Development and Evolutionary Origin of Feathers

RICHARD O. PRUM*
Department of Ecology & Evolutionary Biology, and Natural History Museum, University of Kansas, Lawrence, Kansas 66045-2454

ABSTRACT   Avian feathers are a complex evolutionary novelty characterized by structural diversity and hierarchical development. Here, I propose a functionally neutral model of the origin and evolutionary diversification of bird feathers based on the hierarchical details of feather development. I propose that feathers originated with the evolution of the first feather follicle—a cylindrical epidermal invagination around the base of a dermal papilla. A transition series of follicle and feather morphologies is hypothesized to have evolved through a series of stages of increasing complexity in follicle structure and follicular developmental mechanisms. Follicular evolution proceeded with the origin of the undifferentiated collar (stage I), barb ridges (stage II), helical displacement of barb ridges, barbule plates, and the new barb locus (stage III), differentiation of pennulae of distal and proximal barbules (stage IV), and diversification of barbule structure and the new barb locus position (stage V). The model predicts that the first feather was an undifferentiated cylinder (stage I), which was followed by a tuft of unbranched barbs (stage II). Subsequently, with the origin of the rachis and barbules, the bipinnate feather evolved (stage III), followed then by the pennaceous feather with a closed vane (stage IV) and other structural diversity (stages Va–f). The model is used to evaluate the developmental plausibility of proposed functional theories of the origin of feathers. Early feathers (stages I, II) could have functioned in communication, defense, thermal insulation, or water repellency. Feathers could not have had an aerodynamic function until after bipinnate, closed pennaceous feathers (stage IV) had evolved. The morphology of the integumental structures of the coelurisaurian theropod dinosaurs *Sinosauropteryx* and *Beipiaosaurus* are congruent with the model's predictions of the form of early feathers (stage I or II). Additional research is required to examine whether these fossil integumental structures developed from follicles and are homologous with avian feathers. *J. Exp. Zool. (Mol. Dev. Evol.) 285:291–306, 1999.*   © 1999 Wiley-Liss, Inc.

Avian feathers are a premier example of a complex evolutionary novelty. The evolutionary origin of feathers remains controversial and poorly understood (Brush, '93, '96). Investigation of the evolutionary origin of feathers has been constrained by the lack of any known ancestral feather morphologies or structural antecedents. Feathers first appear in the fossil record in *Archaeopteryx* in completely modern form (de Beer, '54; Griffiths, '96). Interest in the origin of feathers has recently been revitalized by the discoveries of novel epidermal structures in the coelurisaurian theropod dinosaurs *Sinosauropteryx* (Chen et al., '98) and *Beipiaosaurus* (Xu et al., '99) and the description of fully pennaceous feathers on two species identified as nonavian theropod dinosaurs–*Protarchaeopteryx* and *Caudipteryx* (Ji et al., '98). The possibility that these newly discovered integumental structures could be homologous with avian feathers has focused attention on current theories of feather origins and exposed a lack of consensus about the morphology of the earliest feathers.

Early theories of feather origins focused on determining whether the first feathers were plumulaceous (i.e., downy) or pennaceous (i.e., having a planar vane) (for a thorough review of theories of feather origins see Dyck, '85). Evidence for these hypotheses was drawn from the structural variation of feathers and their taxonomic distribution among extant birds (Dyck, '85). This approach was subsequently criticized and abandoned because most extant feathers show derived features that disqualify them as representative of the primitive feather morphology.

Subsequently, theories about the origin of feathers focused on adaptive and functional explanations of the evolution of feathers from primitive reptilian scales (Dyck, '85). The proposed selective explanations include flight (e.g., Parkes, '66;

*Correspondence to: Richard O. Prum, Natural History Museum, Dyche Hall, University of Kansas, Lawrence, KS 66045-2454. E-mail: prum@ukans.edu

Maderson, '72; Feduccia, '93, '96), thermal insulation (reviewed in Lucas and Stettenheim, '72; Dyck, '85), heat shielding (Regal, '75), display (Mayr, '60), and water repellency (Dyck, '85). These theories generally hypothesize an ancestral function for the first feathers, and then propose a primitive feather morphology that can fulfill this function. This functional approach has many obvious problems. Inferring the function or selective advantage of a known structure in the absence of direct observation can be a significant challenge, but hypothesizing the morphology of an unknown structure based on its hypothesized ancestral function is an extremely weak inference.

Current functional theories are insufficient to explain the origin and diversification of feathers and are a hindrance to evaluating homology between feathers and newly described fossil integumental structures. What is required is a theory of the origin of feathers that is based on available evidence and that is independent of hypotheses about their presumed ancestral function. Among the most relevant research questions about the origin of an evolutionary novelty is: What derived developmental mechanisms are required to create the novelty (Müller and Wagner, '91)? A rich and highly relevant source of information about the evolutionary origin of feathers comes from the complex mechanisms of feather development. Although feathers are diverse in form, they all share a common developmental origin in the cylindrical feather follicle. Indeed, since a single follicle can produce feathers of striking structural diversity during the life of a bird, the tremendous structural diversity of feathers is best understood in terms of the control of feather development within the follicle. The development of feathers is also essential to any discussion of feather origins because any complete theory of the origin of feathers must account not only for structure of feathers themselves but for the structure and complexity of the follicle. Thus, hypothesized ancestral feathers must be morphologies that can be grown by some combination of plausible developmental mechanisms within a plausible follicle.

Recently, Brush ('93, '96) emphasized the differences between feathers and reptilian scales and documented the unique aspects of avian feather φ-keratins, feather morphology, and feather development. Brush ('96) concluded that feathers are a hierarchically complex evolutionary novelty and that progress in understanding the evolutionary origin of feathers can come from detailed examination of the distinct features of feathers at the genomic, molecular, developmental, and morphological levels. Subsequently, Brush ('99a,b,c) has further elaborated a model of the origin and diversification of feathers based on consideration of their biochemical, structural, and developmental complexity. Brush ('99a,b,c) proposes that feathers are defined by the presence of feather φ-keratin and a follicle, and that feather morphology diversified rapidly following the origin of the feather follicle. Brush ('99b) further proposes a phylogram of feather diversity that hypothesizes explicit evolutionary relationships among modern classes of feather morphology.

Here, I propose a new theory for the evolutionary origin and diversification of feathers that hypothesizes a transition series from the simplest feather follicle to the modern feather follicle through a series of novelties in feather development. First, I review the structure of extant feathers and how they develop. Second, I present the model in which the details of feather development are used to polarize the sequence of evolutionary novelties in the history of feather evolution. The evolutionary polarities of the events in feather development are inferred from the hierarchical organization of events in feather development, or, in some instances, by the physical necessity of a given structure to subsequent developmental events (Müller and Wagner, '91). In the discussion, I review evidence in support of the model, and evaluate whether the predictions of current functional theories of feather origins are developmentally plausible. Also, I discuss the congruence between the plesiomorphic feather morphologies predicted by the model and recent discoveries of epidermal derivatives in fossil theropod dinosaurs. Last, I discuss the implications of the model for investigations of the molecular mechanisms of feather development.

OVERVIEW OF FEATHER STRUCTURE AND DEVELOPMENT

A feather is a branched, or pinnate, epidermal derivative composed of a matrix of intracellular keratin (Fig. 1A). [This outline of feather terminology, morphology, and development is based on Lucas and Stettenheim ('72). Only a few notable additional details are specifically referenced.] A typical bipinnate (i.e., double branched) contour feather is composed of the calamus, or basal quill, that extends into the rachis, or central shaft of the feather. The primary branches of the rachis are the barbs. The main shaft of a barb is the ramus, and it supports the secondary branches of
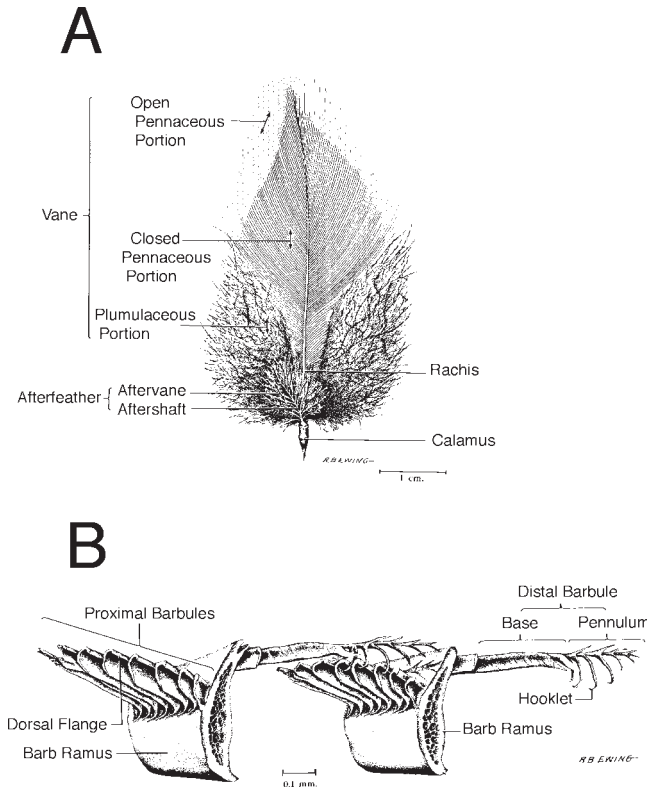
A

B

Fig. 1. (**A**) The structure of a typical pennaceous contour feather with afterfeather. (**B**) Cross-section of feather barb rami from a closed pennaceous feather showing the differentiation between the distal barbules (oriented toward the tip of the feather) and the proximal barbules (oriented toward the base of the feather). The hooked pennulae of the distal ends of the distal barbules interlock with the grooved dorsal flanges of the bases of the proximal barbules from the adjacent barbs forming the closed pennaceous vane. The distal barbules of open pennaceous feathers lack hooked pennulae. Both illustrations from Lucas and Stettenheim ('72).

the feather which are called barbules. Barbules consist of a series of cells, beginning with the short cells of the base and ending with a series of longer, distal cells, called the pennulum (Fig. 1B). The barbules oriented away from or toward the base of the feather are referred to as the distal and proximal barbules, respectively.

The diversity of feathers is a consequence of microstructural variation in the rachis, rami, and barbules. For example, closed pennaceous feathers have continuous, planar vanes that are created by the interlocking interaction of the hooked pennulae of the distal barbules and the simpler, grooved pennulae of the proximal barbules of the neighboring barbs (Fig. 1B) (Dyck, '85). Open pennaceous feathers, or portions of feathers, are bipinnate but lack tightly coherent vanes because

the distal barbules lack terminally hooked pennulae (Dyck, '85). Plumulaceous feathers, or downs, typically have elongate barbules with nodal prongs that interact among barbs to form disorderly tangles that produce a large volume. Other classes of feathers, including flight feathers, bristles, natal downs, filoplumes, and afterfeathers, can be recognized by distinct microstructural features.

Unlike other branched biological structures, such as plants, feathers do not grow from bifurcating tips but from their bases. In all feathers, the distal tips of the feather filaments are produced first, the proximal portions are produced later, and, ultimately, the calamus is produced last. The cells in any horizontal section of a feather develop at approximately the same time.

The feather follicle is the complex organ that provides the spatial organization required to grow feathers. The positioning of the follicle and the control of development within the follicle is determined by a complex cascade of induction and communication between the dermis and epidermis (Sengel, '76; Wolpert, '98). With few exceptions, the follicles that produce all the feathers in a bird's life develop during the first 12 days of life in the egg. First, an epidermal placode appears above a condensation of dermal cells that specify the location of the feather follicle (Fig. 2A). Subsequent proliferation of dermal cells by induction from the epidermal placode produces a finger-like feather papilla, or feather bud. The papilla grows more rapidly on the dorsal side and quickly establishes dorsal and ventral surfaces (Fig. 2B). Next, the dermis induces the epidermis to proliferate around the base of the papilla, creating a cylindrical invagination of epidermal tissue into the dermis around the base of the papilla (Fig. 2C). This cylindrical invagination creates the feather follicle that is uniquely characterized by an outer dermal layer, an outer epidermal layer, a follicle cavity or lumen between the two epidermal layers, an inner epidermal layer, and the dermal pulp at the center (Fig. 2D). The outer epidermal layer becomes keratinized and forms the walls of the socket of the feather follicle, whereas the inner epidermal layer becomes the collar of the feather follicle.

Virtually all feather growth takes place within the epidermal collar of the follicle (also called the ramogenic zone; Lucas and Stettenheim, '72). The dermal pulp at the center of the follicle supplies nutrients for the growth of the feather and is also the source of feather pigments. Feather growth proceeds within the collar by the proliferation of
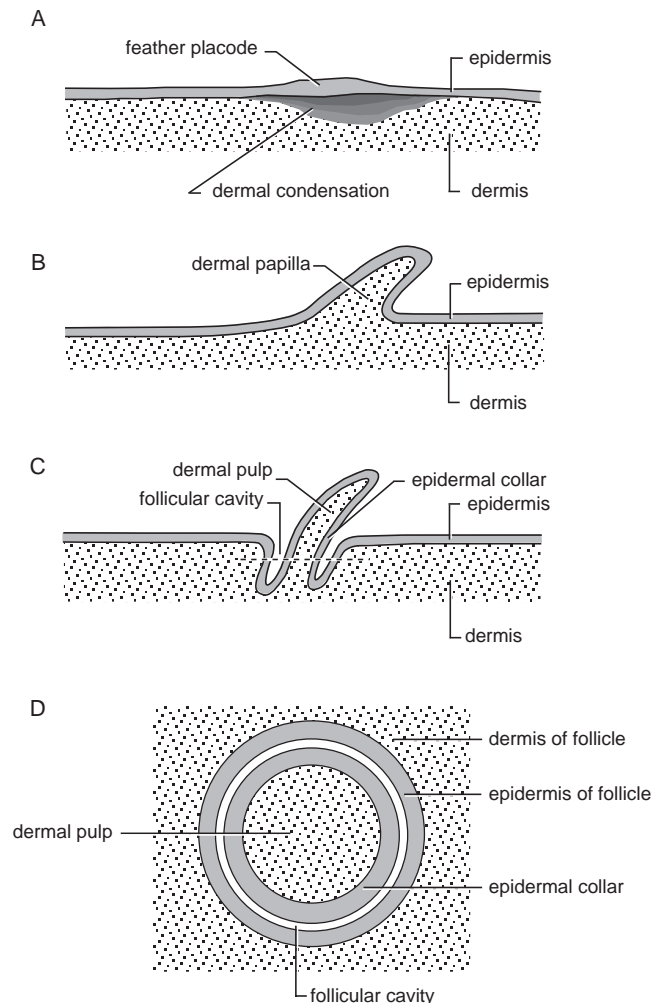
A

feather placode

epidermis

dermal condensation

dermis

B

dermal papilla

epidermis

dermis

C

dermal pulp

epidermal collar

follicular cavity

epidermis

dermis

D

dermis of follicle

epidermis of follicle

dermal pulp

epidermal collar

follicular cavity

Fig. 2. Schematic diagram of the development of a feather follicle. (**A**) Development of the epidermal feather placode and the dermal condensation. (**B**) Development of a feather papilla (or elongate feather bud) through the proliferation of dermal cells. (**C**) Formation of the feather follicle through the invagination of a cylinder of epidermal tissue around the base of the feather papilla. (**D**) Cross-section of the feather follicle through the horizontal plane indicated by the dotted line in C. The follicle is characterized by the juxtaposition of a series of tissue layers (from peripheral to central): the dermis of the follicle, the epidermis of the follicle (outer epidermal layer), the follicle cavity or lumen (the space between epidermal layers), the follicle collar (inner epidermal layer), and the dermal pulp (tissue at the center of the follicle). The proliferation of feather keratinocytes and most of the growth of the feather takes place in the follicular collar.

keratinocytes, which produce intracellular feather keratin. Each layer of cells is pushed upward and out of the collar by younger, more basal cells proliferating below. Gradually, older, more superficial keratinocytes become isolated from nutrients provided by the dermal pulp, and they die, leaving

behind the keratin matrix that constitutes the mature feather.

The different parts of the feather are created by differentiation within the follicle collar. The peripheral layer of the collar produces a cylinder of keratin that forms the superficial, deciduous sheath of the emerging feather. The inner layer of the epidermal collar becomes organized into a series of longitudinal ridges known as barb ridges. Keratinocytes within the barb ridges produce filaments that become the rachis, rami, and barbules of the growing feather.

The primary branched structure of the barbs and rachis of a pinnate feather is produced by helical displacement of barb ridges within the follicle (Fig. 3). Subsequent, younger cells within each barb ridge do not grow directly below the older, more superficial cells. Rather, they are displaced in position within the cylindrical collar toward the anterior midline of the follicle. [I differ from Lucas and Stettenheim ('72) in using "anterior" and "posterior" instead of "dorsal" and "ventral" to refer to the primary axis of orientation

Earliest

Later

Barb Ridges

Earlier Position of New Barb Locus

Rachis

Follicle Collar
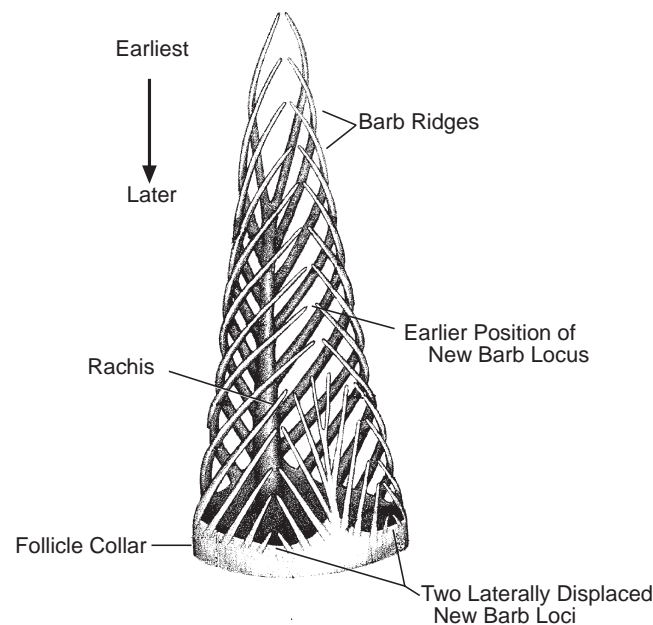
Two Laterally Displaced New Barb Loci

Fig. 3. Diagram of helical displacement of barb ridges within the follicle of a feather with a main feather and an afterfeather (from Lucas and Stettenheim, '72). Initially, barb ridges form at the new barb locus on the posterior midline of the collar and are gradually displaced, as they grow, around the collar toward the anterior midline, where they fuse to the rachis ridge to form the rachis. Following the formation of the paired new barb loci, new barb ridges are helically displaced anteriorly toward the main rachis and posteriorly to form the rachis and vane of the afterfeather. A mature contour feather with afterfeather is illustrated in Figure 1A.

within the follicle. The use of "anterior" and "posterior" avoids confusion between terminology for the orientation within the follicle and the orientation of the vane of the mature feather.] As a consequence, barb ridges are helically displaced as they grow toward the anterior midline of the follicle where they fuse to the largest, anterior-most barb ridge, called the rachis ridge, which becomes the rachis of the emerging feather. New barb ridges form at the new barb locus, a site along the posterior midline of the collar opposite the rachis ridge in symmetrical feathers (Fig. 3). As new barb ridges are formed, the follicle may increase in diameter. From the new barb locus, barb ridges begin their helical displacement around the collar to fuse with the rachis ridge at the anterior midline of the follicle and create the barbs of the left and right sides of the feather vane.

The secondary branched structures of the feather—the barbules—are produced by peripheral-basilar differentiation and cell death within layers of cells of the barb ridges. The inner cells within the barb ridges form the ramus, or main shaft, of the barb while the peripheral cells differentiate into the barbule plates that form the barbules of that barb. Barbule filaments are one cell thick, so each horizontal layer of cells constitutes a single barbule plate that becomes a single pair of barbules. First, the peripheral barbule plate differentiates from the main ramus. Then, the barbule plate differentiates into a lateral pair of plates by the death of the cells along its central axis. The peripheral cells in the paired barbule plates become the distal cells of the barbules, and the more central cells become the base of the barbules, which fuse to the ramus. Since cell proliferation and growth within the collar produces vertical displacement, the distal cells of the barbules are displaced upward out of the follicle as the barbules grow.

As the feather approaches its final size, new barb ridges cease to form at the new barb locus, the follicle decreases in diameter, and the last barb ridges fuse to the rachis ridge. Ultimately, the collar resumes its undifferentiated cylindrical state forming the tubular calamus that is the base of the emerging feather. The center of the tubular calamus is then sealed from the dermal pulp by a keratinaceous pulp cap made from the innermost basilar layer of the epidermal collar. The completed, emerging feather is a cylindrical structure of branched keratin filaments that is covered by a superficial, deciduous keratin sheath, and is commonly called a pin feather. Only after the cy-

lindrical feather emerges from its sheath does it obtain its mature planar, pennaceous, or plumulaceous form. Thus, in a closed pennaceous feather, the hooked pennulae of the distal barbules can only extend to interlock with the unhooked pennulae of the proximal barbules of the neighboring barb (Fig. 1B) after these filaments have emerged from the cylindrical sheath and unfurled into a planar vane. The peripheral surface of a cylindrical pin feather becomes the dorsal surface of the fully emerged feather, whereas the internal or basilar surface of the collar becomes the ventral surface of the feather vane.

The microstructural diversity of feathers is a consequence of the control of developmental mechanisms within the feather follicle. For example, the differentiation between the proximal and distal barbules that creates a closed pennaceous vane originates with differential patterns of growth in the proximal and distal barbule plates within the barb ridges of the follicle. Further, the asymmetrical vane of remiges and rectrices (the flight feathers of the wings and tail) are created by a lateral displacement of the new barb locus from the posterior midline to one side of the collar. This displacement likely occurs through differential recruitment of new barb ridges from the new barb locus to one side of the follicle collar, since asymmetrical vanes are created by differential increase in the width of one side of the feather vane.

Feathers in many birds also have an afterfeather, which is a composed of a second rachis with barbs and barbules connected to the posterior midline of the same calamus (Fig. 1A). The aftershaft originates when the new barb locus divides into two loci that are laterally displaced on opposite sides of the collar (Fig. 3). Barb ridges that form on the anterior sides of these loci are helically displaced toward the rachis and become the barbs of the main feather, whereas barb ridges on the posterior sides of these two loci are helically displaced toward the posterior midline of the follicle collar, and fuse to form the rachis and barbs of the afterfeather (Fig. 3).

Each follicle produces a series of feathers during the life of the bird, and most follicles are capable of producing feathers with a variety of different structures at different times in the life cycle of the bird, indicating the fine regulation of developmental mechanisms within the follicle. The first feathers to emerge from most follicles are plumulaceous natal downs. Most of these same follicles will produce pennaceous contour feath-
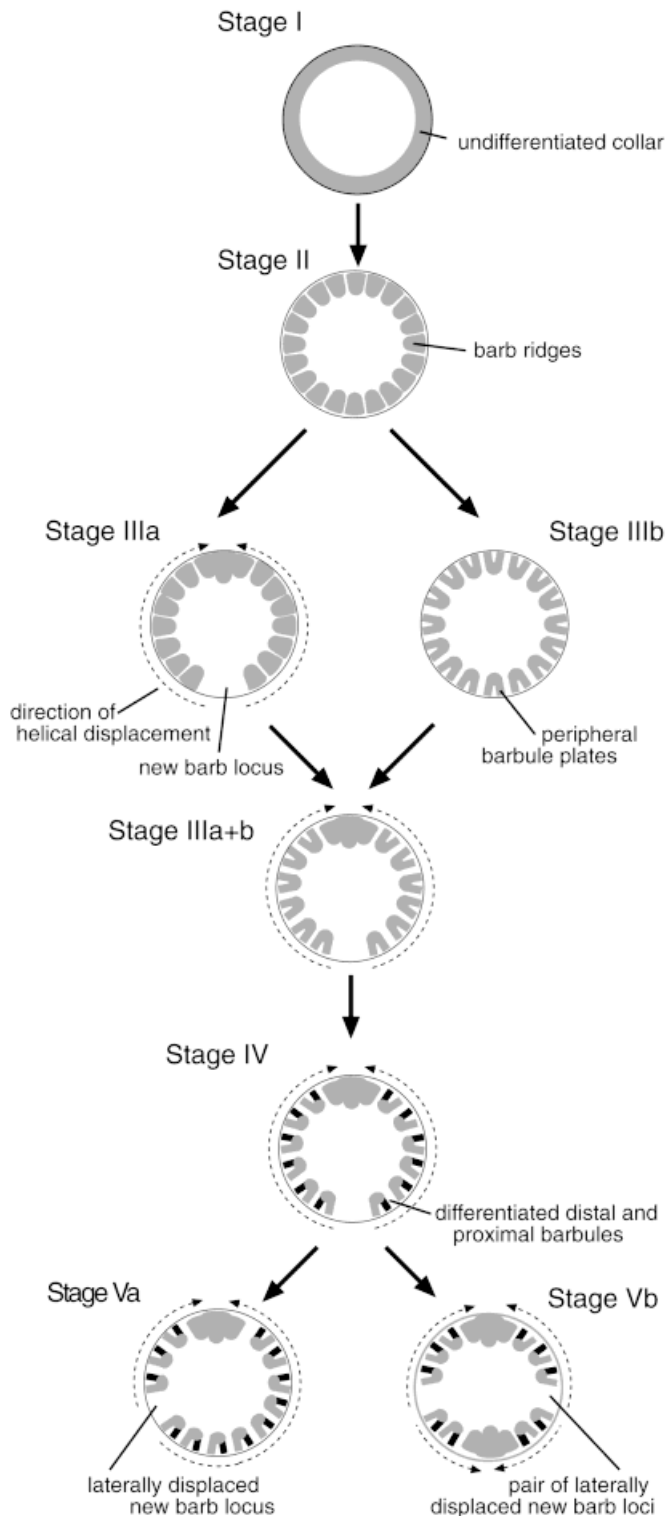
Stage I
undifferentiated collar

Stage II
barb ridges

Stage IIIa
direction of
helical displacement
new barb locus

Stage IIIb
peripheral
barbule plates

Stage IIIa+b

Stage IV
differentiated distal and
proximal barbules

Stage Va
laterally displaced
new barb locus

Stage Vb
pair of laterally
displaced new barb loci

Fig. 4. Developmental model of the origin and diversification of feather follicles. The model is depicted as a transition series of cross-sections of the follicle collar (the innermost layer of epidermal tissue in the feather follicle; Fig. 2D). The consequent transition series in feather morphologies is illustrated in Figure 5. Each diagram is oriented with the ante-

ers in subsequent molts. Feathers can also vary tremendously in morphology from their distal tips to their bases indicating close temporal regulation of developmental mechanisms within single feathers. Most contour feathers are open pennaceous at the tips of the barbs, closed pennaceous toward the base of the barbs, and plumulaceous at the base of the entire feather (Fig. 1A) as a result of fine temporal control of developmental mechanisms of the follicle during feather growth. The structural diversity of feathers is not a consequence of variation in the structure of follicles but of the control of follicular developmental mechanisms that are within the capacity of all follicles.

Bird feathers are usually molted once a year, commonly twice a year, and occasionally once every other year. With each molt, the follicle resumes activity, the collar becomes reorganized into a proliferating tissue with barb ridges, and an entirely new feather of the appropriate structure, shape, symmetry, size, and color emerges. Feathers with a large calamus usually fall out of the follicle as the collar and pulp reorganize. However, the structural continuity of the follicle collar between the subsequent feathers produced by a single follicle is documented by the frequent observation of the calamus of a natal down feather attached to the distal tips of the barbs of the subsequent feather to emerge from that follicle (Lucas and Stettenheim, '72: figs. 229, 230).

A DEVELOPMENTAL MODEL OF FEATHER EVOLUTION

Feathers are hypothesized to have originated with the first feather follicle (stage I), and feather com-

rior surface of the collar upward. The developmental novelties are labeled in the stages at which they originate. Stage I: Origin of the undifferentiated collar through a cylindrical epidermal invagination around the base of the feather papilla. Stage II: Origin of the differentiation of the inner layer of the collar into longitudinal barb ridges and the peripheral layer of the collar into the feather sheath. Stage III: Either of these developmental novelties could have occurred first, but both are required before stage IV. Stage IIIa: Origin of helical displacement of barb ridges and the new barb locus. Stage IIIb: Origin of paired barbules from peripheral barb plates within the barb ridges. Stages IIIa and IIIb: Origin of follicle capable of helical displacement and barbule plate differentiation. Stage IV: Origin of differentiated distal and proximal barbules within barbule plates of barb ridges. Stage Va: Origin of lateral displacement of the new barb ridge locus. Stage Vb: Origin of the division of posterior new barb locus into a pair of laterally displaced loci, and opposing anterior and posterior helical displacement of barb ridges toward the main feather and afterfeather of the follicle. See text for details of additional stages in the evolution of feather diversity (stages Vc–f).
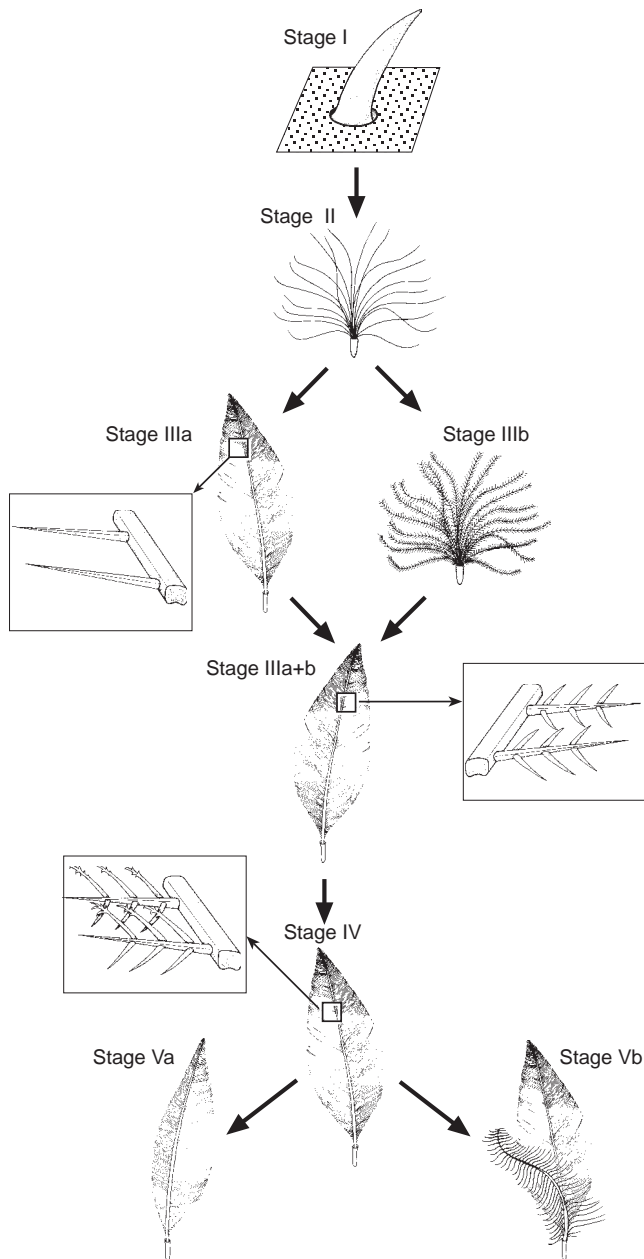
plexity is hypothesized to have evolved through a series of derived developmental novelties within feather follicles (stages II–V). The model is illustrated as a transition series of cross-sections of the collar of the follicle of a developing feather (Fig. 4), and as a parallel transition series of consequent mature feather morphologies (Fig. 5).

Stage I

The follicle originated with the cylindrical epidermal invagination around the base of the feather papilla. The undifferentiated tubular collar yielded the first feather—a hollow cylinder that resembles the calamus, or sheath, of a modern feather.

Stage II

The inner, basilar layer of the collar differentiated into longitudinal barb ridges that grew unbranched keratin filaments. The thin peripheral layer of the collar became the deciduous sheath. The resulting mature feather resembled a tuft of unbranched barbs with a basal calamus.

Stage III

Stage III includes two developmental novelties (IIIa and IIIb), either of which could have occurred first. Both are required prior to stage IV. The evolution of helical displacement of barb ridges within the collar (stage IIIa) resulted in the origin of the rachis, which is formed by the fusion of barb ridges on the anterior midline of the follicle. To create a feather with an indeterminate number of barbs, the posterior new barb locus evolved thereafter. The resulting feather would have had a symmetrical, primarily branched structure with a rachis and unbranched barbs. The evolution of paired barbules within the peripheral barbule plates of the barb ridges (stage IIIb) created the branched barbs with rami and barbules. The resulting

Fig. 5. Developmental model of the origin and diversification of feathers. The proposed transition series of feather follicles is shown in Figure 4. Stage I: The origin of an undifferentiated tubular collar yielded the first feather—a hollow cylinder that resembled the simple sheath or calamus of a modern feather. Stage II: The origin of a collar with differentiated barb ridges resulted in a mature feather with a tuft of unbranched barbs and a basal calamus emerging from a superficial sheath. Stage IIIa: The origin of helical displacement of barb ridges and the new barb locus resulted in a pinnate feather of indeterminate number of unbranched barbs fused to a central rachis. Stage IIIb: The origin of peripheral barbule plates within barb ridges yielded a feather with numerous branched barbs attached to a basal calamus. Stages IIIa and IIIb: The feather possessed a bipinnate, open pennaceous structure with a rachis and barbs with barbules.

Stage IV: The origin of differentiated proximal and distal barbules created the first closed, pennaceous vane. Distal barbules grew terminally hooked pennulae to attach to the simpler proximal barbules of the adjacent barb. Stage Va: Lateral displacement of the new barb locus led to the growth of a closed pennaceous feather with an asymmetrical vane resembling modern rectrices and remiges. Stage Vb: Division and lateral displacement of the new barb loci yielded opposing, anteriorly and posteriorly oriented patterns of helical displacement producing a main feather and an afterfeather with a single calamus. The afterfeather could have evolved at any time following stage IIIb, but likely occurred after stage IV based on modern aftershaft morphology. See text for details of additional stages in the evolution of feather diversity (stages Vc–f).

feather would have been a tuft of branched barbs without a rachis. Following both stages IIIa and IIIb, the feather possessed an open pennaceous structure with a rachis, barbs, and barbules.

Stage IV

The evolution of differentiated distal and proximal barbules created the closed, pennaceous vane. Terminally hooked pennulae on the distal barbules evolved to attach to the simpler proximal barbules of the adjacent barb to form the closed vane.

Stage V

Following the origin of the closed pennaceous feather, subsequent developmental novelties gave rise to additional structural diversity. Asymmetrical flight feathers with vanes of different widths evolved by the lateral displacement of the new barb ridge locus from the posterior midline of the collar toward either side (stage Va). Vane asymmetry could have evolved any time after the origin of a planar vane (stage IIIa), but, prior to stage Va, these asymmetrical feathers could not have been closed and pennaceous or functioned in flight.

The aftershaft originated through the division of the posterior new barb locus into a pair of laterally displaced loci that created opposing, anteriorly and posteriorly oriented patterns of helical displacement, producing a main feather and an afterfeather with a single calamus (stage Vb). The afterfeather could have evolved at any time following stage IIIb, but likely occurred after stage IV, based on modern afterfeather morphology. Modern bipinnate plumulaceous feathers evolved from pennaceous feathers through the origin of nodal prongs in the distal cells of the barbules and other structural features (stage Vc, not illustrated). This stage could either have proceeded from the evolution of bipinnate feathers (stage IIIa and IIIb) or the origin of the closed pennaceous feather (stage IV), but the structure of modern downs indicates that they were derived from closed pennaceous feather morphologies (stage IV).

Additional feather diversity, including filoplumes, powder down, and bristles can also be hypothesized to have evolved by additional developmental novelties. Modern filoplumes consist of a rachis with a terminal tuft of barbs and additional basal barbs that do not fuse to the rachis (Lucas and Stettenheim, '72, p 388–391). They are hypothesized to have evolved through the loss or cessation during development of helical barb ridge displacement and barb ridge formation by the new barb locus (stage Vd). They could have evolved anytime after the origin of bipinnate feather structure (stage IV). Powder downs are derived bipinnate contour feathers that are characterized by elongate barbules covered with powdery particles that are distributed around the plumage by the preening of the adult bird (Lucas and Stettenheim, '72, p 386–387). Powder down feathers evolved through the derived retention of the axial and marginal cells within barbule plates (stage Ve). The differentiation and programmed death of the axial and margin barbule plate cells create the differentiated pairs of barbule plates within the barb ridges of typical bipinnate feathers. In powder downs, these axial and marginal cells are retained until later in development when they become the exfoliating keratin particles between the elongate barbules (Lucas and Stettenheim, '72, p 386–387). Avian bristles are characterized by the increased strength of the rachis and the reduction (sometimes complete) of the barbs and barbules. Bristles evolved through the derived reduction in barb number and barbule structure within the follicle (stage Vf).

DISCUSSION

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. Thus, feathers originated with the evolution of the first follicle. The first follicle was a tubular cylinder with an undifferentiated collar (stage I), and the first feathers were thus hollow keratin cylinders (Figs. 4 and 5, stage I). Depending on the diameter of the follicle, these feathers could have been thin hairlike filaments or substantial cone-shaped structures. Follicles and feathers subsequently diversified through a series of derived novelties in the developmental mechanisms within the follicle (Figs. 4 and 5, stages II–V). Once the inner layer of the follicle collar became differentiated into longitudinal barb ridges (stage II), a feather with a tuft of nonpinnate barbs evolved. With the evolution of helical displacement of barb ridges (stage IIIa), the rachis arose. The differentiation of the peripheral barbule plates within barb ridges (stage IIIb) yielded paired barbules. Only after the origin of an open pennaceous feather with both a rachis and barbules (stage IIIa and IIIb) could structural specialization of the distal and proximal barbules evolve to create a pennaceous feather with a closed vane (stage IV). Subsequent novelties in the de-

velopmental mechanisms of the follicle gave rise to the rest of feather diversity, including asymmetrical flight feathers, the afterfeather, and most modern downs (stage Va–f).

By inferring a hierarchical and causal organization among the events in feather development within modern avian follicles, the model polarizes most of the developmental novelties required to evolve the entire structural diversity of feathers. Thus, filamentous barbs are hypothesized to have evolved before the rachis because the rachis is created within the follicle by the fusion of barb ridges to the presumptive rachis ridge. In pinnate feathers, an initial period of purely axial growth is required in the follicle before the initiation of helical displacement and the formation of the rachis (Lillie and Juhn, '32). In contrast, barbs are hypothesized to have evolved before barbules because barbules are formed by the peripheral differentiation of layers of cells within the antecedent barb ridges. The open pennaceous feather is hypothesized to have originated before the closed pennaceous feather because the rachis, the barb rami, and the barbules of an open pennaceous feather are structural prerequisites of the derived differentiated barbule morphologies that create the closed pennaceous vane. The afterfeather is hypothesized to evolve after the main feather since the paired, laterally displaced new barb loci that produce the afterfeather develop ontogenetically from the division of the single posterior new barb locus (Fig. 3) (Lucas and Stettenheim, '72). The only exceptions are the highly derived contour feathers of the flightless Australo-Papuan ratites, *Dromaius* and *Casuaria,* in which the main feather is equal in length to the afterfeather. A few novelties, such as the origin of helical displacement of barb ridges and the origin barbules, cannot completely polarized within the model (Figs. 4 and 5, stages IIIa and IIIb) because there are no currently justifiable criteria for establishing a causal or hierarchical relationship between these developmental events.

Unlike most previous hypotheses of feather origins, all of the morphologies hypothesized by this developmental model exist among the feathers of extant birds, and are thus known products of avian feather follicles (Lucas and Stettenheim, '72). For example, the undifferentiated cylindrical structure hypothesized as the very first feather is present in the calamus and the sheath of all avian feathers (Fig. 5, stage I). Many barbule-less ornamental feathers, like the display plumes of egrets (*Egretta*, Ardeidae) and birds of paradise (*Paradisaea*; Paradisaeidae), closely resemble feathers in stage IIIa. This developmental model is therefore completely consistent with the data available from modern birds. However, the various morphological classes of extant feathers have had multiple origins and complex evolutionary histories within modern birds. Thus, the barbule-less display plumes of extant birds are secondarily simplified from derived closed pennaceous contour feathers (stage IV). Documenting the evolutionary history of specific modern avian feathers will require detailed phylogenetic analyses of feather structure variation within extant avian clades.

Additional intermediate stages could have occurred between some of the stages of the proposed model. For example, if the evolution of helical growth occurred before the origin of the new barb locus, then stage IIIa would have been composed of two independent stages that produced a distinct intermediate feather type (i.e., a long shaft with a terminal tuft of a finite number of barbs). Furthermore, if a laterally undifferentiated peripheral barbule plate evolved prior to the lateral differentiation of the plate into paired plates, then a single unbranched barbule, or unpaired branch of the ramus, could have evolved prior to the evolution of paired barbules. There are, however, no extant feathers that have this morphology. Asymmetrical feather vanes (stage Va) could also have evolved any time after the origin of the vane (stage IIIa), but these feathers would not have been closed and pennaceous as are modern rectrices and remiges. Given the startling diversity of structures grown by modern feather follicles, it would not be surprising if additional, currently unknown structural diversity may have evolved during the early history of the feather follicle.

In general, the polarities of developmental novelties in the model are congruent with von Baer's rule—the hypothesis that stages that occur earlier in development are phylogenetically more broadly distributed and historically plesiomorphic (e.g., Gould, '77). However, the model does not rely solely on relative timing of events in ontogeny to justify these polarities. The stages of the model are inferred from the hierarchical nature of the developmental mechanisms of the follicle rather than from an analysis of the ontogenetic progression of plumages grown within the follicles of birds. Thus, plumulaceous feathers (stage II) are not primitive to pennaceous feathers (stage IIIa and beyond) because the first plumage of extant birds is usually downy, but because the simplest differentiated follicle collar would have produced

plumulaceous feathers. One detail, however, of feather development appears to violate von Baer's rule. During the development of the first feather papillae in the embryo (before day 12 in the chick, *Gallus gallus*), the barb ridge primordia appear as longitudinal condensations within the feather papillae before the follicle and collar are fully formed (Lucas and Stettenheim, '72). However, this developmental event—the origin of the feather before the follicle and collar—is clearly derived because barb ridges would be unable to grow without the spatial organization provided by the collar.

If the answer to the question of feather origins is to be found in the follicle, then the question remains, "Why did the follicle evolve?" The structure of the invaginated follicle creates a unique cylindrical sandwich of epidermal and dermal tissue layers (Fig. 2D). 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 without continued growth in the volume of the dermal pulp. The follicle may have originated through selection for this complex and indeterminate developmental potential rather than for the cylindrical shape of its products. Interestingly, the cylindrical shape of the follicle did not constrain the morphology of feathers. Rather, subsequent developmental novelties led to the evolution of an astoundingly complex diversity of structures that can be grown from a single cylindrical organ.

Detailed examination of the growth of feathers clearly documents that feathers are not merely derived scales (Brush '93, '96). The current model, however, requires a reevaluation of the homology between feathers and scales and their mechanisms of morphogenesis. Except for differences in their shape, spacing, and biochemical composition (Sengel '76; Brush '93, '96), feathers and scales develop by essentially the same mechanisms from the origin of the placode through the growth of an elongate papilla with an established anterior-posterior axis (Fig. 2A, B). However, with the origin of the epidermal invagination that defines the follicle (Fig. 2C), feathers have distinct and derived mechanisms of development that are not homologous with scales. Given the ubiquity of scales in avian ancestors and their presence in modern birds, it seems unlikely that the shared similarities of the mechanisms of the earliest development of feathers and scales are convergently evolved. Therefore, feathers and scales are apparently homologous as epidermal appendages at the level of the placode and papilla, but not as mature structures. The origin of the follicle created derived developmental mechanisms unique to feathers that grow structures whose details are not homologous with any aspect of a mature scale.

Recently, Alan Brush ('99a,b,c) has investigated the origin and diversification of feathers from a biochemical, cellular, and developmental viewpoint. Brush's analysis independently supports many of the same conclusions of the model proposed here. In the first of three papers, Brush ('99a) defines a feather as a dermal appendage that is composed largely feather φ-keratin (a derived, 10.4 kd form of β-keratin found in large quantities in modern avian feathers) and grows from a feather follicle. Brush hypothesizes that the protofeather was a single, unbranched hollow structure resembling a single barb or a modern bristle feather. Subsequently, Brush ('99b) proposes a phylogram of extant feather diversity based on feather growth, biochemistry, and the fossil record. The phylogram implies that the bristle-like protofeather evolved into natal down, adult down, various specialized plumes, pennaceous contour feathers, and flight feathers. Brush ('99b,c) then concludes that the feather follicle has an inherent potential for diversification and that the diversification of feathers occurred very rapidly within evolutionary history.

Unlike Brush ('99a,b), I hypothesize that feathers are the products of feather follicles, regardless of whether they are made out of modern, 10.4 kd, feather φ-keratin. If the deletion that created feather φ-keratin provided some derived functional advantage, as hypothesized by Brush ('93), it seems most likely that this biochemical novelty evolved after the follicle. The evolution of functionally novel keratin molecule would probably have occurred after the feathers from the first follicles were exposed to natural selection (M. Christianson, personal communication). Thus, it is unlikely that feather φ-keratin evolved before the follicle as hypothesized by Brush ('99a). Furthermore, Brush's combined biochemical and morphological criteria would require that the biochemical composition of fossil structures be ascertained before they are considered as feathers. Accordingly, the "feathers" of *Archaeopteryx* could not be defined as feathers unless they were composed of modern feather φ-keratin. Although feather φ-keratin is an essential component of modern feathers, its evolutionary origin is likely historically independent of the origin of the first structures that could be identified as ancestral feathers

on other morphological criteria. For these reasons, the morphological definition of a feather proposed here should be preferred.

Brush's phylogram of feather diversity ('99b) is largely congruent with the model proposed here. For example, we concur on the unbranched cylindrical form of the earliest feather, that the plumulaceous form preceeded pennaceous morphology, and the flight feathers are highly derived. But Brush's hypothesis describes historical relationships among classes of extant feathers (e.g., natal down, semiplumes, etc.). As mentioned previously, however, many extant feathers are characterized by features that indicate that they are secondarily simplified from more highly derived feathers. For example, the differentiation of distal and proximal barbules in many modern downs implies that they are secondarily derived from derived pennaceous feathers. To avoid conflating the original history of feather complexity and the complex evolution of feather morphology within modern birds, I prefer to hypothesize polarities among classes of feathers that are defined by morphological criteria without reference to modern feathers. Evolutionary history of the diversity of modern feathers should be pursued through comparative phylogenetic analyses within clades of modern birds. Further, Brush's ('99a,b) description of the first cylindrical feather as being like a single barb is evolutionarily misleading. The first feather was likely produced by the whole, undifferentiated collar and would not have been homologous with a single feather barb. Barbs are produced by barb ridges that are differentiated portions of the collar. Barbs evolved through the differentiation of the collar into these barb ridges, and not through the duplication of the growth centers that created the first feather, as implied by Brush ('99b).

Last, Brush ('99b,c) cites the extraordinary diversity of structures produced by single modern follicles as evidence of the omnipotence of this novel integumental organelle, and he advocates a historically rapid diversification of feathers following the initial origin of the feather follicle. However, the presence of complex developmental mechanisms within modern follicles does not imply that these mechanisms evolved rapidly, simultaneously, or as an automatic consequence of the initial evolution of a cylindrical follicular structure. We have no evidence regarding how easy or difficult it may have been to evolve the various developmental apomorphies that led to the diversity of feather morphologies (Figs. 4 and 5). Current evidence is insufficient to support Brush's conjecture.

Many additional topics in feather evolution remain to be studied. For example, it is currently unclear when feather molt first evolved. Molt involves the periodic cessation of growth and disorganization of the follicle collar followed by the subsequent reorganization of the collar and the resumption of growth of a new feather. The emerging large samples of some species of early fossil birds should be scrutinized for indications of molt. Also, the evolution of the pigmentary and structural coloration of feathers, both of which are created during feather growth, is not understood. Further research in these areas would greatly expand our understanding of the evolution of feather diversity.

Functional hypotheses of feather origin

The main contribution of the model is to propose that a transition series for the evolution of avian feathers can be inferred from current developmental evidence available from extant birds without reference to functional scenarios or adaptive hypotheses. Thus, the model is functionally neutral and does not specify which modes of selection may have been involved in any particular stage of the evolution of feather complexity. The model, however, does make specific predictions about the transition series of morphologies that occurred during the evolution of modern feathers, and it is possible to evaluate whether the morphologies hypothesized by previous functional models are consistent with how feathers develop and how the follicle could have evolved.

Flight

Feathers have been hypothesized to have evolved through natural selection on primitive scales for an aerodynamic function (Parkes, '66; Maderson, '72; Feduccia, '93, '96). These models hypothesize that scales became elongate and planar, then fringed, and ultimately pennaceous through continuous selection for increasing aerodynamic efficiency. The aerodynamic hypothesis, however, is basically incompatible with the details of feather development.

First, the developmental similarities between scales and feathers essentially ends with the origin of the follicle. Once the papilla develops a cylindrical, invaginated follicle and collar (stage I), the details of feather development are entirely distinct from those of a scale. The aerodynamic hypothesis requires that ancestral feathers maintained a planar form that could provide an aerodynamic

function during all stages of its evolution, from scale to modern asymmetrical pennaceous flight feather. However, the vane of a pennaceous feather is not historically homologous with, nor functionally contiguous with, the surface of a reptilian or avian scale. The dorsal and ventral surface of a mature feather are created by the peripheral and inner surfaces of the follicle collar, respectively, and cannot be considered homologous with the dorsal and ventral surfaces of a scale, which are formed by the dorsal and ventral surfaces of a scale papilla. From their origin within the follicle until final emergence, all feathers are cylindrical. Any scenario that requires an incremental functional continuity between planar scales and essentially cylindrical feathers is not supported by developmental observations.

Second, a closed pennaceous vane is created by the interlocking interaction of the differentiated proximal and distal barbules of neighboring barbs. As described above, the completely bipinnate, open pennaceous feather must have evolved before the closed pennaceous feather because only after bipinnate structure had evolved were the structural prerequisites of a closed pennaceous feather present. Thus, it was impossible for the feather to maintain an interlocking, planar aerodynamic surface while evolving a bipinnate structure.

Third, for the aerodynamic model to be developmentally plausible, feathers would have had to pass through a stage in which a generally undifferentiated collar was split along the posterior midline of the follicle to create a keratinaceous scale without barbs. There are no avian feather follicles that produce such structures. There are a few examples of modern feathers that somewhat resemble the "fringed scales" hypothesized by the aerodynamic model. For example, the contour feathers of penguins (Spheniscidae) are a terminally pinnate but basally fused into a broad, scale-like rachis. These exceptional and highly derived feathers further demonstrate that the rachis is formed by fusion of barb ridges, and that differentiated barbs originated before the rachis.

Fourth, feathers were unlikely to have been able to perform an aerodynamic function until after the evolution of the closed pennaceous vane—the first feather structure that can conceivably create a coherent aerodynamic surface (stage IV). The only feathers with a primarily aerodynamic function are the rectrices and remiges with asymmetrical vanes, and these feathers evolved through lateral displacement of the new barb locus within the follicle (stage Va). Feathers evolved an aerodynamic

function only after substantial evolution in follicle complexity.

In conclusion, the aerodynamic hypothesis for the origin of feathers is incompatible with the most salient feature of feather development—the cylindrical nature of the follicle. Further, the bipinnate structure of feathers could not have evolved by selection on increasingly elongate scales for an aerodynamic function. Some feathers did ultimately evolve an aerodynamic function, but selection for an aerodynamic function could only have taken place after the evolution of the closed pennaceous, bipinnate feather (stage IV). Of all the diversity and structural complexity of feathers, natural selection for an aerodynamic function probably only gave rise to the asymmetrical vane and robust rachis found in the rectrices and remiges of most flighted birds (stage Va).

Thermal insulation

It has been hypothesized that feathers originated through natural selection for thermal insulation. The first cylindrical feathers (stage I) could have provided significant insulation if they were thin, numerous, and pliable like mammalian hair. The first filamentous, nonpinnate feathers (stage II) could certainly have been plumulaceous and provided thermal insulation.

Heat shielding

Regal ('75) hypothesized that feathers evolved from elongate, crudely pennaceous scales as a shield from excessive solar radiation. As in the flight hypothesis, the protofeathers hypothesized by the heat shielding model, which appear to be structurally intermediate between scales and mature pennaceous feathers, cannot be grown from feather follicles by any plausible developmental mechanism. It is conceivable, however, that the first cylindrical feathers (stage I) could have been behaviorally deployed to provide heat shielding to the organism.

Water repellency

Dyck ('85) hypothesized that feathers evolved through natural selection for water repellency. The very first cylindrical feathers (stage I) could not have provided such a function, but it is plausible that the first filamentous, nonpinnate feathers (stage II) could have functioned in that capacity.

Communication and crypsis

Feathers have been hypothesized to have evolved through natural or sexual selection for communi-

cation (Mayr, '60). It is also plausible that feathers evolved through natural selection for crypsis or camouflage. There is no reason to think that the keratin of the first feathers could not have been pigmented with melanins and carotenoids as in modern feathers. Even the very first keratinized cylindrical feathers could have been either brightly or cryptically pigmented. The simplest possible control of pigment deposition in the follicle (e.g., on, off) could have yielded feathers with horizontal stripes or longitudinal gradients in color. The more complex pigment patterns and structural colors present in modern feathers would have could not have evolved until after the origin of barbs and barbules.

Defense

Although modern feathers do not provide significant physical defense to birds, the first cylindrical feathers could have provided protection to the body by creating an array of pointed keratinaceous structures on the integument, as in a modern hedgehog or porcupine. Subsequent adaptive differentiation in feather morphology would have proceeded through selection for some other function.

Integumental structures of theropod dinosaurs

The discovery of filamentous integumental structures on the coelurisaurian theropod *Sinosauropteryx* (Chen et al., '98) has caused considerable excitement among evolutionary biologist and paleontologists. Given the wealth of support for phylogenetic relationship between birds and theropods, Chen et al. ('98) raised the possibility that these structures could be homologous with avian feathers. The integumental structures of *Sinosauropteryx* have received considerable scrutiny, but many questions about their morphology remain, including whether these structures are epidermal appendages or internal integumental structures; whether they are composed of branched or unbranched filaments; whether they are hollow; and whether they grew from follicles. The more recent discovery of similar but much longer filamentous integumental structures on the therizinosauroid theropod *Beipiaosaurus* (Xu et al., '99) has further intensified speculation on the homology of these integumental structures.

Homology among structures cannot be assessed by functional criteria because adaptive evolution among lineages can produce significant changes in function since common ancestry. Unfortunately, current theories of feather origins directly incorporate functional assumptions that could result in rejecting a hypothesis on purely functional criteria. For example, if we assume that feathers evolved for flight, then homology between feathers and some nonaerodynamic fossil integumental structures could be rejected outright. So, traditional functional hypotheses for the origin of bird feathers can be an impediment to evaluation of the homology of these newly discovered dinosaur integumental structures.

This developmental model provides functionally neutral criteria to evaluate the homology between avian feathers and other fossil integumental structures. The model predicts that feathers with single unbranched keratin structures (stage I) or many unbranched keratin filaments (stage II) preceded the origin of the branched or pennaceous feather. From my direct observations of the two specimens of *Sinosauropteryx* (Chen et al., '98), the integumentary structures appear to consist of unbranched filaments about 20 mm long. Reports of the filamentous structures of *Beipiaosaurus* indicate that they are 50–70 mm long and possibly branched. It is uncertain whether the reported branches in both species are bifurcations of single structures or the merely the appearance of branching created by closely adjacent, separate unbranched filaments within the specimens. However, the length and position of these structures in *Beipiaosaurus* demonstrate convincingly that these were not internal integumental structures. Additional examination of the integumental structures of *Sinosauropteryx* and *Beipiaosaurus* is required to establish: (1) whether the filaments are branched, unbranched, or hollow; (2) whether any calami can be observed; (3) whether these structures grew from follicles; (4) whether single or multiple filaments emerge from a single basal structure; and (5) whether they are composed of keratin or even feather ϕ-keratin. Current descriptions of the morphology of these structures are entirely consistent with homology with avian feathers of stage I or stage II (Fig. 5). If some of these structures prove to be branched, then they could be homologous with feathers of stage IIIa or IIIb. Homology with feathers could be falsified by finding that these structures did not grow from follicles or are not made of keratin.

Given the phylogenetic positions of *Sinosauropteryx* (Chen et al., '98) and *Beipiaosaurus* (Xu et al., '99) within the coelurisaurian theropod dinosaurs, homology between these integumental struc-

tures and feathers would imply a broad phylogenetic distribution for feathers within coelurisaurs, including dromeosaurs, ornithomimids, troodontids, and tyrannosaurs.

The entirely pennaceous integumental structures recently described from the forelimbs and tails of *Protarcheopteryx* and *Caudipteryx* (Ji et al., '98) are doubtless homologous with avian feathers. They are thoroughly modern in morphology although their symmetrical structure implies that they did not function directly in flight. Whether or not these feathers are extraordinary or merely notable depends upon whether these organisms are plesiomorphically flightless theropod dinosaurs or secondarily flightless birds. The original description implied that *Protarcheopteryx* and *Caudipteryx* are the sister taxa to birds (Ji et al., '98) which does not conclusively demonstrate that *Protarcheopteryx* and *Caudipteryx* were plesiomorphically flightless. More detailed phylogenetic analyses including many more taxa are required to further resolve the relationships of *Protarcheopteryx* and *Caudipteryx* to theropod dinosaurs and to birds. If additional phylogenetic analyses confirm that *Protarcheopteryx* and *Caudipteryx* are primarily flightless, then the presence of symmetrical "remiges" and "rectrices" would confirm the hypothesis in the model that symmetrical closed pennaceous feathers (stage IV) preceded the asymmetrical flight feathers (stage Vc).

These recent discoveries rank among the potentially most fascinating fossil finds since the description of *Archaeopteryx*, yet their interpretation is critically related to theories of feather origin. The proposed model provides a new, coherent, and functionally neutral framework for evaluating and testing these hypotheses of homology. In these analyses, it is important to emphasize that early feathers need not precisely resemble any modern feathers, but should be plausibly grown by a conceivable follicle.

Molecular mechanisms of feather development

The development of avian feather placodes and papillae constitutes a historically important model system in developmental biology (Sengel, '76). With the discovery of new molecular methods in developmental biology, feather development has received renewed and intensive molecular investigation (Chuong, '93; Wolpert, '98). The research has confirmed the general paradigm in molecular developmental biology that a common, plesiomorphic set of genes plays an important role in

pattern specification and morphogenesis of structures in a diversity of metazoans. Thus, the broadly distributed *Hox* genes, *Wnt-7a*, *Sonic hedgehog, N-CAM, L-CAM, BMP2,* and *TGF* are now known to be involved in specifying the pattern of feathers placodes within ptyerylae and morphogenesis within the feather placodes and follicles (Chuong et al., '90, '93; Noji et al., '93; Serras et al., '93; Nohno et al., '95; Song et al., '96; Ting-Berreth and Chuong, '96; Crowe et al., '98; Jung et al., '98; Noralmy and Morgan, '98; Viallet et al., '98; Wolpert, '98). The rapid progress in this research will continue to improve our understanding of the molecular mechanisms of feather development.

An important goal of developmental biology is establishing generalizations that contribute to the overall understanding of developmental mechanisms of organisms. Thus, most of the classical (Sengel, '76) and modern molecular (Chuong, '93; Wolpert, '98) developmental research on feathers has focused on the most general mechanisms of induction between epithelium and mesenchyme, and on the determination of spatial patterns. Consequently, a great deal of research has focused on the earliest development of feather placodes and papillae, and substantially less molecular investigation has been done on later stages involved in the differentiation and proliferation of structures within the epidermal collar. One exception comes from the observation that *Sonic hedgehog* is expressed in peripheral collar cells between the barb ridges, and apparently plays a role in the differentiation of barb ridges during the growth of the first natal down (Nohno et al., '95).

It would be extremely fruitful to focus molecular techniques on additional specific hypotheses relevant to the development of morphological components of mature feathers: barbs, barbules, afterfeathers, etc. Many fascinating questions remain to be addressed. For example, what specifies and controls the cylindrical epidermal invagination that creates the feather follicle and, thus, defines the feather? How does the plesiomorphic anterior-posterior axis of the feather yield the positional and temporal information required to produce helical displacement of feather barbs in pinnate feathers? What physical mechanisms are involved in helical displacement of barb ridges? How is the orientation of proximal and distal barbules specified within the barbule plates of barb ridges? How is positional and temporal information used in the development of an aftershaft? How do the developing collar keratinocytes communicate with the

pigment cells in the dermal pulp to determine the pattern of pigment deposition that creates feather pigment patterns? Progress on these questions will substantially contribute to our understanding of developmental mechanisms whose evolution is discussed in this paper.

Modern metazoan developmental biology has produced an apparent contradiction. On one hand, numerous observations document that morphological novelties have arisen through the cooptation of plesiomorphic molecular mechanisms of positional specification and morphogenesis. On the other hand, some morphological novelties also require additional derived alterations of these generalized plesiomorphic mechanisms in order to achieve their novel phenotypes. For example, the development of tetrapod limbs exhibits many striking molecular commonalties with invertebrate limbs, and yet the development of tetrapod digits involves several novel alterations of these plesiomorphic position specification mechanisms (Nelson et al., '96; Shubin et al., '97). As more is learned about the molecular basis of feather development, it will be important to establish a similar distinction of between the plesiomorphic mechanisms that are shared with other epidermal appendages and the derived developmental novelties that are unique to feathers. This distinction will ultimately lead to progress in understanding the relationship between feather development, and the evolutionary origin and diversification of avian feathers.

ACKNOWLEDGMENTS

LITERATURE CITED

Brush AH. 1993. The origin of feathers. In: Farner DS, King JS, Parkes KC, editors. Avian biology. London: Academic Press. p 121–162.

Brush AH. 1996. On the origin of feathers. J Evol Biol 9: 131–142.

Brush AH. 1999a. Protofeathers: what are we looking for? In: Wolberg D, editor. Dinofest International. In press.

Brush AH. 1999b. Evolving a protofeather and feather diversity. Am Zool (in press).

Brush AH. 1999c. The beginings of feathers. In: Gauthier J, editor. New perspectives on the origin and early evolution of birds. New Haven: Yale University Press. In press.

Chen P-J, Dong ZM, Zhen SN. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian formation of China. Nature 391:147–152.

Chuong C-M. 1993. The making of a feather: homeoproteins, retinoids, and adhesion molecules. BioEssays 15:513–521.

Chuong C-M, Oliver G, Ting SA, Jegalian BG, Chen HM, De Robertis EM. 1990. Gradients of homeoproteins in developing feather buds. Development 110:1021–1030.

Crowe R, Henrique D, Ish-Horowicz D, Hiswander L. 1998. A new role for Notch and Delta in cell fate decisions: patterning the feather array. Development 125:767–775.

de Beer G. 1954. *Archaeopteryx lithographica*; a study based on the British Museum specimen. London: Trustees of the British Museum.

Dyck J. 1985. The evolution of feathers. Zoologica Scripta 14:137–153.

Feduccia A. 1993. Aerodynamic model for the early evolution of feathers provided by *Propithecus* (Primates, Lemuridae). J Theor Biol 160:159–164.

Feduccia A. 1996. The origin and evolution of birds. New Haven: Yale University Press.

Gould SJ. 1977. Ontogeny and phylogeny. Cambridge: Harvard University Press.

Griffiths PJ. 1996. The isolated *Archaeopteryx* feather. Archaeopteryx 14:1–26.

Ji Q, Currie PJ, Norell MA, Ji S-A. 1998. Two feathered dinosaurs from northeastern China. Nature 393:753–761.

Jung H-S, Francis-West PH, Widelitz RB, Jiang T-X, Ting-Berreth SA, Tickle C, Wolpert L, Chuong C-M. 1998. Local inhibitory action of BMPs and their relationships with activators in feather formation: implications for periodic patterning. Dev Biol 196:11–23.

Lillie FR, Juhn M. 1932. The physiology of development of feathers: I. Growth-rate and pattern in individual feathers. Physiol Zool 5:124–184.

Lucas AM, Stettenheim PR. 1972. Avian anatomy—integument. Washington, DC: US Department of Agriculture Handbook.

Maderson PFA. 1972. On how an Archosaur scale might have given rise to an avian feather. Am Naturalist 106:424–428.

Mayr E. 1960. The emergence of evolutionary novelties. In: Tax S, editor. The evolution of life. Chicago: University of Chicago Press. p 349–380.

Müller GB, Wagner GP. 1991. Novelty in evolution: restructuring the concept. Annu Rev Ecol System 22:229–256.

Nelson CE, Morgan BA, Burke AC, Laufer E, DiMambro E, Murtaugh LC, Gonzales E, Tessarollo L, Parada LF, Tabin C. 1996. Analysis of *Hox* gene expression in the chick limb bud. Development 122:1449–1446.

Nohno T, Kawakami Y, Ohuchi H, Fujiwara A, Yoshioka H, Noji S. 1995. Involvement of the *Sonic Hedgehog* gene in chick feather development. Biochem Biophys Res Comm 206:33–39.

Noji S, Koyama E, Moyokai F, Nohno T, Ohuchi H, Nishiwaya K, Taniguchi S. 1993. Differential expression of three chick FGF receptor genes, FGFR1, FGFR2, and FGFR3, in limb and feather development. Prog Clin Biol Res 383B:645–654.

Noralmy S, Morgan BA. 1998. BMPS mediate lateral inhibition at successive stages in feather tract development. Development 125:3775–3787.

Parkes KC. 1966. Speculations on the origin of feathers. Living Bird 5:77–86.

Regal PJ. 1975. The evolutionary origin of feathers. Q Rev Biol 50:33–66.

Sengel P. 1976. Morphogenesis of skin. Cambridge: Cambridge University Press.

Serras F, Fraser S, Chuong C-M. 1993. Asymmetric patterns of gap junctional communication in developing chicken skin. Development 119:85–96.

Shubin N, Tabin C, Carroll S. 1997. Fossils, genes and the evolution of animal limbs. Nature 388:639–648.

Song H, Wang Y, Goetnick PF. 1996. Fibroblast growth factor 2 can replace ectodermal signalling for feather development. Proc Natl Acad Sci USA 93:10246–10249.

Ting-Berreth SA, Chuong C-M. 1996. Local delivery of TGFβ2 can substitute for placode epithelium to induce meshnchymal condensation during skin appendage morphogenesis. Dev Biol 179:347–359.

Viallet JP, Prin F, Olivera-Martinez I, Hirsinger E, Pourquie O, Dhouailly D. 1998. Chick Delta-1 gene expression and the formation of the feather primordia. Mech Dev 72:159–168.

Wolpert L. 1998. Pattern formation in epithelial development: the vertebrate limb and feather bud spacing. Philos Trans R Soc Lond B 353:871–875.

Xu X, Tang Z-l, Wang X-l. 1999. A therinzinosauroid dinosaur with integumentary structures from China. Nature 399:350–354.