

# A Feather's Tale

## From tube to plane and back again

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All birds have feathers and feathers are unique to birds.<sup>[1,11]</sup>\* Birds rely upon their feathers for thermoregulation<sup>[7,11]</sup>, flight<sup>[11,15]</sup>, waterproofing<sup>[9]</sup>, communication<sup>[7,9,11]</sup> and more <sup>[9,11,12,13,15]</sup>. To an aviculturist, a bird's feathers represent not only the distinctiveness and beauty of the Class Aves but also a significant investment of a bird's nutritional and physical resources<sup>[1]</sup>.

Feathers are important to birds – and to aviculture. What are feathers and what are they made of? What makes them and how are they made? How are the patterns on feathers made? Summarized here\*\* are some of the amazing answers to these questions, which begin with a unique form of protein and a very special ring.

### What is a Feather?

A feather is an epidermal appendage<sup>[6,7,8]</sup>, which is a structure that is formed by the skin. Examples of other kinds of epidermal appendages are claws<sup>[1]</sup> and beaks<sup>[3]</sup>(rhamphotheca).<sup>[11]</sup>. Feathers are the most complex and highly organized<sup>[15]</sup> epidermal appendages found in vertebrates.<sup>[5,8]</sup>

### What are Feathers Made Of? <sup>[B1]</sup>

*“There are no genes for feathers. The information for their production resides in the timing for production of a set of unique protein molecules. This occurs only in feather follicles during well-defined periods of molt. The conversion of the protein into feathers involves a production-line-like series of events.”*<sup>[1]</sup>

Feathers are about 90% protein, most of which is in the form of keratin<sup>[11]</sup>. There are two basic types of keratin: Alpha-keratin, which forms a helical strand (such as is found in hair) and is very flexible, and beta-keratin, which forms a pleated and folded sheet and is more rigid. All avian epidermal appendages, including feathers, are made from a family of beta-keratin\*\*\* molecules called phi-keratins. Phi-keratins have the special ability to self-assemble into filaments (not all members of the beta-keratin family have this ability).

Genes direct the types of phi-keratins produced and the timing and sequence in which they are made; however it is the physical properties of the phi-keratins that determine how they may assemble from the molecular level to filaments to feather fibers<sup>[15]</sup> (hierarchical organization). By taking advantage of the physical ways in which components

may assemble, fewer genes are necessary to form complex structures such as feathers<sup>[1]</sup>.

Phi-keratins exist in two sizes, one with larger polypeptides and one with smaller. The larger phi-keratins are found in alligator claws<sup>[8,10]</sup> and in avian beaks and claws. The smaller are found only in downs and feathers of birds<sup>[1,8]</sup>. Feather phi-keratins have the special quality of being more flexible than other beta-keratins while retaining their strength<sup>[11]</sup>.

The organization of the phi-keratin filaments in epidermal structures is different: In claws and beaks it is interwoven; in feathers it is linear and branching. The components and structure of beaks and claws combine to make them rigid, durable and resistant to wear. Feathers are flexible but are more easily abraded. This susceptibility may have contributed to the evolution of regular replacement of feathers via molt (as opposed to continuous growth, such as occurs in beaks and claws).

Phi-keratins, like other keratins, are manufactured within specialized cells in the skin called keratinocytes<sup>[6]</sup>. The purpose of these cells is to produce and fill with a keratin, bond to each other to form solid structures (such as developing feather barbs) then die (apoptosis), leaving their keratin behind.<sup>[6]</sup> This is called keratinization. A unique quality of feather keratinization is that the keratinocytes fuse and assume their final shape prior to their death.<sup>[5]</sup> The keratin is not shaped after apoptosis as occurs in hair.<sup>[5]</sup>

### What Makes a Feather?<sup>[A5]</sup>

#### Formation of a Feather Follicle <sup>[A5]</sup>

*“The feather follicle is the complex organ that provides the spatial organization required to grow feathers.”*<sup>[9]</sup>

When a bird is an embryo, feather follicles form<sup>[4,13]</sup> in tracts (pterylae) in the epidermis. The follicles form by the time the embryos of most birds are twelve days old.<sup>[9]</sup> In the pterylae, cells of the epidermis and dermis (second layer of skin, below the epidermis) are chemically signaled<sup>[4,9]</sup> to organize into thickened regions called placodes.<sup>[8,9]</sup> Placodes elongate into fingerlike projections called feather buds<sup>[9]</sup> (or feather germs<sup>[6]</sup>). At this stage, the primary growth zone of the feather bud is at its tip (distal end).<sup>[3,11,13]</sup>

Proliferation of cells in a ring around the feather bud creates a cylindrical dimple (invagination) into the dermis with the feather bud at its base.<sup>[6,9]</sup> As the dimple descends,

the growth zone and stem cells of the germ<sup>[13,14]</sup> migrate from its distal to its proximal (base) end.<sup>[3,13]</sup> The feather germ is now called the dermal papilla, the growth zone is now the follicle collar<sup>[13]</sup> and the dimple is now the follicle cavity or wall<sup>[3]</sup>. Together, these are known as the feather follicle<sup>[3]</sup>. The feather follicles are now permanent features of a bird's skin. Because follicles protect the dermal papillae and stem cells within, they are able to regenerate a virtually unlimited numbers of feathers over time.<sup>[15]</sup>

The feather follicle might be described as looking something like a test tube with a rounded w-shaped base instead of the typical U-shaped base (the central point being the dermal papilla). It might also be described as looking like a cylinder within a tube. The concept of a feather follicle as a cylinder within a tube may be helpful when visualizing how a feather forms.

### Parts of a Feather Follicle<sup>[A5]</sup>

*"The structure of the follicle creates a unique cylindrical sandwich of epidermal and dermal tissue layers. This structure permits: (1) continuous interaction between the epidermis and the dermis, (2) indeterminate growth of the epidermis, and (3) continuous nourishment of the epidermis by the dermis..."*<sup>[9]</sup>

Because the feather follicle and its dermal papilla (tube and cylinder) are formed by the skin, they have layers, as the skin does: outer epidermis, inner epidermis (that interfaces with the dermis), and dermis. Each of these layers is modified to serve a unique function in the formation of a feather:

1). The "tube" is the layer of outer epidermis<sup>[8]</sup> that descends into the dermis and lines the feather follicle (follicle wall)<sup>[3]</sup>.

2a). The "cylinder" is the dermal papilla, which consists of a layer of epidermis covering a core of dermis, "like a thimble covering a finger"<sup>[5]</sup>. The cells of the outer layer of epidermis will form the feather sheath<sup>[9]</sup>. The cells of the inner epidermis will form the feather<sup>[8,9]</sup>. The epidermal layers are termed the "ramogenic zone"<sup>[8,9,13,15]</sup> from "rami" which means "branch" and "genic" which means "forming."

The ramogenic zone and the growth zone are collectively termed the follicle collar<sup>[9]</sup>.

2b). In addition to generating the ring-like growth zone at its base, the dermal papilla is the source of the feather pulp. As such, the core of the dermal papilla (and the feather pulp) is an extension of the dermis; it is nourished<sup>[8]</sup> by an artery and has nerve<sup>[3]</sup> and other connections to the underlying dermis layer of the skin. (So it is easy to understand why blood feathers are sensitive and bleed profusely when broken. The pulp is actually a living part of the dermis).

The pulp is the tissue through which keratinocytes receive nutrients<sup>[7,9]</sup>, and through which other types of cells

interact with the keratinocytes<sup>[9]</sup>.

At the base of the follicle, the dermal papilla induces the keratinocytes of the follicle collar to multiply and produce alpha-keratins that will be utilized to form the feather sheath<sup>[6,8]</sup>, and the phi-keratins that will be utilized to form the feather.

### How is a Feather Made?<sup>[A5]</sup>

*"All feathers develop as cylinders within the tubular epidermal collar of the feather follicle. The cylindrical organization of the follicle is the defining developmental and morphological characteristic of feathers."*<sup>[9]</sup>

It may be difficult to visualize how feathers form from reading a description; therefore, it may be helpful to view an Internet animation of how a feather forms<sup>[6]</sup> at <http://falon.anatomy.wisc.edu/feather.html>.

To summarize, the feather follicle has developed to the stages where the feather forms: A follicle, follicle collar and pulp have developed, and the keratins necessary to construct the feather are being produced. Now the specialized construction of the feather begins.

The epidermal region of the follicle collar begins to differentiate<sup>[15]</sup> into longitudinal ridges called barb ridges.<sup>[6,7,8]</sup> These ridges form what could be described as a mold for barbs and barbules. The height of the layers of cells within the barb ridges determines the length of the feather parts formed there<sup>[9]</sup>. For example, "the length of the single cell wide individual barbule depends on the "height" of the barb ridge"<sup>[13]</sup>.

In a symmetrical pennaceous feather (such as a contour feather), the collar begins the formation of a feather barb ridge at a point located on the center of its back (posterior midline)<sup>[7,9]</sup>, called a new barb locus<sup>[7,8,9]</sup>. As each barb locus develops, the cells of the growth point are offset toward the opposite side of the collar (anterior displacement)<sup>[8]</sup>. This causes each barb to grow at an angle, and not straight up resulting in a helical growth pattern<sup>[6]</sup>. In an asymmetrical feather (such as a primary feather), the new barb locus is offset from the posterior midline of the collar.<sup>[3,13]</sup>

Keratinocytes move through the pulp into the developing barb ridge and sheath layers. They produce the appropriate type of alpha or phi-keratin and die, leaving deposits of keratin within the ridges and sheath.<sup>[6]</sup>

The growth point of an individual barb continues to be displaced around the collar until it reaches the opposite side (anterior margin)<sup>[7,8]</sup>. There, the end of the barb is fused to the ends of prior barbs to form the shaft (rachis) of the feather<sup>[6,8]</sup>. In a down feather, which has no (or a very short) rachis<sup>[3]</sup>, the barb ridges grow straight, not helically, and do not fuse at the back<sup>[6,7]</sup>.

The feather continues to grow, with barbs developing from their tips to the rachis as the new barb loci move around the ring of the follicle collar, emerging from the fol-

licle inside its protective sheath<sup>[6]</sup>. The dermal pulp at the center of the feather is gradually resorbed and the sheath flaked away (usually by the preening activity of the bird). Removal of the sheath releases the feather, allowing it to unfurl from the tubular position it was constructed into the flat (planar) feather vane<sup>[6,7,8]</sup>. When the development and growth of the feather is complete, the follicle forms the quill (calamus)<sup>[6,9]</sup>, the pulp is fully resorbed, and growth activity within the follicle stops.

Interestingly, the barbules form as a tube<sup>[7]</sup> on the barb ridges. This tube consists of three plates of keratinocytes: the barbule plate<sup>[6]</sup>, the marginal plate (edge) and the axial plate (center, opposite the rachis)<sup>[7,15]</sup>. The marginal and axial plates shrink and die separating the barbs from one another and leaving the barbs free to unfurl as the feather sheath is flaked away<sup>[3,15]</sup>.

The same follicle is able to produce different types of feathers<sup>[9]</sup>. For example, a follicle may form down when a bird is a chick, contour feathers when an adult, and in adults of some species, may form courtship feathers of specialized color or form in season<sup>[7]</sup>. It can also produce multiple barb structures on the same feather: a downy base on a contour feather, the soft edges of owl flight feathers, the hairlike tips of Eclectus parrots' feathers or the array of iridescent structures and forms of the feathers of a Peacock's (*Pavo cristatus*) tail.

The quill will remain in the follicle until physiological changes signal the follicle to again begin the proliferation of cells at the follicle collar and commence the formation of a new feather. This proliferation and growth push the old feather out of the follicle: The molt<sup>[11]</sup>.

### How are the patterns on feathers made?<sup>[A5,C7]</sup>

*"The challenge in conceptualizing feather pigment pattern development is to reconcile the tubular nature of the feather follicle and germ and the helical growth of pennaceous feather barbs with the final planar form of the mature pennaceous feather."* [7]

As described in the previous section, feathers form from the tip down and from the outer (distal) tips of the barbs to the rachis<sup>[9,11]</sup>. The barbs form sequentially as they grow helically around the follicle collar. This is important to understanding how pigment patterns may and may not form on individual feathers (within-feather pigment patterning<sup>[7]</sup>).

#### *How the Feather Keratin Becomes Pigmented*

Although there are several pigment families, carotenoids (red and yellow) and melanins (black, gray and brown) appear to be most commonly used to color avian plumage. Carotenoids appear to be found in at least half of all avian orders, and melanins are found in all avian orders<sup>[2]</sup>. Here, melanin is used to illustrate one mechanism for delivery of pigment to feather keratin. While other pig-

ments are not brought to the keratinocyte or incorporated into it in the same way as melanin is<sup>[2,5,11]</sup>, the pigmentation of the keratin at the follicle collar<sup>[2,5]</sup> to create the in-feather pattern may be the same regardless of the pigment utilized.

Melanin pigment producing cells called melanocytes reside in the dermal pulp of the developing feather. During feather formation, melanocytes migrate from the dermal pulp to the collar of the developing feather. The melanocytes release melanin (in structures called melanosomes) to the keratinocytes at the forming barb ridges via hose-like extensions called pseudopodia. The keratinocytes then take up the pigment and incorporate it into the keratin they are producing. Feedback-regulated chemical "on-off" switches (reaction-diffusion system of activating/inhibitory signals<sup>[7]</sup>) govern the amount and length of time pigment is taken up by the keratinocytes.

#### *Patterning a Feather*

Individual feathers may have different patterns on them, including dots, patches, stripes, bars, and combinations of these. The patterns may be symmetrical or asymmetrical. How are these patterns made? Are there any limitations to the kinds of patterns that can be formed on an individual feather?

The key to visualizing how a feather may be patterned with pigment is to recall that the follicle collar is a ring, and the barbs grow helically out of it. To illustrate, if all the keratinocytes at the follicle collar of a single uncolored feather (white tube) were to accept pigment from melanocytes (black pigment) at the same moment in time for the same length of time and then stop at the same time (isochronic), the result at that moment would be a black stripe around the ring of the tube. But as the feather barbs continue to grow in their helical fashion, the stripe would become more and more offset. When growth is completed and the tube opened and laid out flat (planar), the black pattern on the barbs would not form a stripe across the feather, but would form a chevron (V) with the legs of the chevron the same angle as the angle of the barbs to the rachis.

Patterns of pigmentation observed on a mature, unfurled feather are the result of how the pigment was taken up by the keratinocytes and incorporated into the keratin of the feather barbs<sup>[9]</sup> at the follicle collar, and further, by the growth rate and angle of the feather barbs.

To determine what kinds of patterns might be possible within feathers, a mathematical model was devised which includes barb growth angle and rate, length of time pigments are and are not applied, and a simulation of how the "on-off" feedback signals operate.<sup>[7]</sup>

The model generated patterns of dots, bars, stripes, central "hollow," "eye," transitional, combinations of pattern elements and other patterns that are found in natural feathers. The models could be further expanded to simulate

more pattern types and include colors and differences in feather shape.[7]

Data was input into the model to generate patterns not known to appear in natural feathers. This was done in an attempt to understand what kinds of patterns are not produced by follicle collars. It appears that in nature, barbs are not utilized as elements of pattern or the pattern itself. For example, a feather patterned with a series of completely pigmented barbs and completely unpigmented barbs does not appear to exist in nature. Also, the follicle collar does not appear to pigment "around itself" in barber-pole or candy-cane stripe fashion (bar sinister).[7]

### Conclusion

From tube to plane and back again, rings of growth within specialized follicles organize and pattern unique phi-keratins into the most highly organized and intricate epidermal appendages found in vertebrates. These remarkable structures are found only on birds: Feathers. ❖

### End Notes

\*Examination of fossilized bipedal theropod (primarily) dinosaurs, such as those found in China and Germany, indicates that feathers or similar structures were present on dinosaurs that may be unrelated to modern birds.[1,3,7,8,9]

\*\*Much of this article is a summary of information contained in three primary references below. These are noted in the section headings as A5 (Lucas and Stettenheim 1972); B1 (Brush 1993) and C7 (Prum and Williamson 2002).

\*\*\*Beta-keratins are proteins and, like all proteins, are constructed from amino acids. Beta- and other keratins must not be confused with beta-carotene or carotenes. Carotenes, including beta-carotene, are a family of red or yellow unsaturated hydrocarbon pigments that are found in cells of plants, and the fatty tissues of plant-eating organisms. Beta-carotene is a precursor of vitamin A; it is not a protein.

### References

- [1] Brush, A., 1993. The origin of feathers. In Farner DS, King JS, Parkes KC, editors. Avian biology Vol IX. London: Academic Press. p 121-162
- [2] Brush, A., 1978. Avian pigmentation. In Chemical Zoology, Vol X, Aves (ed. AH Brush), pp 141-161. New York: Academic Press
- [3] Cheng-Ming, C et al 2003. Adaptation to the Sky: Defining The Feather With Integument Fossils From Mesozoic China and Experimental Evidence From Molecular Laboratories, J. Exp. Zool. (Mol. Dev. Evol.) 298B:42-56
- [4] Jiang, T-X. et al. 1999. Self-organization of periodic patterns by dissociated feather mesenchymal cells and the regulation of size, number, and spacing of primordia. Dev. 126:4997-5009
- [5] Lucas, A and Stettenheim, P., 1972. Avian Anatomy – Integument. Washington DC: US Department of Agriculture Handbook
- [6] Prum, R. and Brush, A., 2003. Which Came First, the Feather or the Bird?. Scientific American Vol. 288 No. 3 84-93
- [7] Prum, R and Williamson, S., 2002. Reaction-diffusion models of within-

feather pigmentation patterning. Proc R Soc Lond B Biol Sci 269 (1493):781-92

- [8] Prum, R. and Brush, A., 2002. The Evolutionary Origin and Diversification of Feathers, The Quarterly Review of Biology Vol. 77, No. 3 261-295
- [9] Prum, R., 1999. Development and Evolutionary Origin of Feathers, J. Exp. Zool. (Mol. Dev. Evol.) 285:291-306
- [10] Sawyer, R. et al. 2000. The expression of beta-keratins in the epidermal appendages of reptiles and birds. Am. Zool. 40:530-539
- [11] Stettenheim, P., 2002. The integument of modern birds: an overview. Am. Zool. 40:461-477
- [12] Welty, J. and Baptista, L., 1988. Skin, scales, feathers, and colors. In The Life of Birds 4th ed. Saunders. New York
- [13] Widelitz, B et al. 2003. Molecular Biology of Feather Morphogenesis: A Testable Model for Evo-Devo Research, J. Exp. Zool. (Mol. Dev. Evol.) 298B:109-122
- [14] Yong Mei, X., et al. 2003. Establishment of Feather Follicle Stem Cells as Potential Vehicles for Delivering Exogenous Genes in Birds. J. Reprod. Dev. 49:213-219
- [15] Yu, M. et al. 2002. The morphogenesis of feathers. Nature 420:308-312.

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