected key avian taxa, including some recently discovered ones [7], indicates that a transitional beak already had evolved in early-branching ornithurine birds [3]. Furthermore, morphological features associated with a fully functional bird cranial kinetic system, including mobile connections between various cranial bones, are all present in *Ichthyornis*, and indicate that a modern-form feeding apparatus evolved earlier than previously thought [3].

However, the feeding apparatus of *Ichthyornis* retains some unexpected plesiomorphic features. For example, it has a large tooth-bearing maxillary bone absent among extant birds. Most strikingly, *Ichthyornis* has a plesiomorphic dinosaurian temporal region wherein it has a large upper temporal fenestra, though perhaps just as a remnant. That fossa is indicated by the presence of a nearly complete upper temporal bar formed by a large postorbital ossification and a deinonychosaur-like squamosal peripheral to the braincase. Together with several other features, the morphology of the temporal region suggests the presence of well-developed jaw adductor muscles in *Ichthyornis* [3].

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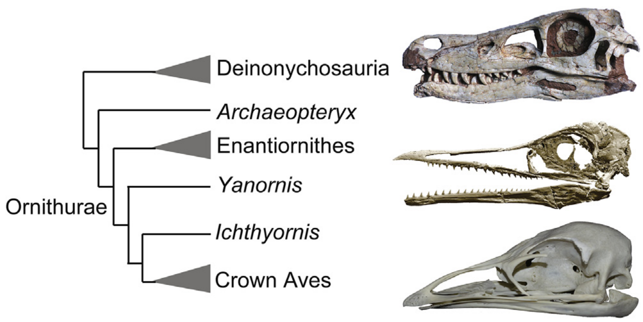

Fig. 1. A simplified avialan phylogeny showing several evolutionary stages for head evolution. Skull and mandible in left lateral view of the deinonychosaurian *Linheraptor exquisitus* (top), the early-branching ornithurine *Ichthyornis dispar* (middle), and the crown-group bird *Dromaius novaehollandiae* (bottom).

It is not surprising to see that the brain of *Ichthyornis* evolved faster than the feeding apparatus, and that birds acquired a modern brain earlier than a modern feeding apparatus. However, to see a nearly diapsid temporal configuration retained in *Ichthyornis*, as a close relative of modern birds, is surprising, given that feeding apparatus is among the most varied structures among living birds. Furthermore, presence of a nearly diapsid condition musculatory system in a large-brained bird is in conflict with the prediction from development models that the enlargement of the avian brain drove jaw adductor muscle reduction, as the result of spatial restriction [8]. In this macroevolutionary scenario with *Ichthyornis*, it appears we can reject that hypothesis for the loss of the diapsid condition in birds and its related reduction in musculature.

It is not known why birds took longer to evolve the modern-type feeding apparatus, relative to their faster acquisition of modern brain components, but the relationship of the brain to selection in favor of modern flight capability in *Ichthyornis* and more crownward birds [3] may be the source. However, it should be noted that the mosaic pattern of evolution demonstrated here is not fully modular with the relatively slowly evolving feeding apparatus of *Ichthyornis* exhibiting features such as a (partial) beak and a fully functional cranial kinetic system seen in modern birds.

Conflict of interest

The author declares that he has no conflict of interest.

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