S06-5 Selection for feather structure

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Abstract We focus here on possible selection pressures that acted on the protofeather to create the structural complexity and diversity of modern feathers. The need for water repellency may have influenced the spacing and structure of barbs and barbules. Thermodynamics may have been critical to the development of downy barbs and the subsequent formation of semiplumes and down feathers. Aerodynamics probably influenced the twisting of barbules that provides for the overlap of adjacent barbules and the resistance of the vane of flight feathers to air flow. Air pressure may also have selected for the elliptical, cross-sectional shape of the ramus, since such a shape would reduce the tendency of the barb to rise into the low pressure over the dorsal surface of the flight feather. Because the elliptical shape would resist bending, it would also reduce material fatigue from repeated flexing. Resistance to abrasion by airborne particles would favor larger feather parts and increased strength of the protofeather. Melanin deposited in the keratin increases its strength and increases the thickness of the cortex of the ramus of the barb and of the rachis. While these selection pressures have been invoked as affecting modern feathers, their potential importance to the evolution of feather structure has been largely overlooked. We briefly discuss new data on ectoparasites and feather-degrading bacteria which suggest that both parasites and bacteria have had a long association with feathers and may have selected for the deposition of melanin and the thickening of the cortex among birds inhabiting humid environments. Ultraviolet damage to feathers is almost unstudied, and damage from icing has been mentioned only anecdotally. Exploring selection pressures that act on modern feathers may be key to understanding the evolution of feather structure and diversity.

Key words Feather, Evolution, Selection, Feather structure, Feather diversity

1 Introduction

To understand the evolution of feathers we must answer two related, but different questions: how the protofeather originated and how it evolved into the structural complexity and diversity of modern feathers. The most primitive feathers are filamentous structures projecting from the integument of *Sinosauropteryx*, a basal coelurosaur (Chen et al., 1998; Zhou, 2006), and *Beipiaosaurus*, a therizinosaurid theropod (Xu et al., 1999). The integumentary appendages of both dinosaurs are single filaments. Such structures correspond to stage I in the evolution of the feather as predicted by Prum (1999) and Prum and Brush (2002).

Attention so far has focused on the evolutionary origin of feathers (Feduccia, 1999; Prum, 2002; Zhou, 2006), and on mechanisms by which the structure and form of modern feathers evolved (Prum, 1999; Prum and Williamson, 2001), with but little attention to the selection pressures that shaped that structure and diversity. With the appearance of protofeathers (Xu et al., 2001; Zhou, 2006), an array of biotic and abiotic pressures began to select for particular modifications to their filamentous structure. Like the reptilian skin and scales that preceded this evolutionary novelty, the protofeather needed to resist abrasion, degradation by bacteria and consumption by ectoparasites. Similarly, ex-posure to the damaging effects of ultraviolet radiation necessitated a structure that could resist UV-damage and protect sensitive underlying tissues. As protofeathers enlarged, they needed to be flexible so as to move with the limbs, but also resilient in order to recover their position and shape. These and other pressures could not have acted until the original feather appeared. Some of these pressures acted in concert, for example resistance to abrasion, feather-degrading bacteria and ectoparasites. Others acted in opposition, for example flexibility versus resiliency. But over time these actions and interactions selected for the structural complexity and diversity of modern feathers.

Accordingly, we review here those selection pressures we believe played a role in the evolution of complex and diverse modern feathers from filamentous protofeathers and summarize the supporting data. The discussion is based necessarily on evidence from modern feathers. We realize that selection on protofeathers may have been different from that on modern feathers, but we are convinced that a better understanding of selection on modern feathers will lead to new insights concerning the evolution of feather structure and diversity generally. To set the stage, we summarize structure and diversity in modern feathers.

1.1 Brief review of feather structure and diversity

Modern feathers include contour feathers,

semiplumes, filoplumes, bristles, down, those with and without aftershafts and come in a bewildering array of colors and shapes. All have a basal calamus that is anchored in a follicle below the surface of the skin. All have a central structure from which branches, the barbs, extend; and the barbs have secondary branches, the barbules. Growth patterns are similar and all growing feathers are enclosed temporarily in a sheath. There the similarity ends. Contour feathers and semiplumes have a central shaft, the rachis, flanked by barbs that form a flat vane on either side of the rachis. Flight feathers and coverts have barbs that interlock rigidly, whereas body contour feathers have barbs that interlock weakly; and semiplumes have barbs that do not interlock at all. Filoplumes have a rachis that thickens distally and ends in a tuft of 1–6 short barbs. Bristles have a stiff tapered rachis and a basal tuft of barbs. Most down feathers have flexible barbs and barbules that extend directly from the calamus to form a loose tangle that entraps air. However, some down feathers, especially those of waterfowl, may have a rachis that is as long as the longest barbs. With this brief sketch of the structural diversity of feathers we can now ask what are the selection pressures acting on feathers that might account for their evolution from primitive filaments to the complex, diverse structures described above.

2 Selection pressures

2.1 Water repellency

Theropods had protofeathers that were thin filaments, some of them branching in a pattern similar to the open pennaceous feathers that cover the bodies of modern birds. These fibers were 30–40 mm long, but less than 0.5 mm in diameter and possibly as little as a 0.1 mm in diameter. When such long, thin filaments were struck by raindrops they would not have had the mechanical strength to resist the forces exerted by the surface tension of the water droplet and would have adhered to each other in clumps, such as seen in wet fur. Such clumped filaments would be less able to shed further rain and would provide reduced insulation. In addition, the water that clung to the coalesced bundles of fibers would conduct heat away from the body. Thus rain would have wet a body covering of branching, filamentous protofeathers, which would have lost their ability to shed additional water and their ability to insulate.

Both problems can be eliminated by evolving a structure that resists the forces of surface tension. One way to do this is to arrange the filaments so that the distance between them remains constant despite the presence of water droplets and the forces of surface tension (Cassie and Baxter, 1944). On contour feathers, barbules from adjacent barbs link to each other and maintain relatively constant spacing between barbs. Furthermore, the barbules and barbs of overlapping feathers (e.g. coverts, body feathers) maintain an open porous structure such as envisioned by Cassie and Baxter who point out "... it is surprising how closely the structure of feathers conforms with the theoretical requirements for water-repellency."

Rijke (1970, 1987, 1989) developed a model for water repellency based on the model for porous surfaces developed by Cassie and Baxter (1948) and Cassie (1958) for textiles. However, Elowson (1984, 1987) found that the vane of a modern feather is considerably more complex and variable than the geometry of the textile model, that the model's predictions were not met, and that the spacing of barbules appeared to influence the shape of droplets more than the spacing of barbs. The open branching structure of protofeathers described by Xu et al. (2001) and modeled by Prum and Williamson (2001) may more closely approach the conditions assumed by the textile model. Possibly water repellency shaped the early or later evolution of feather structure.

2.2 Resistance to water penetration

When a bird floats on the surface of the water or dives beneath it, pressure may force water between the barbs. Mahoney (1984) showed significant differences in the penetration of water into the plumage of different aquatic species. She and Rijke (Rijke et al., 1989) calculated and measured penetration on isolated feathers and found that spacing of the barbules was an important factor in limiting water penetration whereas spacing of the rami of the barbs was critical to shedding rain drops. Water penetration under pressure is critical to water birds whereas water repellency is critical to water birds and terrestrial birds alike. Furthermore, water penetration and water repellency select for different structural adaptations in the feather. The relative contributions of each to the evolution of feather structure is open to exploration.

2.3 Damage from freezing

Water that freezes after penetrating the network of barbs and barbules can bind feathers together and cause barbs to be ripped from the rachis when a bird moves, thereby pulling the feathers apart as, for example, when opening a folded wing in the morning after a night of sleet (pers. obs.). How the feather can evolve to minimize such damage and how important such damage is to birds are unknown. The topic is unstudied.

2.4 Durability

We do not know whether protofeathers grew continuously or reached a predetermined length after which the follicle became quiescent and growth ceased until the follicle resumed activity and a new protofeather replaced the old. In either case, the filament had to be sufficiently durable to resist wear so that the organism could maintain a functional coat. Durability of the filaments and simple branching structures evident in the early fossils is unknown, but selection should have favored resistance to abrasion by airborne particles.

Particulate abrasion has been measured experimentally for feathers by Burtt (1986) who used an aerodynamic model to predict which areas of a flying bird receive the most intense particulate abrasion. Melanic feathers, which

are the most resistant to particulate abrasion, occur disproportionately often in those areas (most notably the wing tips) predicted by the aerodynamic model (Burtt, 1986). The cortex of the rachis and of the ramus is thicker when melanin is present than when not (Voitkevich, 1966), and melanic keratin has greater tensile strength than non-melanic keratin (Bonser, 1993, 1995).

Recent isolation of feather-degrading bacteria from the plumage of wild birds raises the possibility that bacteria, which can be seen associated with feather impressions of fossil birds (Davis and Briggs, 1995), may have catalyzed selection for characteristics that resisted bacterial degradation. Feathers with melanin degrade more slowly than those that lack melanin (Goldstein et al., 2004). Furthermore, Burtt and Ichida (2004) have shown that the darker color of song sparrows (*Melospiza melodia morphna*) from the humid forests of the Pacific northwest of USA is associated with a somewhat higher incidence and more active strain of feather-degrading bacteria (*Bacillus licheniformis*) than in the pale song sparrows (*M. m. fallax*) of arid southwestern USA. Here again, the presence of melanin is associated with greater cortical thickness. Other structural differences between feathers with more or less melanin have not been studied.

2.5 Resiliance

The rachis, rami, and barbules will bend as the feather moves through the air, as it interacts with neighboring feathers when limbs, head and neck move, and as feathers brush against grass, twigs, and other objects in the environment. How far can the feather bend without breaking? How does the structure of the feather respond to repeated bending?

Flexibility can be advantageous. Slight bending of the tips of the primaries reduces wing tip vortices in soaring birds such as vultures, increasing the efficiency of the wing at slow speeds. Similar bending of the coverts into the airstream over the wing creates the micro-turbulence that helps to hold the laminar flow of air close to the wing at slow speeds and steep angles of attack. In both these cases, limited bending of the feather into the airstream of a flying bird is essential to the function of the feather. Too much bending would create excessive turbulence and reduce aerodynamic efficiency.

The square cross-sectional shape of the rachis with its thickened dorsal and ventral cortex suggests selection for limited flexing of the feather in dorsal and ventral directions, the very directions in which the primaries and coverts would flex into the air stream. The elliptical cross-sectional shape of the ramus, reinforced dorsally and ventrally, permits bending toward the tip or base of the feather, but restricts bending above or below the plane of the vane of the feather. What selection pressures favored flexibility in certain directions and not others? Can we infer selection acting on the primitive open structure hypothesized by Prum and Brush (2003) from measurements on modern feathers?

2.6 Ultraviolet damage

As the outermost covering, protofeathers and modern feathers were and are exposed to solar radiation. Bergmann (1982) provided qualitative evidence that ultraviolet radiation damages feathers, but quantitative evidence for relating exposure to damage is lacking. Also lacking is evaluation of ultraviolet damage to differently structured and colored feathers. Melanin is present more often in the dorsal cortex of the rachis, rami, and barbules than in the ventral cortex. Is melanin distribution an adaptation to limit ultraviolet damage to feather structure? Is thickening of the dorsal cortex of the rachis and rami an adaptation to reduce potential ultraviolet damage to the feather? If we can document how modern feathers resist damage from ultraviolet radiation, that may help us understand the role played by ultraviolet light in the evolution of modern feathers from protofeathers.

Adaptations of the feather may not be limited just to preserving structural integrity. The feather may shield underlying tissue from ultraviolet radiation. The open structure of the primitive feather, as hypothesized by Prum and Brush (2003), would be a poor shield and closure of the structure would be strongly selected by the need to absorb potentially damaging UV-radiation.

2.7 Thermodynamics

Regal (1975) makes a strong case for the evolution of feathers as insulation to prevent heat loss. Indeed, the filamentous structures found on theropod dinosaurs and postulated by Prum (1999, 2002), Prum and Williamson (2001) and Prum and Brush (2002, 2003) as stage 1 in the evolution of feathers would have trapped air among the many overlapping filaments. The multiple barbs extending from a calamus or the branches extending from a rachis would have improved the ability of the primitive feather to capture warm air near the body of protobirds. Additionally, the air-filled structure of the feather is ideal for reducing conduction of heat through the feather itself, as pointed out by Dyke (1985) in his discussion of feather evolution. Thus the form of primitive feathers and their internal structure could have been selected for their thermodynamic advantages. Protofeathers could have helped retain metabolic heat, thereby increasing the efficiency of energy conversion in a small active organism. Alternatively, they could have helped protect the organism from overheating in warm, sunlit, but breezy conditions (Walsberg, 1982).

Thermodynamics may explain evolution of multiple barbs (down) or the open branching structure (semiplume), but there seems to be no thermodynamic advantage to the closed branching structure of contour feathers. However, selection based on thermodynamic requirements would seem to provide strong reasons for the origin of filamentous protofeathers and for their elaboration into structures with multiple branches.

2.8 Aerodynamics

Much has been written about the role of aerodynam-

ics in the origin of birds and feathers. If we accept the developmental model for the origin of feathers, then aerodynamics has no role to play. Novel changes in the integument resulted in the evolution of a papilla surrounded by germinal tissue that produced a hollow tubular structure such as seen in *Sinosauropteryx* (Chen et al., 1998; Zhou, 2006) and *Beipiaosaurus* (Xu et al., 1999). Such structures are not aerodynamic. Not until the open branching stage of development did the feather reach a point at which selection for aerodynamics might have played a role in selecting for the closed structure that characterizes modern remiges.

However, several characteristics of feathers are ideally suited for flight. Feather keratin is lighter than the keratin that covers the bill and feet. The tubular structure of the rachis and rami of barbs is light but strong, and more resistant to bending than a solid rod of the same weight. The elliptical shape of the rami allows the barbs to flex only toward the tip of the feather and the thickened dorsal and ventral surfaces of the rachis allow only slight lifting of the feather tip into the airstream above the wing. The slight lift creates a thin layer of turbulence over the wing, which helps hold the laminar flow of air on the wing at slow speeds. Such control of the airflow enables the bird to lower its stalling speed and thereby maneuver and land at low, safe speeds.

The remiges and rectrices of many birds are further modified so that each feather has an airfoil shape that contributes to lift and propulsion. These changes must have occurred after the feather had become a closed branching structure, stage 4 in the scheme laid out by Prum and Brush (2003), but when? Could earlier, more open stages in the evolution of the feather have conferred advantages on a gliding protobird?

3 Conclusions

Protofeathers were probably unbranched, tubular structures such as found on several of the Chinese fossil theropods and predicted by Prum and Brush (2003). Selection for the origin of such filaments was probably thermodynamic, but may also have been protection from ultraviolet radiation or rain. Once this tube of keratin came into existence, it became subjected to selection to improve its thermodynamic properties, to better shed rain, and to better shield the underlying skin and organs from harmful radiation. These pressures could have favored the evolution of a branching structure. Selection to resist abrasion, brushing against stationary objects, degradation by microorganisms, and consumption by lice and mites would have influenced the shape and reinforced the structure of the protofeather.

At some point, the primitive feather evolved into a branched structure, at which time its evolution as an aerodynamic appendage could begin. Were tubular protofeathers made of ß-keratin, or did incorporation of a light, strong keratin occur during evolution of an aerodynamic appendage? Bristles and filoplumes have sensory and pro-

tective functions (Gill, 1994); but were such functions critical to their evolution? We are now beginning to understand the origin of feathers, but we are barely on the threshold of understanding the selective pressures that account for the evolution of the structure and diversity of modern feathers. Exploration of such pressures acting on modern feathers may provide insight into the pressures that transformed the ancient protofeather into the structurally and functionally diverse feathers of today.

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