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S06-3 The theropod origin of feathers: congruence between development, paleontology, and phylogeny

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Abstract Progress on the evolutionary origin of feathers has been hampered by conceptual problems and by the lack of primitive feather fossils. Recently, both limitations have been eliminated. A new developmental theory proposes that feathers evolved through a series of novelties in developmental mechanisms of the feather follicle and feather germ. Recent analyses of the integumental appendages of theropod dinosaurs from the early Cretaceous Liaoning formation of China (~124 million years ago) have confirmed that these integumentary structures share several unique features with avian feathers: multiple filament structure, branching at the base, and serial branching. In combination with robust phylogenetic evidence supporting the theropod origin of birds, the details confirm that these integumentary structures are homologous with avian feathers. The discovery of primitive and derived fossil feathers on a diversity of coelurosaurian theropod dinosaurs documents the evolution and diversification of feathers in non-avian theropods before the origin of birds and before the origin of flight. The morphologies of these primitive dinosaur feathers are exactly congruent with the predictions of the new developmental theory. The aerodynamic theory for the origin of feathers is falsified, but other proposed functions remain developmentally and phylogenetically plausible. Feathers are inherently tubular structures. Whatever their initial function, they evolved by selection for a follicle that would grow an emergent tubular appendage.

Key words Feather, Evolution, Theropod, Fossil

1 Introduction

Despite more than a century of research, the evolutionary origin of feathers has long remained a mystery (Prum and Brush, 2002). Progress was hampered by two long-standing problems: the lack of primitive, fossil feathers, and the limitations of conceptual models of feather evolution. The earliest and most basal bird fossil, *Archaeopteryx lithographica* from the Late Jurassic, exhibits entirely modern feathers that are indistinguishable from those of extant birds. So, traditionally, paleontology has contributed little so far to the debate on how feathers evolved. The conceptual problems arose largely from the adoption of inappropriate concepts of the primitive feather, for example the interpretation of feathers as elongate scales, as well as unproductive approaches to the study of macroevolution and speculative assumptions that feathers evolved for a specific function, such as flight.

These traditional problems have been eliminated by recent advances in the developmental biology of feathers (Prum, 1999; Harris et al., 2002), and by fortuitous discoveries of feathered, non-avian, theropod dinosaurs from the early Cretaceous Yixian formation of Liaoning, China, summarized in Prum and Brush (2002). Together, these studies document the origin and diversification of feathers within carnivorous, bipedal theropod dinosaurs before the origin of birds or the origin of flight.

2 The feather origin problem

The origin of feathers, conceptually, exemplifies the more fundamental questions raised by the origin of evolutionary novelties. Evolutionary novelties are derived structures that have no homologs, or antecedent structures, in ancestral or related organisms (Müller and Wagner, 1991). Evolutionary theory provides a robust understanding of the evolution of minor or continuous variations in organismal size and shape. But where do entirely novel structures, such as digits, limbs, eyes and feathers come from?

Understanding the evolutionary origin of feathers has been hampered by several common conceptual problems. First among these is the neo-Darwinian view of *macroevolution* as merely *microevolution* writ large. Since 1960s, biologists have theorized that novelties originated through a series of small, micro-evolutionary stages, each of which is ecologically, functionally, and selectively plausible. Since such adaptive micro-evolutionary approaches never focused specifically on what is *genuinely* novel about the two transformational end points, they are unlikely to contribute to a realistic understanding of the origin of novel structures.

A favorite micro-evolutionary theory for the origin of feathers has been that planar feathers evolved from elongate scales through natural selection for flight within ancestral birds. Such theories have a persistent flaw which was first pointed out in the 19th century (Davies, 1889), but which has been ignored for most of the last century (Prum, 1999; Prum and Brush, 2002). That error is the assumption that the two planar surfaces of a scale develop from the top and bottom of the initial epidermal outgrowth that forms the scale. In actual fact, however, the two planar surfaces of a pennaceous feather are created by the *outer* and *inner* surfaces of the tubular feather germ only after the feather emerges from its cylindrical sheath. The planar surfaces of an elongate scale and a pennaceous feather are not, and could not have been, homologous. Feathers could never have evolved by elongation and division of a planar scale. The unchallenged persistence for most of the 20th century of the flawed concept of the primitive feather as an elongate scale has contributed greatly to the delay in achieving an understanding of the origin of feathers.

3 The developmental theory

An alternative approach to the study of the origin of feathers posits that the detail of feather development can be used to reconstruct plausible antecedent feather morphologies (Prum, 1999). It maintains that any theory of the origin of feathers should also provide a complete and consistent theory of the evolution of the complex mechanisms of feather development. This alternative “developmental” theory of the origin of feathers is based entirely on the hierarchical details of how feathers grow, and provides a detailed, testable model of the evolutionary origin and diversification of feathers.

The developmental model hypothesizes that the first feather (Stage I) originated with a tubular elongation of the placode and the first feather follicle, a cylindrical epidermal invagination around the initial feather papilla. Subsequent feather diversity evolved through a series of derived developmental novelties within the ring-shaped epidermal collar of the follicle that generates the tubular feather germ. After the origin of the tubular feather germ came the differentiation of the tubular epidermis into the barb ridges that generate the barbs (Stage II). The model proposes two alternative stages next: (1) the origin of helical growth and the rachis (Stage IIIa), or (2) the origin of barbule plate differentiation (Stage IIIb). Evolution of both of these developmental novelties established the capacity to grow both the branched structure of modern feathers (Stage IIIa+b). The origin of differentiated distal and proximal barbule plates followed (Stage IV).

This hypothesized series of five developmental novelties predicts an explicit transition series in the morphologies of the feathers grown from such follicles. Stage I follicles would produce an unbranched, hollow, tubular feather. A Stage II follicle would produce a tuft of barbs fused basally to the calamus. A Stage IIIa follicle would grow a feather with a rachis (formed by the initial fusion of feather barbs on the anterior side of the follicle) and a series of fused barbs. A Stage IIIb follicle would produce a tuft of barbs from which barbules branched. Stage IIIa+b follicles would grow the first bipinnate (double-branched) feathers with a rachis, barbs, and barbules. In the absence of differentiated barbules, a Stage IIIa+b feather would be diffusely pennaceous, i.e. lack a coherent vane. Stage IV follicles would grow a pennaceous feather with a coherent vane produced by the interlocking of the differentiated hooks and grooves of the distal and proximal barbules of neighboring barbs.

4 Support for the developmental model and theropod origin of feathers

Support for the developmental theory of feather origins comes from the hierarchical nature of feather development itself (Prum, 1999) and the diversity of feathers among extant birds (Prum, 1999). Furthermore, exciting new molecular data from the developmental biology of feathers (Harris et al., 2002) now corroborates both the morphologies and the sequence of the first three stages predicted by the developmental model (Prum, 1999).

The last decade has also produced startling new paleontological discoveries from the early Cretaceous (~124 million years old) Yixian formation in Liaoning Province, north China, yielding a diversity of theropod dinosaur fossils with well-preserved integumentary structures. These discoveries have produced a revolution in our understanding of the origin and evolutionary history of feathers. Feathers first appeared in a lineage of coelurosaurian theropod dinosaurs and diversified into essentially modern structural variety within subsequent lineages of non-avian theropods (Zhou, 2003). Among the numerous feather-bearing theropod dinosaur lineages, one particular group evolved the ability to fly with the feathers of its specialized forelimbs and tail: the birds.

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