

THE ROLE OF PIGMENTS AND STRUCTURAL COLORS IN THE EVOLUTIONARY ORIGIN OF FEATHERS

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ABSTRACT: I propose that the “aerodynamic features” of modern feathers, including a distinctive combination of flatness, light weight, resilience, and smooth-contour, initially evolved in a context unrelated to flight. Instead, flatness and lightness evolved in response to selection favoring a maximally effective shape for the exhibition of pigments and structural colors. Pigments shield the body surface from damaging ultraviolet radiation and produce many colors involved in communication and crypsis. In flat shape and dense pigmentation, contour feathers converge on plant leaves and flower petals, two other ubiquitous structures that display pigments for photosynthesis and the attraction of pollinators, respectively. Lightness evolved in response to selection for (1) ease of angular movement of individual feathers and groups of feathers by a complex system of shallow dermal musculature and (2) a matrix of keratin infiltrated with melanins and air vacuoles that enabled the production of structural colors. The physical characteristics and individual mobility of feathers, serving to expose pigments and iridescence during display, were preadaptive for the eventual use of feathers in flight and thermoregulation. The intimate relationship of pigments to feather microstructure, strengthening, gross appearance and molt-plumage cycles points to a tightly co-evolved system. The earliest feathers were probably heavily melanized and may have been iridescent.

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Introduction

Decades of debate have failed to explain convincingly the origin of feathers, the most complex epidermal derivative known in any vertebrate (Spearman and Hardy 1985) and a structure widely regarded as a premier evolutionary novelty (Mayr 1960, Brush 1996). Continuing hypotheses of origin emanate largely from the obvious functions of modern feathers: aerodynamic surfaces for flight (Parkes 1966, Maderson 1972, Feduccia 1995, 1996, Homberger 1999); thermoregulation (Mayr 1960, Lucas and Stettenheim 1972, Regal 1975, Dyck 1985); communication (Quinn 1997), sexual display and intraspecific combat (Mayr 1960, Cowen and Lipps 1982), crypsis (Prum 1999); and waterproofing (Dyck 1985, 1999).

Despite the variety and logic of these explanations, key pieces of the puzzle remain missing. The light, strong, flexible, and resilient feather with its smooth contours has a “near-perfect aerodynamic design” (Feduccia 1996). Therefore, as Feduccia emphasized, if feathers did not evolve for flight, an alternative explanation must account for their unique combination of structural features.

The purpose of this paper is to marshal evidence that pigmentary and structural colors were crucially involved in the evolutionary origin of feathers. Because it is not immediately obvious why either should have anything to do with feather origin, neither has been discussed previously in this context. Evidently, authors have felt that the physical basis of color is subsumed satisfactorily under the hypothesis that feathers serve an epigamic (Mayr 1960) or communicative role (Cowen and Lipps 1982, Quinn 1997). Nonetheless, the fact that feathers display colors during communication does not adequately address the issue of why colors are exhibited by structures of this particular “aerodynamic design” when other conceivable devices could have sufficed for this function. Here I argue that multiple lines of evidence support the view that feathers initially evolved as two-dimensional, movable surfaces that exhibit pigments and structural colors away from the body.

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Why Display Pigments?

Feathers and feather pigments block harmful ultraviolet radiation.--Burt (1979) reminded ornithologists that ultraviolet (UV) radiation is harmful and potentially lethal to living systems, including birds, by causing rupture of chemical bonds and mutation through alteration of DNA (Witkin 1966, Resnick 1970). Burt (1979) suspected that birds shield themselves from lethal intensities of ultraviolet light by absorption of such radiation into feathers, which are dead tissue. In unique experiments comparing relative transmission of UV radiation, Burt (1979) demonstrated that feathers with melanins block transmission of 80% of available UV radiation to the avian body surface; feathers pigmented with carotenoids reduce transmission by 50%. White feathers, which lack pigments, lowered UV transmission by 40%, showing that keratin alone provides significant shielding. I interpret Burt's findings to support the hypothesis that feathers evolved as structures to hold pigments away from the body as a first line of defense against UV radiation. Melanins in the skin, which are common both in epidermis and dermis of birds (Lebedinsky 1929, Lucas and Stettenheim 1972), probably serve as a second line of defense, although I am unaware of experiments in which plucked live birds have been exposed to UV radiation to test the possible role of the skin in screening.

Pigments form the proximate basis for colors used in communication and crypsis.--A brief review of the basis of coloration in birds is necessary for the discussion beyond. Feather biochromes, predominantly melanins, carotenoids and porphyrins, often in combination with unpigmented, white feathers and pigmented bare skin on the head, legs, and feet, are the basis for pigmentary coloration and hence appearance in birds. Structural colors (schemochromes) also serve intimately in display and communication; these colors may or may not involve pigments. Structural colors fall into three classes (reviewed by Lucas and Stettenheim 1972, updated by Prum et al. 1999): (1) Unpigmented, white feathers that scatter all visible wavelengths of light; (2) iridescent structural colors, as in hummingbird gorgets, that result from constructive interference of light by feather barbules containing melanin granules and air vacuoles suspended in barbule keratin, colors that change in hue with the angle of incidence or observation; and (3) non-iridescent structural color, as in blue feathers of jays, that are produced by constructive interference of coherently scattered light waves by the spongy medulla of feather barbs, consisting of keratin rods, air vacuoles, and a basal region of melanin granules. This latter pithy matrix surrounded by discrete spaces filled with air is reminiscent of styrofoam (Fahrenback 1977) and reflects non-iridescent blue, violet, and turquoise, but in combination with carotenoids reflects green (Fox 1976). These colors remain stable in hue regardless of viewing angle.

Birds use colors and patterns of feathers routinely in communication, courtship, and crypsis. A vast literature documents such use but to save space it will not be reviewed here.

Pigments are Best Displayed on Flat Surfaces

The exhibition of pigments in or upon two-dimensional flat surfaces is ubiquitous in the biotic world. Two of the most commonplace structures on earth, plant leaves and flower petals, both evolved their respective shapes for the display of pigments, the former exhibiting chlorophyll to sunlight for photosynthesis and the latter displaying pigments which attract pollinators. The similar shape and dense pigmentation of contour feathers, plant leaves and flower petals represent one of the most striking examples of convergent evolution ever described. Most feathers, many leaves, and some flowers share a further similarity in being flat surfaces supported by central and lateral stiffened rods, the rachis and barbs in feathers and the petiole and veins in leaves. Convergence between feathers and leaves and flowers can be extended further to include their development. All three structures develop by the unfurling of two-dimensional flat surfaces from cylinders--follicles for feathers, and leaf buds and flower buds for leaves and flowers, respectively. Furthermore, pigmentation of feathers and plant leaves share an additional similarity in that the upper, exposed surfaces of both are more heavily pigmented than the lower surfaces, indicating that selection for maximally effective exposure

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of pigments in both dictated the placement and density of the pigment.

The exhibition of pigments in or upon two-dimensional flat surfaces is also commonplace in the abiotic world. Witness paintings, billboards, signs, solar panels, newspapers and manuscript pages.

Feather Pigments are Best Displayed on Lightweight Surfaces

I hypothesize that lightness in feathers, rather than evolving for the purpose of flight, developed in response to selection for (a) mobility of surfaces that enable maximally efficient exposure of plumage signals and (b) the production of structural colors, all of which, either white, iridescent or pigmentary, require air vacuoles.

Devices adapted for exposure of pigments and structural colors away from the body surface must be light in order to be mobile.--Both pigmentary and structural colors and patterns are maximally effective when exhibited away from the immediate body surface in flexible structures whose orientation can be altered in relation to the angle of incidence of solar radiation. In feathers this is accomplished by an intricate system of feather muscles (e. g. erectors) that serve to raise and rotate individual feathers. Resilient, structural fat tissue in the dermis and associated elastic membranes return feathers to their resting positions (Homberger 1999). Retractors also are part of this complex system. These function to expand and contract entire fields of follicles (see exquisite illustrations and thorough discussion in Lucas and Stettenheim 1972). Thus, small or large blocks of feathers can operate as a unit, quickly exposing or hiding color patches in various behavioral contexts.

The most complex feather muscles operate follicles in the dorsal cervical tract, where feathers can be erected rapidly (Lucas and Stettenheim 1972). In hostile contexts, erection of the neck hackles changes the outline of the bird, making it appear larger and more formidable. Based on this fact, I speculate that the first feathers probably arose on the crown, hind neck, and upper back, areas with blocks of feathers that are frequently used in displays by modern birds. Moreover, skin muscles in other vertebrates (e. g., bony fishes, lizards, and mammals) elevate dorsal fins, spines, or back hair, respectively, especially in aggressive contexts, suggesting that integumentary muscles operating epidermally derived dorsal structures are widespread and ancient in vertebrate groups and doubtless were available very early in evolutionary history to be co-opted for use in feather orientation by birds. The "soft and pliable" integumentary structures on the dorsal surface of the neck and back, reported for the Upper Jurassic or Lower Cretaceous theropod dinosaur *Sinosauropteryx prima* (Chen *et al.* 1998, see also Prum 1999), serve as an appropriate structural analogue.

Although the feather muscle system effectively moves single feathers or groups of feathers, it cannot manipulate heavy structures because of simple biomechanical principles. Feather muscles in birds are located dermally. In the Domestic Chicken (*Gallus domesticus*), the thickest portion of the dermis is only .214 mm (Lucas and Stettenheim 1972). Feather muscles in such a shallow layer of dermis would have lever arms of a few millimeters at most, stretching from the bulb (basal end) of the follicle to the fulcrum located at the calamus near the skin surface (Lucas and Stettenheim 1972). Because typical body feathers are a minimum of 50-100X the length of the longest muscle lever arm, lightness of feathers was mandatory in the evolution of this system if their motion was to be achieved.

I interpret feather muscles as a refined, co-evolved system that initially was selected for as the mechanical basis for orientation of feathers to effect maximal display of dull melanins, vivid carotenoids and brilliant structural colors. This suggests that the presentation of pigments by two-dimensional flat structures whose mobility is controlled by an intricate system of muscles is a fundamental role of feathers that may be traceable to their evolutionary origin. In addition, the early feather muscle system would represent a major preadaptation allowing the eventual use of blocks of elevated and depressed feathers for thermoregulation (Parkes 1966).

Air-filled keratin, the proximal basis for the production and exposure of structural colors, results in light feathers.--I suggest that the production of structural colors by this matrix easily could have been the selective force promoting the spongy structure of medullary barb keratin to begin with. Air-filled barbules attached to barbs also may have evolved specifically for the display of melanin

pigment. Melanin, in combination with appropriate structure of keratin, is always associated with iridescence (Elsässer 1925, Craig and Hartley 1985) and is probably required for its production. This leads to the logical inference that iridescence was the selective force leading also to the design of barbule fine structure. Thus, natural selection could have favored the evolution of a light, flexible, air-filled matrix of keratin in both the barbs and the barbules, specifically for the adaptive advantages it offered in the production of both iridescent and non-iridescent structural colors for display and communication. Such construction directly provided the lightness and buoyancy so crucial to eventual aerodynamic function.

Feathers and Pigments Represent a Tightly Co-evolved System

Melanin and carotenoid pigments influence the structure of feather keratin .-- Feather keratin is strengthened (Carr 1957, Burt 1986) and hardened (Bonser 1995) by the presence of melanin pigment granules, perhaps reflecting the fact that granular fillers in polymers increase their resistance to abrasion (Lancaster 1973). Carotenoids are also "very strongly bonded to the keratin proteins" (Stradi *et al.* 1995). From this I infer that melanins and carotenoids are present in feathers not merely as passive inclusions but instead should be regarded as fundamentally important structural materials.

Carotenoid pigments in high concentration also can alter feather structure, resulting in flattened barbs, missing barbules, a reduced or absent medulla, and a thickening of the exterior cuticle, all resulting in a glossy appearance (Olson 1970). The intensified reflectance of such feathers enhances their effectiveness in communication. Carotenoids usually are confined to distinctive cells in the barb cortex and are lacking in barb medulla. Elimination of barbules and reduction of barb medulla in feathers with heavy carotenoid infiltration, sites where melanin is concentrated, suggests that carotenoids and melanins compete for space. The fact that both carotenoids and melanins can be bonded to and alter the form of feather keratin is a strong line of evidence for the intimate association of keratin mobilization and pigmentation during feather morphogenesis. Furthermore, the fact that keratin filaments and keratin-strengthening melanins and carotenoids, when present, are mobilized essentially simultaneously in the feather follicle during morphogenesis (Lucas and Stettenheim 1972) points to a close adaptive synergism and thus a probable contemporaneous evolutionary origin for these intertwined processes.

Natural selection favored the co-evolution of a finely-tuned mechanism for periodic switching of the visible phenotype in birds.-- The genetic-hormonal control of follicles during feather morphogenesis is enormously flexible in birds. As inspection of any field guide will show, the diversity of avian plumages is bewildering. Striking differences according to sex, age, and season and other morphisms within species, and a myriad of differences in patterns of pigmentation among species, are commonplace. Feathers of different shapes, colors, and patterns can be replaced iteratively via molt from a single follicle. Diet also readily influences appearance in many species through the simple ingestion of carotenoids which are deposited in growing feathers either in unmodified form or after metabolic alteration (Stradi 1998). In addition to replacing worn feathers, molt often strikingly alters the visible phenotype even when feathers are apparently fresh and *not in need of renewal* (e. g., the "eclipse" plumage of dabbling ducks, particularly the Mallard [*Anas platyrhynchos*] Sibley 1957). This suggests that switching of phenotypes can be a primary role of molt and that the presentation of colors and patterns is a fundamental role of feathers. Morphism in general is probably mediated in many instances by single genes with Mendelian effects (e. g., Snow Goose [*Chen caerulescens*], Cooke 1987; Sooty-capped Bush-tanager [*Chlorospingus pileatus*], Johnson and Brush 1972, Buckley 1987). I regard the existence of a simple yet flexible and diverse genetic-hormonal-molt mechanism for easy plumage change as strong indication that this finely-tuned system co-evolved, another major line of evidence that color and pattern expression is a major function of feathers. The origin of this system is probably as old as are feathers themselves.

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Melanins and pigmentary structural colors in feathers are ancestral in birds.--Melanins are ubiquitous in the natural world (Majerus 1998), including the skin of vertebrates, and there is every reason to suspect their presence in the earliest integumentary derivatives that led to feathers. Early feather melanins served to block harmful ultraviolet radiation and simultaneously provided the basis for crypsis and display, the latter through the expression of structural colors, including iridescence. The fact that melanins are taxonomically widespread and occur in all orders of living birds is strong evidence that they are primitive. Therefore, bright plumage based in part or completely on melanins may have been ancestral, a view that is receiving increasing support (Kimball and Ligon 1999). Feather carotenoids, in contrast, occur commonly in relatively few unrelated avian orders (N. K. Johnson unpubl.) and therefore are probably derived.

The Earliest Feathers

Several recent contributions have negated important aspects of earlier theory on origin. For example, the predominant hypothesis of recent decades, that feathers evolved from modified, flat reptilian scales (Maderson 1972), has now been falsified. Not only are feathers comprised of a unique phi keratin unknown in reptiles, but many other facets of their molecular development are incompatible with such an origin (Brush 1993, 1996). Furthermore, feathers develop from a cylindrical follicle, also unique to birds (Brush 1996). Prum's (1999) analysis of developmental sequences (from Lucas and Stettenheim 1972 and references cited therein) also disallows origin from a flat scale because flight requires bipinnate feather structure, a form impossible to derive "by selection on increasingly elongate scales for an aerodynamic function" (Prum 1999).

If not modified flat scales, what did the earliest feathers look like? Two current papers address this issue. Brush (1996) hypothesized that linearly associated monomers of phi-keratin led first to highly oriented filaments and then to keratinous fibers. In contrast, Prum (1999) proposed initial origin as a hollow cylinder arising from an undifferentiated tubular collar that was not "homologous with a single feather barb." Although either scenario is plausible, the fossil record provides no clear evidence for feather origin. Furthermore, there is no reason to believe that the earliest feathers would have been recognizable as such. Finally, the degree to which modern feather development offers clues to the evolution of a structure that appeared over 150 Mya is dubious.

Despite the complexity and structural variety of definitive feathers, Brush (1996) has emphasized their fundamentally simple design as "structures of serial repetition." Thus, the repeated shaft-barb organization of "crystallographic arrays" of keratin filaments applies to all feathers which, in essence, are a "two-dimensional surface of variable dimensions constructed from a single family of proteins" (Brush 1996). Expanding Brush's remarks, I speculate that the development of simple dendritic branching of keratinous filaments was of fundamental importance. This design permitted the eventual evolution of a light, flat latticework comprised of a stepwise series of repetitive keratinous structures: the pre-rachis producing pre-barbs, pre-barbs growing pre-barbules, and pre-barbules bearing hooked pre-barbicels. The latter allowed interlocked barbs, a key step in the evolution of flat feathers with solid vanes. Thus, definitive complexity was achieved by repetition of a simple dendritic process extending beyond the "repeated shaft-barb organization" to include barbules and barbicels with their all-important hooklets.

I propose that the earliest feathers originated as short, single filaments of flexible keratin emanating from small patches of melanized reptilian skin on the head, neck, or back. Initially, these short filaments were controlled by sparse dermal musculature. Over time, selection favored increasingly intricate musculature to control longer single filaments of pigmented keratin, then dendritic, flattish, buoyant filaments and, finally, filaments that hooked together to form flat, leaf-shaped structures. The latter resulted from selection promoting effectiveness in exposing pigment because branching would enlarge the signalling surface and increase fitness. Eventually, elongated patches of protofeathers became distributed into tracts, both antero-posteriorly on the body, including the caudal region, and laterally onto the forelimbs. Early simple feathers in the caudal and forelimb

regions were poised for eventual evolution into complex aerodynamic surfaces.

As Bock (1986) has correctly reasoned, when a novel structure evolves, *every* stage of its evolution must be adaptive with respect to the selective milieu in which it functions at that time. In keeping with Bock's requirement, I emphasize that *even a single filament or small group of protofeathers could have had a signalling function*, as is evident in modern birds. Consider the 7 cm crown adornment of the Mountain Quail (*Oreortyx pictus*), composed of only *two* long plumes. In contrast, a few feathers could not have functioned effectively either for flight or thermoregulation.

Two key elements are missing from the above discussion, elements that were crucial in the initial evolution of the protofeather: early filaments were highly pigmented and filled with air. In addition to blocking ultraviolet radiation, the pigments produced colors used in crypsis and communication. Air vacuoles were selected for because they both allowed the lightness that mobility required for efficient posturing of single filaments or groups of filaments during communication and display. Furthermore, the air pockets formed an essential part of the matrix necessary for the production of structural colors through their interaction with keratin microstructure and pigments. I conclude that the principal force that changed the initial protofeather from a single-axis filament or cylinder into a light, flexible, dendritic, pennaceous, feather was selection for a flat, air-filled, mobile surface that effectively exhibited pigments and structural colors.

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