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Complexities and novelties in the early evolution of avian flight, as seen in the Mesozoic Yanliao and Jehol Biotas of Northeast China

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Abstract

Recently reported specimens from the Mid-Late Jurassic Yanliao (or Daohugou) Biota and Early Cretaceous Jehol Biota of Northeast China suggest that the early evolution of avian flight involved a surprising amount of homoplasy and evolutionary experimentation. Pennaceous feathers of variable size, structure, and extent occur on the hindlimbs of numerous Jehol and Yanliao paravian theropods, including some basal birds, and clearly had an aerodynamic function at least in the dromaeosaurid *Microraptor*. However, their function in many cases may have been primarily ornamental, and it is unclear whether aerodynamically useful hindwings represent a widespread paravian feature or an evolutionary novelty limited to *Microraptor* and possibly a few other taxa. Clearer examples of novelties related to aerial locomotion are the tail plumage of the basal bird *Jeholornis*, in which a proximal fan of feathers is present and the ancestral distal frond is somewhat reduced, and the membranous wings of the Yanliao scansoriopterygid *Yi*. Early paravian evolution evidently involved a rapid diversification of aerodynamic structures, and ancestral paravians may have been volant. It is also possible that the avian lineage passed through a four-winged "tetrapterygian" stage, but current phylogenies suggest that aerodynamic hindwings were more likely acquired independently by different paravian groups.

Keywords: Theropoda; Paraves; Aves; Flight; Feathers; Mesozoic

1. Introduction

Archaeopteryx, from the Upper Jurassic Solnhofen Limestone of Bavaria, has been central to discussions of avian origins since first being reported by Meyer (1861). Until almost the end of the 20th century, the iconic Urvogel was in fact the only known taxon recognised as being close to the emergence of birds, leading Ostrom (1976, p. 93) to assert that "*Archaeopteryx* holds the key to bird origins". On the basis of careful comparisons between *Archaeopteryx* and other reptiles, he built a persuasive case that birds were descended from among small non-avian theropod dinosaurs (Ostrom, 1973, 1975, 1976).

Dromaeosaurids and troodontids, groups classified together as the Deinonychosauria, were subsequently identified as particularly close relatives of birds (Currie, 1985, 1987; Padian, 1985; Gauthier, 1986). However, the dromaeosaurids and troodontids that were known in the 1980s have emerged in recent phylogenetic analyses (Xu et al., 2011; Turner et al., 2012; Agnolín and Novas, 2013; Godefroit et al., 2013a, 2013b; Brusatte et al., 2014; Lee et al., 2014; Tsuihiji et al., 2014; Cau et al., 2015) as relatively derived members of their respective lineages, and most of them date from the Late Cretaceous. Similarly, the roster of Mesozoic birds known at the time was limited, apart from *Archaeopteryx* itself, to a handful of taxa that current avian phylogenies (M. Wang et al., 2014; X.L. Wang et al., 2014; O'Connor et al., 2016) place within the derived clade Ornithothoraces. Furthermore, *Archaeopteryx* stood alone as the only Mesozoic theropod with reasonably well-preserved plumage. As a result, the ability of other taxa to shed light

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on either the origin of avian flight or morphological evolution during the transition to birds was limited, although some information could be gleaned from articular surface geometries, limb bone proportions, and other skeletal features. This relative paucity of data made the transition difficult to study, and also encouraged simple and linear hypothetical reconstructions of how various characteristics might have evolved on the line to birds. For example, Padian (1985) argued that the pattern of mobility in the joints of the deinonychosaur forelimb had been co-opted with minimal change to serve the needs of flapping flight, and Jenkins (1993) used the morphology of the shoulder joint in *Deinonychus*, *Archaeopteryx*, and modern birds as the basis for inferring a gradual change in the orientation of the glenoid fossa from ventral to dorsolateral.

Beginning in the mid-1990s, scientific understanding of the origin of birds was transformed by a wealth of new fossil evidence, particularly from western Liaoning Province and adjacent parts of Northeast China. In this region the Yixian and Jiufotang Formations of the Lower Cretaceous Jehol Group began to yield basal (i.e., non-ornithothoracine) birds (Hou et al., 1995; Chiappe et al., 1999) and enantiornithines (Sereno and Rao, 1992; Zhou et al., 1992; Zhou, 1995), along with compsognathid (Ji and Ji, 1996; Chen et al., 1998), therizinosaurian (Xu et al., 1999a), oviraptorosaurian (Ji et al., 1998), and dromaeosaurid (Xu et al., 1999b) non-avian theropods. These specimens often comprised complete, articulated skeletons accompanied by preserved feathers, in keeping with the exceptional taphonomy of the Jehol Biota (Zhou et al., 2003). The presence of filamentous feathers in the basal therizinosaurian *Beipiaosaurus* (Xu et al., 1999a) and even the compsognathid *Sinosauropteryx* (Chen et al., 1998) not only provided powerful support for the theropod hypothesis of avian origins, but showed that rudimentary feathers first appeared in theropods that were phylogenetically remote from the origin of birds and clearly incapable of flight. Furthermore, the equally non-volant basal oviraptorosaurs *Caudipteryx* and *Protarchaeopteryx* both sported pennaceous feathers comparable to those of extant birds (Ji et al., 1998), with a central rachis flanked by vanes composed of parallel barbs. Notwithstanding suggestions that oviraptorosaurs should be regarded as secondarily flightless birds (Jones et al., 2000; Maryańska et al., 2002), the most straightforward and plausible interpretation of the evidence was that pennaceous feathers appeared prior to the origin of flight and were subsequently exapted for aerodynamic purposes.

In the current millennium, the Jehol Biota has continued to produce both avian and non-avian theropods, with the known count now exceeding sixty species (Zhou and Wang, 2010). Furthermore, an older assemblage also from Northeast China and characterised by similar exceptional preservation, the Mid-Late Jurassic Yanliao Biota, was discovered by local farmers in 1998 (Sullivan et al., 2014). The Yanliao Biota contains several non-avian theropods, although no unequivocal avians have so far come to light. The Yanliao Biota resembles the Jehol Biota in encompassing faunas and floras that existed over a period of millions of years, and can be partitioned into a slightly older Daohugou Biota and slightly younger Linglongta Biota (Huang, 2015). However, the term "Daohugou Biota" has also been used to refer to the Yanliao Biota as a whole (Sullivan et al., 2014).

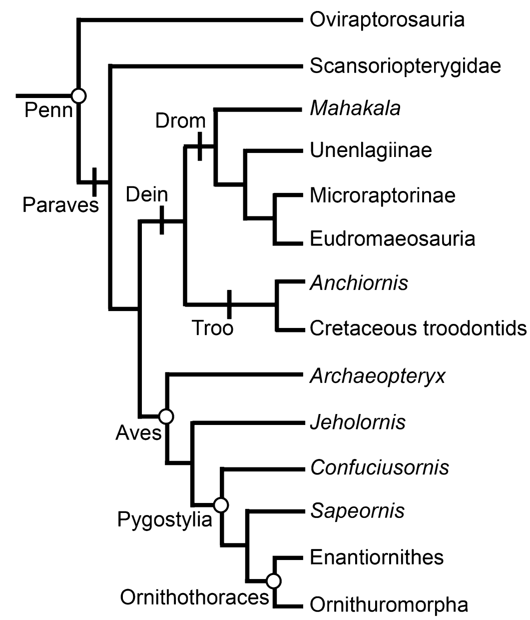

Fig. 1. Simplified phylogenetic relationships of pennaraptoran theropods, based on informal consensus of selected recently published cladograms (Turner et al., 2012; Xu et al., 2015; O'Connor et al., 2016). Vertical bars identify stem-based clades, and open circles identify node-based clades. Several plausible alternative arrangements exist, but this single phylogenetic hypothesis is presented for simplicity. Abbreviations: Dein, Deinonychosauria; Drom, Dromaeosauridae; Penn, Pennaraptora; Troo, Troodontidae.

Crucially, many of the birds from the Jehol Biota are non-ornithothoracines, and some resemble *Archaeopteryx* in retaining long bony tails. Among non-avian theropods, some of the species from the Jehol Biota and all of those known from the Yanliao Biota represent relatively basal members of major branches within Pennaraptora, the clade that is primitively characterised by the presence of pennaceous feathers and contains avians (avialans of many authors) alongside oviraptorosaurs, scansoriopterygids, and deinonychosaurs (Fig. 1). Accordingly, the two biotas provide abundant information on the osteology and plumage of both avian and non-avian theropods that are extremely close in evolutionary terms to the origin of birds. *Archaeopteryx* is no longer an isolated transitional form, but stands firmly embedded in a well-documented radiation of early pennaraptorans that spanned the Late Jurassic and Early Cretaceous.

The new finds from Northeast China, together with other recent discoveries from such places as Madagascar (Forster et al., 1998), Spain (Sanz et al., 1996), and Argentina (Novas and Puerta, 1997; Makovicky et al., 2005; Novas and Pol, 2005) have provided abundant new information about both the diversity of Mesozoic pennaraptorans and the origin of flight, clarifying some issues and inevitably complicating others. One clear conclusion to have emerged during approximately the last decade of research is that at least some non-avian members of Paraves, the clade including deinonychosaurs and birds, were equipped for controlled gliding if not for powered flight. Several Yanliao and Jehol taxa, including the possible troodontid *Anchiornis* (Hu