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Research Highlight

Feather evolution: looking up close and through deep time

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The last two decades have witnessed significant advances in our understanding of the evolution of major avian characteristics [1–6]. In particular, the spectacular discoveries of fossilized feathered dinosaurs from China and elsewhere have provided key insights into feather evolution [1,2]. These fossils indicate that many non-avialan dinosaurs were feathered animals just like living birds, and when we map the different types of feathers present in various dinosaurs onto their phylogeny, we see a clear evolutionary trend of increasing morphological complexity towards the origin of birds, with even highly specialized asymmetrical flight feathers having evolved before the first birds [2]. Even with these significant new fossils and associated data, important issues such as when the first feathers evolved [7] and the microscopic composition of early feathers [8] remain unclear (Fig. 1), although two recent studies provide new information on these issues [9,10].

The first study, published in *Nature Ecology and Evolution* by Yang et al. [9], presents unexpected new data relevant to the evolution of the earliest feathers. Although numerous feathered dinosaur fossils have been discovered over the last twenty years, they are mostly restricted to the clade Tetanurae [2] (a major theropod sub-group within which birds are deeply nested), suggesting that feathers originated within theropod dinosaurs. However, there are a few dinosaur species outside of Tetanurae that preserve simple, mono-filamentous integumentary structures, which have been interpreted as the first feathers [2]. Similar structures also are known in several species of pterosaurs, a group of flying reptiles closely related to dinosaurs, raising the possibility of a deep origin for feathers (Fig. 1). In other words, the first feathers might have evolved in the most recent common ancestor of dinosaurs and pterosaurs during the Early Triassic [2], but, this hypothesis has not been examined in depth for various reasons.

However, Yang et al. [9] present new evidence suggesting that we need to seriously consider the possibility of an early evolutionary origin of feathers. The most compelling evidence presented in their study is that the filamentous integumentary structures preserved in two pterosaur fossils display one key defining feature of feathers: feather-like branching. Some fossilized integumentary structures in these pterosaur specimens are composed of multiple filaments joined at their base, and some comprise multiple filaments attaching to a central filament. Those morphologies suggest the presence of barbs and a rachis (main components of a feather) outside of Dinosauria. Furthermore, the authors have demonstrated that these pterosaur filamentous integumentary structures likely represent the first feathers from a phylogenetic perspective as well, thus supporting the deep-origin hypothesis for the evolution of feathers.

The conclusions from the second study, which was published by Pan et al. [10] in the February 19, 2019 issue of *Proceedings of the National Academy of Sciences of the United States of America*, are even more unexpected. Pan et al. [10] examined the ultrastructure and molecular composition of fossil feathers and claw sheaths of several non-avialan dinosaurs and early birds by using scanning electronic microscope (SEM), transmission electronic microscope (TEM), and immunohistochemistry methods. Surprisingly, they find that: (1) the simple filamentous structures of *Shuvuuia*, an early-diverging maniraptoran theropod, lack feather β-keratins; (2) the pennaceous feathers of *Anchiornis* (either an early-diverging deinonychosaurian theropod or an early-diverging avialan) are formed mainly by α-keratins with only a small proportion of feather β-keratins. This second result is truly unexpected given that *Anchiornis* feathers are pennaceous and nearly identical in general morphology to the flight feathers present in modern birds, which are dominated in composition by β-keratins. The dominance of β-keratins in flight feathers adds structural rigidity. Nevertheless, this result led these authors to suggest that *Anchiornis* feathers lack some molecular characteristics of modern feathers, potentially required for powered flight.

If confirmed, the results derived from these two studies will significantly advance or even revolutionize our knowledge of feather evolution. However, there are challenges to both studies. For example, while the primary homology (based on morphological criteria) of the filamentous structures in pterosaurs and dinosaurs can be established, the secondary homology of these structures (i.e., being derived from a single phylogenetic origin) will be doomed to controversy, given the extremely patchy fossil records of integumentary structures among dinosaurs and pterosaurs. Some of those fossils indicate the possibly extremely restricted distribution of feather-like structures on the body of some species, highlighted by the horned dinosaur *Psittacosaurus*, and they suggest that some otherwise scaled dinosaurs, such as stegosaurs and ankylosaurs, may have had feathers or feather-like structures

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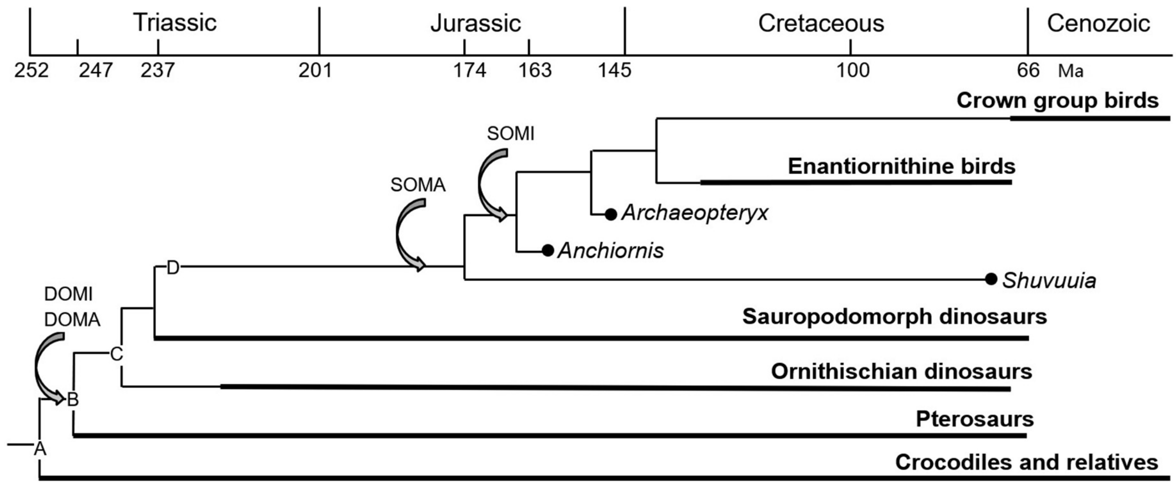

Fig. 1. Time-calibrated archosaurian phylogeny showing different evolutionary scenarios for feathers in both macroscopic or microscopic levels. At the macro-level, feather-like structures (filamentous and branching morphologies) evolved independently in pterosaurs, ornithischian dinosaurs, and theropod dinosaurs, and true feathers originated within the Theropoda (shallow-origin hypothesis). Alternatively, feathers have a single phylogenetic origin at the most recent common ancestor of dinosaurs and pterosaurs (deep-origin hypothesis). At the micro-level, feather β-keratins originated in the first pennaraptoran theropod; or alternatively, feather β-keratins evolved early in archosaurian evolution, associated with the appearance of simple filamentous feathers. Abbreviations: A, Archosauria; B: Avemetatarsalia (the dinosaurs + pterosaurs clade); C, Dinosauria; D, Theropoda; DOMA, deep origin at macro-level; DOMI, deep origin at micro-level; SOMA, shallow origin at macro-level; SOMI, shallow origin at micro-level.

(only) on certain parts of their bodies. In that situation, the absence of (preserved) feathers in these dinosaurs could be the result of taphonomy or incomplete fossil preservation. Thus, the combination of a patchy fossil record and patchy preservation of feathers in a fossil specimen makes the confirmation of the secondary homology of feather-like structures in different groups outside of Tetanurae extremely difficult.

The second study by Pan et al. [10] will face even more challenges. The dominance of α-keratins in the feathers of *Anchiornis* is unusual because the same study indicates that other fossil feathers from both non-avialan theropod dinosaurs and early birds, and even the fossil claw sheath of earlier-branching theropods are dominated instead by β-keratins. However, the main ultrastructural components of *Anchiornis* feathers are thick filaments, unlike the thin and short ones in other fossil and modern feathers, and therefore are consistent with this chemical interpretation. The absence of feather β-keratins in *Shuvuuia* also is unusual given that even some non-feather integumentary structures in extant archosaurs have feather β-keratins [11,12]. The identifications of fossil keratins are based on immunohistochemical methods, and application of this methodology in fossils recently has been questioned [13], possibly leading to further scientific debate.

Do feathers have a deep origin in archosaurian phylogeny and evolution? Did feathers really evolve differently at the macroscopic and microscopic/molecular levels? The available evidence seems to provide affirmative answers to both questions (Fig. 1), but more and better-preserved fossils, along with the application of new techniques and methods are needed to resolve these controversial questions about feathers, fibers, and flight.

Conflict of interest

The author declares that he has no conflict of interest.

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