

## Evolving a Protofeather and Feather Diversity<sup>1</sup>

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**SYNOPSIS.** It is likely that feathers evolved from a conical shaped tubercle rather than a plate-like structure. Although the morphology of the presumably most primitive feather is unknown, minimal conditions for its production include the cellular capacity to synthesize feather proteins (=  $\phi$ -keratin) which provides the molecular phenotype, and a follicular mechanism for production and assembly of molecular and gross structure. Once the minimal structural element, presumably recognizable as a barb, existed, a variety of phenotypes followed rapidly. A tubercular growth center of appropriate size could produce a simple barb-like element, with cortex and medulla. This might be recognized externally as a bristle, but need never existed as a separate morphological unit. Rather, if individual placodes gave rise to multiple barb ridges that fused proximally, a structure resembling natal down would have resulted. Subsequent differentiation is controlled by the follicular symmetry, and the feather shape is regulated by barb length. Barb length is directly related to growth period. As feathers appear to grow at roughly similar, size independent rates, shape is determined by individual barb growth periods. The simple fusion of individual proto-barbs would produce a morphology identifiable as natal down. Although this might be the simplest feather structure, others could emerge quickly, perhaps simultaneously, a consequence of the same redundant processing. Once the machinery existed, broad phenotypic plasticity was possible. I constructed a feather phylogram based on these conditions, the fossil record, and ontogeny. I organized the subsequent changes in morphology by perceived complexity. The changes are simply individual responses to similar processes that might be time (when in ontogeny) and space (where on body) dependent.

### INTRODUCTION

There are almost as many candidates for the primitive feather as there are extant morphological types. The variety of biological roles ascribed to feathers is equally impressive. Uncountable numbers of words have been written in attempts to combine structure and function in attempts to reconstruct the primitive feather and explain *why* feathers evolved; *e.g.*, for flight, insulation, waterproofing, display, etc. (*e.g.*, Feduccia, 1995). The arguments often overlook the fact that the entire range of phenotypic plasticity in feathers is generated from a single set of structural proteins, predicated on very few identifiable structural elements, and uniformly produced by a common mechanism. The differences in the morphogenesis

of the various feather shapes are small and, to a large degree, correlate with differential growth and a high degree of repeated, but highly similar, events.

Flight feathers are found on the oldest known avian fossil, *Archaeopteryx* (Feduccia and Tordoff, 1979). At least two recognizable feather types are found on bird fossils from the early Cretaceous (Carroll, 1997; Padian and Chiappe, 1998). Interest in the origin of feathers was renewed recently with the discovery in China of *Sinosauropteryx prima* (Ji and Ji, 1996, original in Chinese). Originally thought of as “the earliest bird in the world,” and reported in the press as a ‘feathered dinosaur’, Ji and Ji (1996) considered it avian with feathers that “are small and short, and are not differentiated, not possessing the structures of other birds.” Chen et al., (1998) described *Sinosauropteryx* as a compsognathid dinosaur. The structures are essentially filaments and have “no structures showing the fundamental morphological

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features of modern bird feathers, but they could be previously unidentified protofeather which are not as complex as either down feathers or even the hair-like feathers of secondarily flightless birds.” (Chen, et al., 1998). The structures are clearly epidermal in origin, unbranched, probably tubular, and may cover most of the body. In addition to their implications regarding the ancestry of birds, the existence of a protofeather has profound implications for our understanding of the evolution of feathers.

The Yixian formations have subsequently yielded *Protarchaeopteryx robusta* (Ji and Ji, 1997) and *Caudipteryx zoui* (Ji et al., 1998), both considered theropods with essentially modern contour and primary feathers. Although probably younger than *Archaeopteryx*, these finds establish the presence of feathers in an avian ancestor and demonstrate that their origin was followed quickly or accompanied by the potential for great phenotypic plasticity. More than a single feather type exists in both the chronologically younger Chinese specimens and in the more advanced, but older, *Archaeopteryx*. This provides evidence for the appearance of feathers generally, but not one type in particular. In essence, we have no way to polarize the sequence in the evolution of feather morphology and by implication, feather function.

The feathers on *Archaeopteryx lithographica* are essentially modern in their morphological features (Griffiths, 1996). Only the finest ramifications of the vaned primaries are unanalyzed. The seven specimens are from the Late Jurassic period (Tithonian) of Bavaria (145–150 MYA). By comparison, the most primitive animals to possess feathers are the maniraptorian dinosaurs, *Protarchaeopteryx* and *Caudipteryx* (Ji et al., 1998). The feathers on these specimens are recognizable as symmetrical primaries and semiplumes on the body. The Yixian formations of Liaoning province in NE China are probably not older than 120 MYA (Smith et al., 1995; B. Edelman, personal communication) and, hence, early Cretaceous (Lucas and Estep, 1998). Although perhaps chronologically more recent, *Caudipteryx* is phylogenetically closest to *Archaeopteryx*, but may not be com-

pletely avian (Padian, 1998). The Yixian dinosaurs were cursorial, bipedal, and not capable of flight. Presumably, at this stage the role of feathers was probably other than for flight. Although there is no evidence as to how widespread feathers were in maniraptors, feathers clearly existed prior to the existence of *Archaeopteryx*. This recent and exciting discovery is important in understanding avian origins and ancestry. Documenting the origin of feathers, in fact, remains a distinct—and only partially resolved—issue.

It is possible to define and describe the minimal conditions necessary to produce a protofeather based on the analysis of the construction, ontogeny, regulation, and design of modern feathers. Minimally, just two conditions are necessary: the presence of the typical feather  $\phi$ -keratin (=feather  $\beta$ -keratin) and the existence of a follicle capable of fabrication. The chemical, cellular and regulatory factors involved were described recently (Brush, 2000). This discussion of the conditions implicit in the protofeather will be summarized below and, along with information based on modern feathers a phylogram developed. This exercise facilitates discussion of the nature of the phenotypic plasticity of feathers, allows speculation on the processes of feather origins, and accounts for their apparently rapid evolution.

Feather structure is both periodic and hierarchical (Edelman, 1988). Feathers display different kinds of structural symmetry that has functional significance and originates in development. Feathers have undergone shape changes during their evolution, but there is disagreement regarding the primitive shape. Edelman (1988) identified four processes that are key to feather morphogenesis. By extension, these processes may also apply to the evolutionary origin of feathers. The processes involve the formation of periodic symmetrical structures as the result of induction between germ layers; mechanical events derived from the motion of cells and sheets of cells; periodic boarder or boundary formation within single epithelial layers; and the correlation of histogenetic events (e.g., keratinization) in precise fashion within such boundaries. All

these pattern-producing processes, at some level, are ultimately regulated genetically. The combination of symmetry, reiterated structure, and gradients of operation all contribute to a high evolvability of the system (Gerhart and Kirschner, 1997).

The essential design of feathers must have been constrained by geometric rules, the properties of the constructional materials, and the process of growth and development (for a recent general discussion, see Authur, 1997). The fossil record helps understand this design. The elements of feather configuration must be considered quite stable. The rules that govern their construction and assembly are not completely known for all levels of organization, but some (*e.g.*, molecular folding, filament formation, chemical aspects of morphogenesis) are understood because of their general nature and almost universal occurrence (Oster and Alberch, 1982). The initial conditions for the appearance of feathers also probably resides in processes common to all ammonites and include placode formation, invagination, and mesenchymal–epithelial interactions. In addition to the similarities in the keratins used in construction, many of the chemical signals in development are shared broadly among animals. Molecular regulatory mechanisms mediate cell surface conditions and the various cell–cell interactions. They can be place specific, cellular, and extracellular. These processes together integrate the structural elements and reflect adaptations to environmental conditions. The diversity of feathers reflects opportunism constrained by structural limitations and historical events.

Feathers are chemically initiated and regulated. Topography and geometry define the overall and individual growth patterns. Structural elements are produced in transformed cells within the follicle. There are repeated patterns of cellular shape and activity at each level. Coordination of these processes is molecular. Feathers are not weight-bearing elements, and they are flexible, not jointed. The geometry of the essentially tubular structure is determined by physical features; the overall shape by growth patterns. Hence, the rachis, which provides the central support has a variable

diameter and tapers distally. The heaviest portion is at the base and a consequence of the slowest growth rates. Overall shape of each feather is defined by barb length and determined by growth patterns. The high keratin composition provides adequate strength for repeated bending and flexing, but is subject to abrasion. The semi-crystalline filamented structure provides internal support (Brush, 1978), superimposed on the structural interactions of branched structures that produce the vane of body contour and flight feathers. While all feathers wear, they are replaced regularly by the molt processes.

What emerged is a complex structure produced from relatively simply organized materials. Multiple, repeated interactions such as self-recognition and self-organization combine to yield mechanical strength and increase size in common geometric elements. Patterns of differentiation and cellular functions are, in turn, regulated by genes and chemical growth factors that regulate segmentation of the repeated, linear occurrence of simple elements. The appearance of feathers in the avian ancestor marked the emergence of a flexible design that included an internal geometry and structure that afforded phenotypic plasticity. Through various combinations and serial repetition of existing parts, morphological complexity proliferated.

The very early steps in the evolution of a protofeather largely reflect the development of modern epidermal structures. However, rather than being derived directly from a flat Archosaurian scale (Maderson, 1972), a tubercle-like morphology was involved. Similar structures have been found on dinosaurs and living reptiles. Tubercles afford the formation of a filament, quite possibly one that is hollow. The early feather bud would have been radially symmetrical. The growth centers (*i.e.*, barb ridges) would have produced columns rather than plates of cells. The basal cells would have synthesized  $\phi$ -keratins rather than primarily alpha-keratins. Hence, the tubercle would have represented a rather complete morphogenic unit. Anatomically and functionally, the follicle is partitioned internally and isolated

from the environment by the sheath (Sengel, 1976).

Comprehending the nature and the potential of a feather-generating structure is based on the proposition that a set of structural genes and their proteins are semi-isolated and internally coordinated. Development is regulated by discrete cell-based centers through inductive signals. The protein products from genes that influence morphogenesis pattern act as local signals. Genes, such as HOX, BMP, and CAM, that regulate patterns of growth are co-opted from existing programs and activated internally. Other molecules act as chemical signals to control formation and growth of margins and other landmarks in development. This has become a standard model in developmental biology (Lawrence, 1992; Slack *et al.*, 1993). Subsequent processes such as gene duplication and deletion provide redundancy in a system that grows primarily by repetitive events. The feather bud, from the start, included the part or potential parts for production and assembly of the final structure. It had become a follicle. Even the orientation on the body surface of the follicles is controlled chemically (Normaly and Morgan, 1998). The morphological unit, now visible on the skin, *in ovo*, has changed from an early association of specialized cells through physical processes (contraction, movement, folding, involution, etc.). Once the follicle formed, its modular nature allowed change semi-independently of the organism. In the case of feathers, the developmental plasticity was maintained through various spatial and temporal controls of gene activity and differential rates of processes. In turn, these processes have direct implications for determining feather size and shape. Consequently, morphological diversity can be generated rapidly.

An early follicle would have conserved specific molecules and developmental pathways. The regulatory genes (*i.e.*, various growth factors) are not unique to feather evolution, but shared widely among animals (Raff, 1996; Gehring, 1998). Simple process such as the modification of growth rates would have affected size and shape appropriate to body size and feather func-

tion. The spatial and temporal regulatory mechanisms which control structural gene expression are relatively free to vary and, in turn, are subject to selection. Changes of both types produce patterns of gene expression that result in alterations of growth patterns and, further downstream, morphology. A simple case is the proportion of pinnaceous and plumulose portions of contour feathers (Brush, 1972).

Whether or not the structure on *Sinosauropteryx* represents a protofeather may be moot. Regardless, a protofeather would have occurred first on a flightless animal. The feathers of flightless extant taxa are often modified in shape and reduced in complexity. McGowen (1989) illustrates such feathers, parts of which could be considered hair-like. Other phenotypically simple feathers include bristles (Stettenheim, 1973), filoplumes (also called secondary feathers), and numerous decorative feathers. Examples include the crown and tail feathers of birds-of-paradise, drongos, Bristle-thigh Curlew (*Numenius tahitiensis*), etc. As far as is known, all are produced by a follicle and constructed of feather keratin. Perhaps the most unusual of the modified structures is the beard of the Turkey, *Meleagris gallopavo*, (Lucas and Stettenheim, 1972, Stettenheim, 2000). These structures are bristle-like, grow continually, and have an extraordinary papillary organization. Their protein composition is unknown. Nevertheless, there is nothing to indicate that any of these bristles, which essentially lack barbs along most of their length, is in any sense primitive among feather morphologies (*e.g.*, plesiomorphic).

It is not likely, that a complete, detailed fossil record of feathers will ever exist. However, the occurrence of primitive and advanced species bearing common features is informative. Fossils provide some interesting insights to possible evolutionary events. Present knowledge of molecular composition, ontogeny, and follicular activity could provide important clues to the evolutionary mechanisms, even if the actual taxa involved remain unknown. For some purposes, the precise taxa are not important, nor are the exact times. It is possible to use extant information to reconstruct what



might have been a primitive feather and understand the modifications necessary to produce the observed historic morphological changes.

#### FEATHER PHYLOGRAM

Not surprisingly, numerous candidates have been suggested as primitive among feather phenotypes (for summaries see Lucas and Stettenheim, 1972; Feduccia, 1996; Chatterjee, 1997, Fig. 8.5). The interpretation of the nature of a primitive feather has often been related to function. One argument associates feather evolution with the evolution of flight, but these are clearly separate events. Feathers are necessary for flight, but myriad other conditions would be sufficient for their evolution. What seems to be lacking is an attempt to establish polarity in the feather phenotypes. The archetypical ancestral phenotype may, or may not be, a bristle-like feature as found in *Sinosauropteryx*. Although structurally simple, bristle-like feathers in extant species are almost all modified from contour-like feathers (Stettenheim, 1973). It is possible, however, that a stage which resembles a simple bristle might have occurred in the evolutionary morphogenesis of feathers. After all, an elongated tubercle, if it met the conditions described above, would have the appearance of a simple, single filament. A default internal organization that included a cortex and medulla is typical of epidermal structures. Externally, the sheathed natal down of many birds resemble just such a structure.

Assuredly, all feathers share a common ancestor. However, it is conceivable that no neornithine feather retains this very primitive morphology. Feather morphology is varied, whereas the apparent genetic basis that produces it is uniform. Variation in structural morphology may imply a 'default' form. Actually, a structure with multiple functional roles may be polymorphic with genetic switching between two or more equally likely states. This may be the case in feathers. Certainly, the follicle can produce different morphologies dependent on its location. Further, individual follicles produce feathers of different morphologies over the course of their life. They shift from

one morphology to another, albeit it in a linear sequence. What follows, is my attempt to integrate the massive amounts of new information in a diagram that reflects current thinking on the phenotypic evolution of feathers. Figure 1 is derived from the following arguments.

#### Outgroup

Structures that contains the  $\alpha$ -keratin base common to amminotes. The  $\alpha$ -keratin construct is older than the  $\beta$ -keratins included in reptilian scales and ultimately feathers. In mammals,  $\alpha$ -keratin is found in hair, bristles, hooves, nails, and claws as well as in soft skin. In birds, in addition to the soft skin,  $\alpha$ -keratin is the major component of the reticular scales of the planar surface of the foot and the membranes that cover the developing feather. It forms the soft skin and scales in all reptiles.

#### Sister group

The closest related protein structures to bird feather proteins constitute the scutellate scales, claws, and beaks (Brush, 1980, 1985). The  $\phi$ -keratins in this structural group are larger (14.5 kd) than in feathers (10.4 kd). Although they share a placode stage in early development, the subsequent morphogenesis is different, no follicle is present, and the structures grow continuously. Feather follicles display a different pattern as they are replaced through a typical molt cycle. Chemically the keratin of these structure differs consistently in the presence in the presence of a repeated tripeptide.

#### Protofeather

A protofeather would be the simplest filament-like structure unit made of  $\phi$ -keratin. Morphologically and developmentally it may have resembled a barb. It had an hollow internal portion with the medulla occupied by fluid with blood and nerve supply. It might have grown continuously, but evidence on this point is lacking. The overall growth pattern was the result of early coalescence of multiple growth centers. The individual growth centers were structured internally and functioned like the extant barb ridge. The visible structure was tuber-

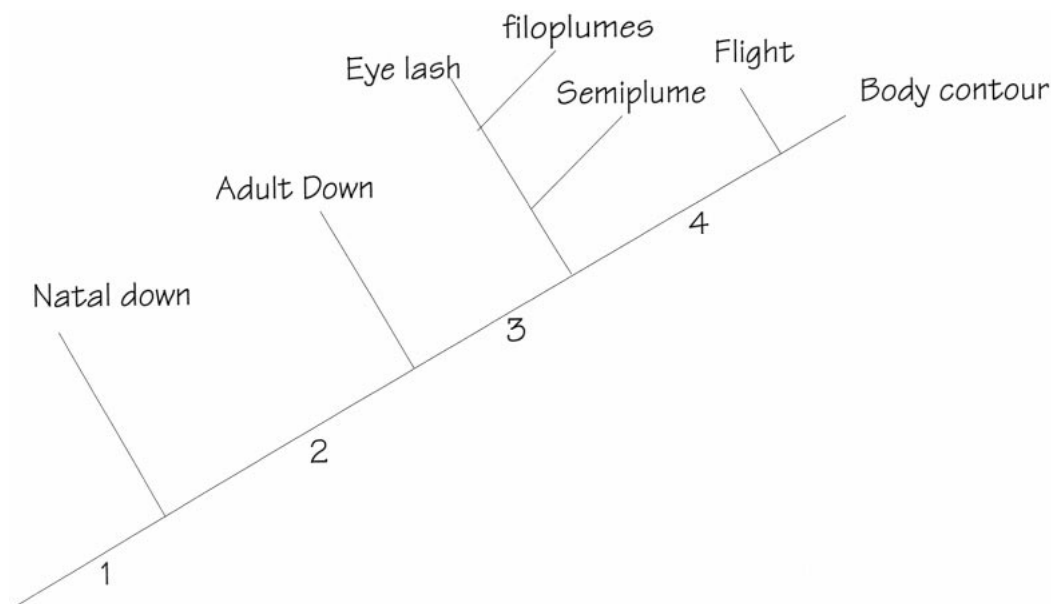


FIG. 1. Major branches of feather evolution. The pattern reflects increased morphological complexity, but branch length is arbitrary. The outgroup includes scutes, claws, and scales, and is based on a larger (14.4 kd) keratin and differ in patterns of production and development. The most primitive structure may have been a protofeather. Node 1: all structures are constructed from 10.5 kd  $\phi$ -keratin, fabricated by a follicle, with barbs fused at the base. Natal down is the first generation ontogenetically in all extant birds. Morphology is relatively simple. There is no rachis, and barbs lack further ramification. Node 2: second generation feature (separated by a molt from the first). In adult down, barbs can be simple with reduced or incomplete barbules; rachis present; follicle asymmetrical; vane unorganized. Node 3: includes pennaceous and plumulose barbs; rachis central structure, shaft often curved on long axis; full array of barbule morphology; barbs reduced or absent in selected areas. Node 4: vane fully formed; symmetrical inbody contour feathers, asymmetrical in remiges and rectrices.

cle-like. Individual filaments, when adequately elongated, may have provided functional surface features. Sculpting in the ramogenic center was under chemical control. Eventually, the barbs, as they move during synthesis towards a center point, fused at the proximal ends and formed a downy feather-like structure (Brush, 2000).

#### *Natal down*

Natal down is the earliest feather (first) generation in ontogeny. Barbs of natal down have structural subdivisions which might not occur in a protofeather. Natal downs frequently lack a rachis, but numerous barbs come together at a common point. This convergence and fusion is a consequence of the follicular structure. An interlocking vane is lacking, so the structure is entirely plumulose in character and keratinized in composition. In essence only one degree of branching is present.

#### *Adult down*

Adult down is a plumulose structure, based essentially on barb construction. Adult down is a second generation product. There is a small rachis, always shorter than the barbs, which implies a break in the symmetrical structure of the follicle. Symmetry is broken when one presumptive barb ridge enlarges and becomes the focus of barb fusion. No vane is present. The downs themselves are quite variable in shape.

#### *Semiplume*

Semiplumes have a rachis longer than the barbs, and are plumulose throughout. Well defined, functional barbules are absent. These numerous feathers are typically open structures that underlie body contour feathers and originate in the contour feather follicle. They make little or no contribution to the external surface of the bird. Ratite body feathers are plumulose.

*Contour feather*

Contour feathers are abundant and typically consist of both plumulose and pennaceous portions. They are symmetrical, but highly variable in overall shape. Flight feathers are essentially an asymmetrical contour feather and grow specifically on the hand.

*Filoplumes*

Pennaceous distally, but proximal barbs lack barbules. Becker (1959) considered this to be the original feather. They often share a follicle with a contour feather.

*Modified feathers*

This category includes feathers that exist in various combinations of structural elements. The bristle and eyelash consist of a rachis void of barbs, except at the innermost base. Small feathers that boarder featherless areas often have an extended, barbless rachis. Various display feathers consist of fused barbs or selective elimination of barbs. Examples include display feathers on the head of many birds-of-paradise, tips of the Cedar Waxwing (*Bombicilla cedrorum*) primaries, and racquet-shaped tail feathers (e.g., Motmots, flycatchers). When coupled with pigment patterns, the visual effect of these feathers can be stunning.

## DISCUSSION

The existence of diverse feather morphology even on individuals is quite consistent with a single genetic construction. There is a close correlation of the protein data among individual structural components and among feather types. Feathers are all constructed from the same protein set and undergo the same biochemical transformations, such as filamentation and keratinization. Moreover, barbs on single feathers can have identical protein composition, but with modified filament arrangements and strikingly different shapes (Brush, 1978). The choice between alternative forms in feather morphology may depend on simple epigenetic or environmental factors. Compare, for example, the feathers produced on different parts of the body. It is possible, in principle, that heri-

table genetic changes would bias such choices and lead to distinct morphological varieties. By implication, once a primitive feather emerged, the subsequent morphological evolution could have been implemented by the selective stabilization of particular forms within the ontogenetic repertoire.

The follicular mechanism marks the appearance of a modular unit capable of generating the complete range of feather shapes. Selection may act to modify ontogeny and ultimately determine morphology and function. Although follicles in different locations on the body produce different feathers, they are all the result of uniform processing within the module. Further, some follicles produce both a contour feather and an afterfeather simultaneously. In this case, the same follicle generates two structures of different morphologies. Many of the phenomena encompassed in follicular activity involve chemical or mechanical processes, are repetitive, and may themselves generate significant forces at the tissue level. Adjustments in timing, especially growth, are effective, especially as simple cellular events are repeated, amplified, or undergo changes in periodicity. The universal processes in the epidermis include thickening, placode formation, and histological organization for growth. These are in turn modified by epithelio-mesenchymal interactions. Growth factors and other intercellular messengers participate at various organizational levels and over time. One example is the repeated induction of structural subdivisions in the linear structural elements.

Because of these features, the most primitive feather, whatever its morphology, had an innate potential for structural variation. Its potential for change would have been high, a feature that characterizes evolutionary novelties (Gerhart and Kirschner, 1997). An event such as the appearance of feathers must involve a hierarchical array of events and changes. An event of this type not only involves the appearance of unique genes, but modifies the way genetic variation maps onto phenotypic variation (Wagner and Altenberg, 1996). Structural redundancy at the level of genes, proteins, and

structural elements is inherent. The existence of follicular capacity to produce morphological diversity existed prior to the complex external morphology. In the model presented here, the follicle produced and assembled linear, hollow structures. The primary structures are subject subsequently to variable degrees of branching. Externally, growth translated into elongation would be adequate to transform the primary tubercle (now the feather bud) into something like a bristle or a large filament.

At a finer scale, the follicle consists of ramogenetic centers, distributed symmetrically, and capable of producing columns of cells. Internally, as the incipient barbs grow in length, moving laterally within the follicle and outward along its length, the structural cells undergo keratinization, which, among other things, involves the production of filaments through the self-assembly of protein chains. Protein synthesis and folding occur within the cell. At appropriate concentrations, they assemble into filaments. There are the essential elements of histogenesis, and support the standard epithelial model of feathers. Feather morphology is an emergent feature of these processes, plus the assembly mechanism inherent in the follicle. Ultimately many individual feathers combine to fashion the plumage, which may be considered another emergent feature.

The system behaves as if its individual elements were an amalgamation of smaller, simple units. Feathers, however bizarre or morphologically complex, consist essentially of a rachis, barbs, and barbules. Combined, they can generate even the most complex plumage. In a sense feather structure is polymorphic, and genetic switching can occur between equally likely states (Wake and Roth, 1989; Newman, 1994). This is the observed pattern of the molt cycle, with modifications on the time axis. In the extreme, one could argue that there is no simple default state for feathers, but that a polymorphic structure develops from the same embryological source. I submit that the default structure was likely a proto-feather (in this case a simple filament) or a simple natal down. Nevertheless, feathers are also unique in that sequential variability

in feather structure is produced from the *same* follicle. This implies that the numerous morphological forms are consistent with a single genetic constitution. That is, each morphological generation is read off the same genetic instructions and generated in by the same processing. Choices among the forms are heritable and depend on epigenetic process (*e.g.*, vane formation emerging from the combined structural elements on adjacent barbules) or internal factors that influence gene expression (West-Eberhard, 1989).

The question of why a relatively complex machinery was necessary to produce a relatively simple object is not directly answerable (Feduccia, 1985, 1995). Perhaps the most primitive structure unit was cable-like and reflected the filamented keratin macromolecule. At each level, the follicle and the feather is an amalgamation of smaller, simpler units. Emergent properties, such as the curve in the rachis, while functionally significant, are the result of simple processes such as differential growth. From the elemental barb, all other morphology follows, as the barb is the simple structural unit.

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