

THE QUARTERLY REVIEW *of* BIOLOGY



THE EVOLUTIONARY ORIGIN AND DIVERSIFICATION OF FEATHERS

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KEYWORDS

feathers, evolution, development, paleontology, birds, dinosaur

Although paleontological evidence is revealing the origin of birds, neither paleontological nor developmental evidence yet speaks more than a whisper about the origin of feathers (Hall 1998:266).

ABSTRACT

Progress on the evolutionary origin and diversification of feathers has been hampered by conceptual problems and by the lack of plesiomorphic feather fossils. Recently, both of these limitations have been overcome by the proposal of the developmental theory of the origin of feathers, and the discovery of primitive feather fossils on nonavian theropod dinosaurs. The conceptual problems of previous theories of the origin of feathers are reviewed, and the alternative developmental theory is presented and discussed. The developmental theory proposes that feathers evolved through a series of evolutionary novelties in developmental mechanisms of the follicle and feather germ. The discovery of primitive and derived fossil feathers on a diversity of coelurosaurian theropod dinosaurs documents that feathers evolved and diversified in nonavian theropods before the origin of birds and before the origin of flight. The morphologies of these primitive feathers are congruent with the predictions of the developmental theory. Alternatives to the theropod origin of feathers are critiqued and rejected. Hypotheses for the

The Quarterly Review of Biology, September 2002, Vol. 77, No. 3

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0033-5770/2002/7703-0001\$15.00

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initial function of feathers are reviewed. The aerodynamic theory of feather origins is falsified, but many other functions remain developmentally and phylogenetically plausible. Whatever their function, feathers evolved by selection for a follicle that would grow an emergent tubular appendage. Feathers are inherently tubular structures. The homology of feathers and scales is weakly supported. Feathers are composed of a suite of evolutionary novelties that evolved by the duplication, hierarchical organization, interaction, dissociation, and differentiation of morphological modules. The unique capacity for modular subdivision of the tubular feather follicle and germ has fostered the evolution of numerous innovations that characterize feathers. The evolution of feather keratin and the molecular basis of feather development are also discussed.

FEATHERS are the most complex integumentary appendages found in vertebrates (Lucas and Stettenheim 1972; Bereiter-Hahn et al. 1986). They have complex branched structure, and grow from their bases by a unique mechanism (Figures 1 and 2). The evolutionary origin of feathers has been a persistent and intractable question for more than 140 years (Lucas and Stettenheim 1972; Dyck 1985; Feduccia 1999; Maderson and Homberger 2000). Two important sources have contributed to the fundamental difficulty of studying this problem: the intellectual limitations of available models, and the lack of any antecedent fossil feather structures. Over the last few years, both problems have been addressed in ways that have fundamentally changed our conception of and answers to these evolutionary questions. Recent proposals of the developmental theory (Prum 1999; Brush 2000), and startling new paleontological discoveries of primitive feathers in nonavian theropod dinosaurs (Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a, 1999b, 2000, 2001; Ji et al. 2001), have made it possible to make the first concrete conclusions about the evolutionary origin of feathers.

The earliest known feathers appear in the fossil record in *Archaeopteryx lithographica*, known from the 140 million-year-old Solnhofen Limestone of Germany (de Beer 1954). The discovery of these spectacular fossils in the 1860s stunned scientists because of their mosaic of primitive reptilian and modern avian features, including essentially modern feathers (Griffiths 1996; Martin and Czerkas 2000). Most specimens of *Archaeopteryx* are preserved with impressions of the remiges and rectrices (flight feathers of the wings and tail, respectively) that exhibit asymmetrical, closed pennaceous vanes indicative of advanced flight capability. The closed pennaceous struc-

ture of the remiges and rectrices of *Archaeopteryx* demonstrates an entirely modern morphology, however, including differentiated distal and proximal barbs that interlock between neighboring barbs to create the planar vane of modern feathers (Griffiths 1996; Martin and Czerkas 2000). Thus, the oldest known fossil feathers give no more clues as to the ancestral morphology and ultimate origin of feathers than do the feathers of extant birds. (In this paper, the terms Aves, birds, and avian refer to members of the most inclusive clade including *Archaeopteryx* and modern birds. For a discussion of alternatives, see Gauthier and de Queiroz 2001.)

Research on the origin of feathers requires a backward extrapolation from the complex, entirely modern feathers of *Archaeopteryx* and modern birds to propose plausible ancestral feather morphologies. Unfortunately, the development of a heuristic theory of the origin of feathers has been limited by many of the same conceptual problems faced by macroevolutionary biology over the last century. Early workers attempted to reconstruct primitive feather morphologies based on variations in feather structures found among "primitive" lineages of extant birds (reviewed in Dyck 1985). In absence of an explicit concept of phylogeny, these theories overlooked the fact that all modern birds share a common ancestor with *Archaeopteryx* that already had fully modern feathers. Therefore, extant variations were derived, secondarily simplified feather morphologies. Since 1950, many theories focused on constructing functional theories for the origin of feathers (reviewed in Dyck 1985; Feduccia 1999). These theories used speculations about the plausible function of ancestral feathers to predict their morphology, despite the paucity of evidence about the biology of avian ancestors. Func-

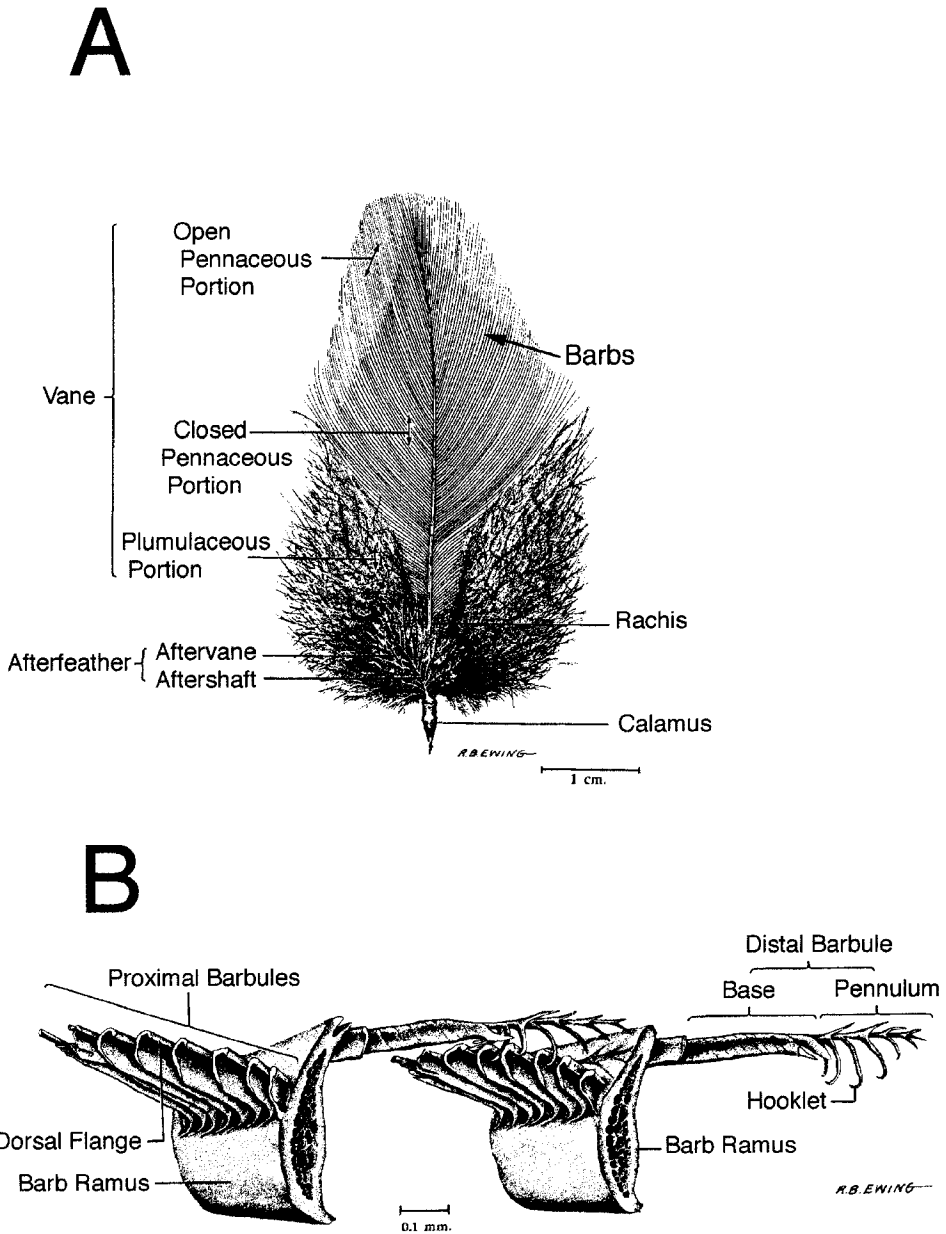
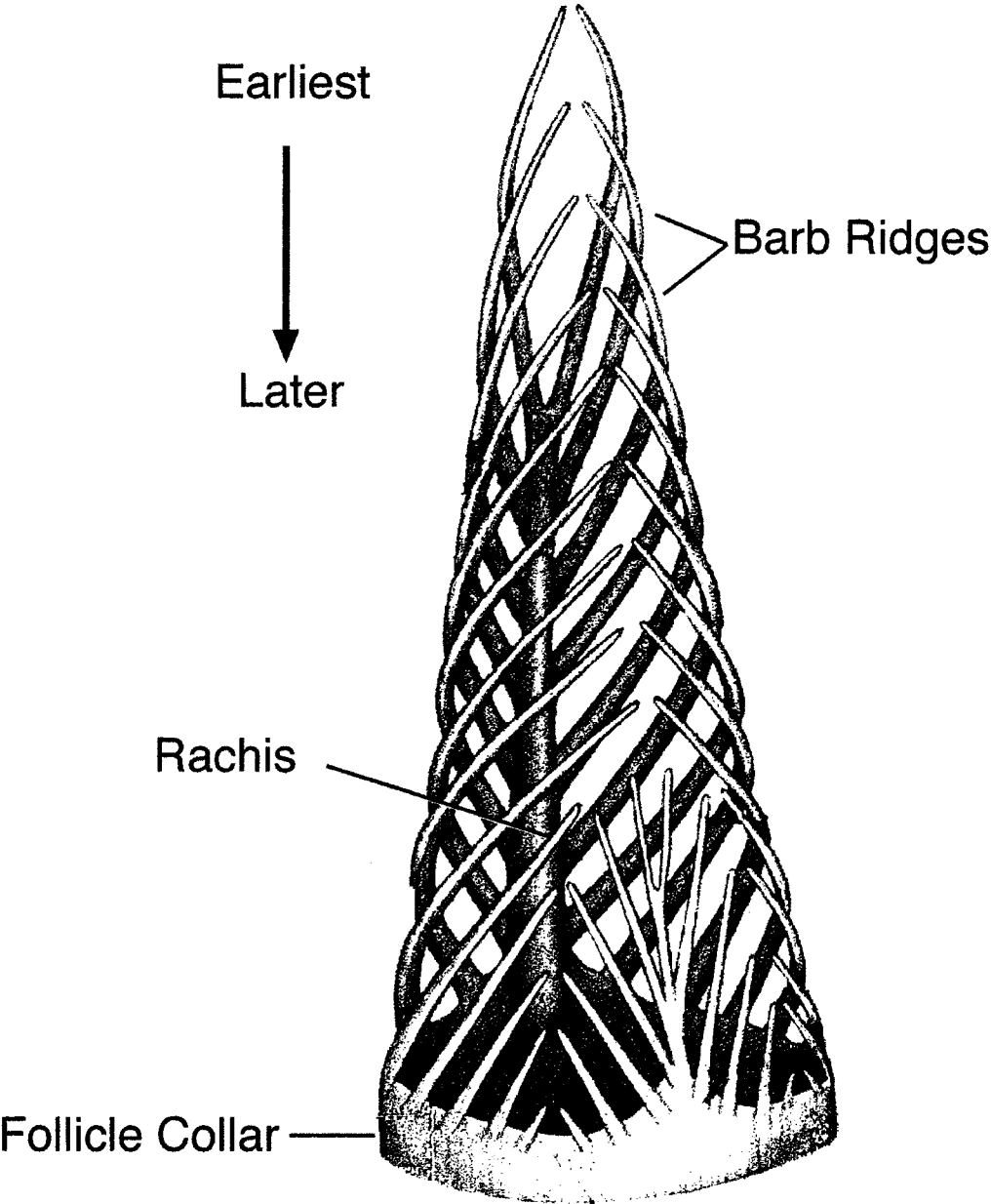


FIGURE 1. THE BRANCHED STRUCTURE OF A PENNACEOUS FEATHER

(A) The structure of a typical pennaceous contour feather with afterfeather, from Lucas and Stettenheim (1972). (B) Cross section of two adjacent feather barbs from the closed pennaceous portion of a feather vane (orientation as in the labeled barbs in A). Distal barbules are oriented toward the tip of the feather (extending right) and the proximal barbules are oriented toward the base of the feather (extending left). The hooked pennulae of the ends of the distal barbules extend over the obverse (upper) surface of the vane to interlock with the grooved dorsal flanges of the bases of the proximal barbules of the adjacent barbs to form the closed pennaceous vane. The distal barbules of open pennaceous feathers lack hooked pennulae. Both illustrations are from Lucas and Stettenheim (1972).



tional theories of the origin of feathers have failed to establish a consensus on either the original function or original morphology of feathers.

Over the last half of the 20th century, neo-Darwinian approaches to the origin of feathers, exemplified by Bock (1965), have hypothesized a microevolutionary and functional continuum between feathers and a hypothesized antecedent structure (usually an elongate scale). Feathers, however, are hierarchically complex assemblages of numerous evolutionary novelties—the feather follicle, tubular feather germ, feather branched structure, interacting differentiated barbules—that have no homolog in any antecedent structures (Brush 1993, 1996, 2000; Prum 1999). Genuine evolutionary novelties are distinct from simple microevolutionary changes in that they are qualitatively or categorically different from any antecedent or homonomous structure (Nitecki 1990; Müller and Wagner 1991; Raff 1996). Consequently, Wagner (2000; Wagner et al. 2000; Chiu and Wagner 2001) has argued that macroevolutionary research on homology and the origins of evolutionary novelties should ask different questions that are focused on uncovering the mechanisms that generate morphological novelties. Traditional neo-Darwinian approaches to the origin of feathers have focused on creating theoretical continuity with antecedent structures, and as a consequence, few of these theories have adequately appreciated the many novel aspects of feather morphology and feather development, and none have formulated adequately detailed hypotheses about the origin and evolution of these morphological and developmental novelties. In contrast to neo-Darwinian approaches, and in congru-

ence with a macroevolutionary concept of novelty, the developmental theory of feather origins is focused specifically on reconstructing the transition of developmental *novelties* required for the origin and diversification of feathers (Prum 1999).

Another conceptual problem has been the tendency to propose complex evolutionary scenarios as intellectual “package deals” that include correlated and interdependent hypotheses about the origins of birds, avian flight, and feathers. One package features birds as an early nondinosaurian lineage of archosaurs, the arboreal theory of the origin of flight, and the aerodynamic theory of the origin of feathers (e.g., Feduccia 1999). An alternative package offers birds as a lineage of theropod dinosaurs, the cursorial theory of the origin of flight, and the thermal insulation theory of the origin of feathers (e.g., Ostrom 1974). These two packages have been promoted inaccurately as reflecting “ornithological” and “paleontological” schools of thought, respectively (e.g., Feduccia 1999). Clearly, the solutions to these complex questions are ultimately interrelated (i.e., there is only one history of life). But the fundamental problem with these combined scenarios is that they conflate the analysis of these complex issues and eliminate many plausible combinations. These macroevolutionary questions can only be productively and rigorously pursued independent from one another. By approaching the questions of phylogenetic relationships and evolutionary functional morphology independently, emergent historical patterns can be used to test hypotheses of morphological homology and evolutionary process (Lauder and Liem 1989; Larson and Losos 1996). Perhaps unsurprisingly, the recent theoretical

FIGURE 2. SCHEMATIC DIAGRAM OF HELICAL GROWTH OF BARB RIDGES OF A PENNACEOUS FEATHER

The branched structure of the barbs and the rachis of a feather form by helical growth and fusion of barb ridges within the tubular feather germ. Feathers grow from the base. Barb ridges form at the new barb locus on the posterior midline of the collar and grow helically around the collar toward the anterior midline where they fuse to form the rachis ridge. Subsequent barb ridges fuse to the rachis ridge. In feathers with an afterfeather, the new barb locus divides into two laterally displaced new barb loci. Subsequently, new barb ridges grow helically both anteriorly to the main rachis and posteriorly to form the hyporachis and vane of the afterfeather. The main vane and the afterfeather form separate vanes united within a single feather by the calamus (Figure 1A). Pennaceous feathers obtain their planar form only after emerging from the cylindrical feather sheath when growth is complete. The obverse (upper) and reverse (lower) surfaces of the vane develop from the outer and inner surfaces of the cylindrical feather germ. Illustration based on Lucas and Stettenheim (1972).

progress on the evolutionary origin of feathers has come from outside these entrenched scenarios.

In this paper, we present a conceptual review of the previous theories of the origin of feathers and a synopsis of the recently proposed developmental theory of the origin of feathers (Prum 1999; Brush 2000). We review recent paleontological evidence that supports the theropod origin of feathers prior to the origin of birds or flight, and the congruence between these newly discovered theropod feather morphologies and the morphologies predicted by the developmental theory. In light of these findings, we discuss the homology of feathers and scales, plausible and implausible functional theories of the origin of feathers, feathers as evolutionary novelties, and the molecular basis of feather development and evolution.

CONCEPTUAL REVIEW OF PREVIOUS THEORIES

Previous theories of the origin of feathers can be categorized in terms of four conceptual approaches: analyses of the "primitive" feathers of extant birds, functional theories, scale-to-feather transformation theories, and theories based on the details of keratin biochemistry and keratinogenesis. These four approaches are not mutually exclusive, but have often been combined in different ways to advocate a variety of hypotheses. Here we review the conceptual bases for these theories.

Many early predictions of the ancestral morphology of feathers were based on analyses of the variation in extant feather morphology and its distribution among modern birds (Dyck 1985). These attempts were unsuccessful for several reasons. First, researchers attempted comparative evolutionary analyses without historically explicit concepts of monophyly and phylogeny. This conceptual vacuum led to incongruous arguments that the feathers of specific extant groups represent the primitive morphology of all avian feathers. For example, ratites (Lowe 1935), penguins (Ewart 1921), and megapodes (Becker 1959) were each hypothesized at various times to be a basal lineage of birds that actually possess primitive feathers. These

authors did not understand explicitly that an extant lineage within the monophyletic clade of modern birds could not be more closely related to the lineage in which feathers evolved than *Archaeopteryx*, and that the phylogenetic distribution of feather variation in extant bird clades could not be used to identify primitive feather morphologies. Other researchers argued that the simpler structure of certain extant feather types, commonly either plumulaceous downs or open pennaceous contour feathers, supported the hypothesis that such morphologies were likely to be primitive (Ewart 1921). These hypotheses were countered by evidence that some of these modern feathers show obviously derived features (Steiner 1917). For example, some downs have differentiated distal and proximal barbs that indicate that they may be secondarily derived from pennaceous feathers in which the differentiated barbs interconnect to form a closed vane (Dyck 1985). Of course, both arguments incorrectly imagined that the ancestral morphology of all feathers could be found within extant feather diversity. Structurally modern feathers have been present since at least *Archaeopteryx*, and they have continued to evolve, diversify, and simplify in various ways. The presence of differentiated barbs in some modern downs may constitute evidence that they are secondarily derived from pennaceous feathers, but this finding is irrelevant to the question of whether plumulaceous or pennaceous structure was primitive to the initial radiation of feather morphology. Theories of the origin of feathers based on nonphylogenetic analyses of extant feather diversity have confounded the evolution of feathers among extant birds with the initial origin and diversification of feathers preceding *Archaeopteryx*.

A second conceptual current has been the development of functional theories of the evolutionary origin of feathers (reviewed in Dyck 1985; Feduccia 1999). These theories propose plausible initial functions for ancestral feathers, and then hypothesize a suitable ancestral morphology to fulfill that function. Plausible initial functions have been justified based on notions about the natural history and ecology of ancestral birds, and notions about what functional transitions in mor-

phology are evolutionarily possible. Recent evidence of biologically convergent, analogous instances of the intermediate functional states proposed by the models have been used to support the plausibility of specific functional theories (e.g., the hairy arms of *Propithecus* lemurs as an aerodynamic model of early feather evolution: Feduccia 1993). The list of functional theories of feather origins includes the hypotheses that feathers evolved for flight (e.g., Steiner 1917; Heilmann 1926; Blaszyk 1935; Parkes 1966; Feduccia 1985, 1993, 1999), thermal insulation (e.g., Davies 1889; Ewart 1921), heat shielding (Regal 1975), water repellency (Dyck 1985), communication (Mayr 1960), and tactile sensation (Broman 1941).

The conceptual basis of functional theories of the origin of feathers is weak because these theories rest upon hypotheses about the function of an ancestral structure whose morphology is unknown. Biologists can actively debate the "functional significance" of some well-known morphological structures from extant organisms, yet the ability to make inferences about the function of specific morphologies without direct experimental tests is limited. Functional theories of feather origins presume that current knowledge of the identity and natural history of the lineage in which feathers initially evolved, and the evolutionary mechanisms that shape morphology and function, are sufficient to permit a confident reconstruction of the ancestral morphology of feathers. Given that it can be difficult to understand the function of known structures, it is essentially impossible to confidently infer the ancestral function of feathers in absence of an independent hypothesis on their form. Alternative functional theories of the origin of feathers have been justified by restating the initial functional speculations in absence of supporting evidence from the organism's biology. Over the past 20 years, it has been recognized that historical analysis in evolutionary biology requires an independent documentation of the *pattern* of evolutionary events before testing alternative functional hypotheses about the evolutionary *process* that explain those events (Lauder 1981; Lauder and Liem 1989; Lauder 1990; Larson and Losos 1996; Padian

2001). Based on nonphylogenetic, neo-Darwinian evolutionary theory (e.g., Bock 1965), functional theories of the origin of feathers have failed because they attempt to do exactly the opposite: they use presumed knowledge of adaptive evolutionary process to reconstruct historical pattern.

An additional problem with functional theories of the origin of feathers is that functional criteria are explicitly incompatible with the recognition of the homology of structures. Even enthusiastic advocates of the concept of the "homology of functions" have recognized that function cannot be used to elucidate structural homology (Lauder 1994; Hall 1999:205). Thus, if a primitive homolog of modern feathers were discovered that did not meet the criteria of a specific functional model, its homology with modern feathers would be rejected based on *functional* criteria alone rather than whether its structure shared some unique or special similarities that reflect their historical relationship. For example, the homology between feathers and the integumentary appendages of *Sino-sauropteryx* may have been initially rejected because they did not meet the expectations of functional theories of the origin of feathers (Gibbons 1997; Feduccia 1999). Likewise, an entirely analogous structure with a convergent function could be proposed as a feather homolog based entirely on meeting some of the *functional* criteria of a proposed theory. For example, the proposed homology between feathers and the appendages of *Longisquama* (Jones et al. 2001) are based entirely on functionally convergent aspects of their planar structure. A fundamental aspect of the concept of structural homology is that it explicitly excludes similarities of function, and thus allows the recognition of homologous structure that have evolved in form as a consequence of an evolutionary change or transference in function. Incorporating a priori functional criteria into models for the origin of feathers has created fundamental problems for the field.

A third, important concept in many previous theories of the origin of feathers has been the hypothesis that feathers evolved from scales (reviewed in Lucas and Stettenheim 1972). Numerous ancestral feather morphol-

ogies have been proposed as hypothetical intermediates between planar reptilian scales and feathers. These scale-based scenarios have been incorporated into various functional theories, usually in the form of an elongate, planar scale (e.g., Heilmann 1926; Parkes 1966; Maderson 1972; Regal 1975; Dyck 1985; Feduccia 1999; Maderson and Alibardi 2000). Scale-based hypotheses of the origin of feathers create a developmental and topological conundrum that was first pointed out by Davies (1889) and still has not been adequately addressed by any elongate-scale-to-feather transformation theory. Scales are inherently laminar or planar folds of the skin, whereas feathers are essentially tubular epidermal appendages (Prum 1999). A planar pennaceous feather obtains its planar shape *only* after emergence from the cylindrical sheath. The obverse (outer) and reverse (under) surfaces of a pennaceous feather vane develop from the outer and inner surfaces of the tubular epidermal feather germ, respectively (Figure 2). In contrast, the dorsal and ventral surfaces of a planar scale develop from the dorsal and ventral surfaces of the original epidermal outgrowth. Thus, the planar surfaces of scales and feathers are not homologous (Davies 1889; Prum 1999). One planar form cannot be evolutionarily transformed into the other while maintaining a continuously functional planar configuration (Prum 1999). Steiner (1917) attempted to reconcile this contradiction by homologizing the ventral surface of a scale with the afterfeather (Lucas and Stettenheim 1972). This hypothesis, however, is not congruent with how the afterfeather develops (Lillie and Juhn 1938; Lucas and Stettenheim 1972). No other scale-based model for the origin of feathers has even attempted to resolve this fundamental problem (Heilmann 1926; Parkes 1966; Maderson 1972; Regal 1975; Dyck 1985; Feduccia 1999; Maderson and Alibardi 2000).

Scale-based theories of the origin of feathers have also been justified by the general premise that pennaceous feathers, with barbs and a rachis in a planar form, constitute the primitive feather morphology. This conclusion has been supported by the observation that many plumulaceous (downy) feathers of

extant birds have derived structures (Steiner 1917; Parkes 1966; Dyck 1985; Feduccia 1999). As described above, this conclusion is based on faulty phylogenetic reasoning, and is contradicted by the more general tubular nature of feathers (see below).

Scale-based models of the origin of feathers have not adequately recognized the suite of unique evolutionary novelties that characterize feather structure and development, nor have they attempted to explain their evolutionary origins. Any comprehensive theory of how feathers evolved should also explain the evolution of how feathers grow (Prum 1999). Scale-based models have failed to propose a cogent explanation for the origin of the follicle itself. Maderson and Alibardi (2000) accurately describe the function of the feather follicle in feather development, but they suggest no mechanism by which it might have evolved from a scale or what appendage morphology might grow from any such intermediate. Furthermore, scale-based models have repeatedly hypothesized the evolution of the branched structure of feathers as a process of the division of a planar scale (Heilmann 1926; Regal 1975; Dyck 1985; Maderson and Alibardi 2000). Like the proposed homology of the planar surfaces of feathers and scales, these scenarios are incongruent with the basic details of how feathers grow (Lucas and Stettenheim 1972; Prum 1999). Barb ridges form by the proliferation and outfolding of the basal layer of the feather germ epithelium, creating the longitudinal epidermal compartments that become the barbs (Lucas and Stettenheim 1972). The proliferation of barb ridges on the ventral side of a feather follicle during the growth of a pennaceous vane demonstrates clearly that barb ridges do not form by the division of a plane but by the proliferation, differentiation, and compartmentalization of epidermal tissue within the follicle collar (Strong 1902b; Lucas and Stettenheim 1972). In addition, the role of the barb ridge fusion in the creation of the rachis and hyporachis ridges during development further demonstrates that the rachis ridge is not homologous with a thickened medial axis of a scale (Lillie and Juhn 1938; Lillie and Wang 1941; Lucas and Stettenheim 1972; Prum 1999).

Scale-based models of the origin of feathers have proposed only the vaguest scenarios for the evolution of the complex structure of barbs and barbules (Regal 1975). Dyck (1985) made the most explicit attempt but concluded, "When and how the interlocking system of the barbules formed is difficult to suggest." The absence of these crucial details in scale-based models has frequently been covered with an unsatisfying caveat that feathers did not *actually* evolve directly from scales (Maderson 1972; Regal 1975; Maderson and Alibardi 2000). Yet these same authors still maintain that pennaceous feathers evolved from the elongate, planar, scale-like structure—which is the source of these conceptual problems.

Recently, Zhang and Zhou (2000) proposed that the thick, flat rachi of the elongate central rectrices of *Protopteryx fengningensis*, an Early Cretaceous enantiornithine bird, provide support for a scale-like origin of feathers. This hypothesis has two substantial problems. First, similar "scale-like" feathers occur in living birds, such as penguins (Spheniscidae) and tropicbirds (Phaethontidae). These enlarged rachi are formed by the fusion of barbs and are only superficially scale-like. Nearly identical rectrices are also present in the Early Cretaceous confuciusornithine birds that are phylogenetically even more basal than *Protopteryx*, but in *Confuciusornis* these feathers are distally branched just like the analogous feathers of modern birds (Chiappe et al. 1999). Unfortunately, the tips of the remiges of the only specimen of *Protopteryx* are missing, so these critical data are unavailable. A second, more critical problem with this hypothesis is that *Protopteryx* and other enantiornithines are not the most basal birds in avian phylogeny (see Figure 6; Chiappe et al. 1999). Because feathers must have evolved in a lineage prior to the differentiation of *Archaeopteryx* from other birds, the rectrices of the enantiornithine *Protopteryx* must be secondarily derived. Like variations in feather morphology among modern birds, these fascinating early bird feathers document the diverse developmental capabilities of ancient feather follicles, but they do not constitute retained plesiomorphic morphologies. Given its phylogenetic position and the equivocal nature of

the evidence, the rectrices of *Protopteryx* do not provide evidence of a scale-like origin of feathers.

A fourth approach has been to use details of patterns of keratinization in reptiles and birds to support hypotheses of the origin of feathers. Maderson (1972) and Maderson and Alibardi (2000) have proposed that the similarity in vertical alternation of α and β -keratins in feathers and lepidosaur scales justified the use of the lepidosaur scale as a "model system" for the evolution of feathers. Maderson (1972) made no proposals about the origin of the branched structure of feathers, but Maderson and Alibardi (2000) propose that branched feathers evolved through the subdivision of an elongate scale into barbs and barbules, as proposed by Regal (1975) and others (reviewed in Dyck 1985). This approach is conceptually superior to purely functional theories because it is based on observable and testable details of integumentary biology and development. Unfortunately, the patterns of α -keratin and β -keratin expression in the reptilian dermis lead to few detailed predictions about the origin of feathers and evolution of feather morphogenesis that are not merely consequences of the assumption that feathers are broadly homologous with scales (including their planar surfaces), that feathers evolved directly from an elongate scale, and that pennaceous feathers are primitive. Thus, these models have all the previously discussed problems inherent in strictly scale-based theories. Furthermore, the proposed relationship between vertical alternation of keratin in lepidosaur scales and bird feathers is based on a misconception of phylogenetic relationships of birds and reptiles. Birds and crocodylians are archosaurs. The scales of both crocodylians and birds lack the vertical stratification of α -keratin and β -keratin expression in the epidermis, and the shedding or molt associated with it in both lepidosaurs and bird feathers (Maderson and Alibardi 2000). It is not parsimonious to conclude that molt in lepidosaur scales and bird feathers is somehow homologous when it is absent from crocodylian and avian scales. If the vertical alternation of keratin expression in lepidosaur scales and feathers is evolutionarily convergent, it remains to be demon-

strated how any analogous aspects of lepidosaur scales can function as an appropriate "model system" for the study of the origin of feathers, as proposed by Maderson and Alibardi (2000). The evolution of vertical alternation of keratin expression in feathers ultimately requires explanation. There is no reason to conclude, however, that the patterns of α -keratin expression in lepidosaur scales, crocodilian and avian scale-hinge regions, and the feather sheath are not proximate adaptations for their current physical functions.

Brush (1993, 1996) provided an alternative "keratin-based" theory of the origin of feathers. He reviewed the origin of the novel keratins found in feathers, and the evidence and theories about their evolution, and concluded that feathers are complex hierarchical novelties that incorporate numerous unique molecular and developmental features. Brush (1993, 1996) also directly questioned the homology of scales and feathers, and pointed out the essential novelties of the many details of feather biochemistry and development. Although he did not propose an explicit scenario for the origin of the complex branched structure of feathers, these discussions were based on testable details of feather development and anticipated subsequent models based on feather development.

A DEVELOPMENTAL THEORY OF THE ORIGIN OF FEATHERS

We have recently proposed an alternative approach to the origin of feathers that uses the details of feather development to reconstruct plausible antecedent morphologies (Prum 1999; Brush 2000, 2001). This approach suggests that any theory of the origin of feathers should also provide a complete and consistent theory of the origin of the complex mechanisms of feather development. Furthermore, the details of feather development support an hypothesis of feather evolution that is independent of phylogenetic and functional assumptions. We have each independently proposed developmental theories of the origin of feathers. Prum (1999) analyzed the complex, hierarchical mechanisms by which feathers grow, and hypothesized a transition

series of developmental novelties from the first feathers through modern feather morphological diversity. Brush (1993, 1996, 2000, 2001) used feather biochemistry and the hierarchy of feather development and structure to define the conditions for recognizing the original "protofeather," and to propose a "phylogeny" of feather types. The implications of these two independent approaches are extensively congruent, and represent a conceptually new direction in the study of the origin of feathers.

The details of feather development provide a rich source of information about feather biology (reviewed in Lucas and Stettenheim 1972, summarized in Prum 1999). Feathers are branched, filamentous keratin structures uniquely characterized by a tubular follicle which forms by a cylindrical invagination around the elongate feather papilla or short bud (Figure 3). Rather than growing from bifurcating tips like a plant, feathers form a branched structure from the base using two unique mechanisms. The branching of the barbs and rachis is a consequence of the helical growth of barb ridges around the tubular epidermal cylinder of the feather follicle and feather germ, and the fusion of the barb ridges to the rachis ridge on the anterior side of the follicle (Figure 2). In contrast, the branched structure of the barbules and barb rami involves the differentiation of keratinocytes within the peripheral barbule plates of the developing barb ridges into a paired series of cells that connect basally to the barb ramus.

By focusing on the evolution of the mechanisms of feather development, Prum (1999) proposed a detailed, testable model of the evolutionary origin of feathers that is independent of functional or phylogenetic assumptions. The model proposed a five-stage transition series in the history of feather diversity as a hypothesized sequence of novelties in feather development (Figure 4). The model hypothesizes that the first feather (Stage I) originated with the first feather follicle—the cylindrical epidermal invagination around the initial feather papilla. Subsequent feather diversity evolved through a series of derived developmental novelties within the tubular intermediate epidermal

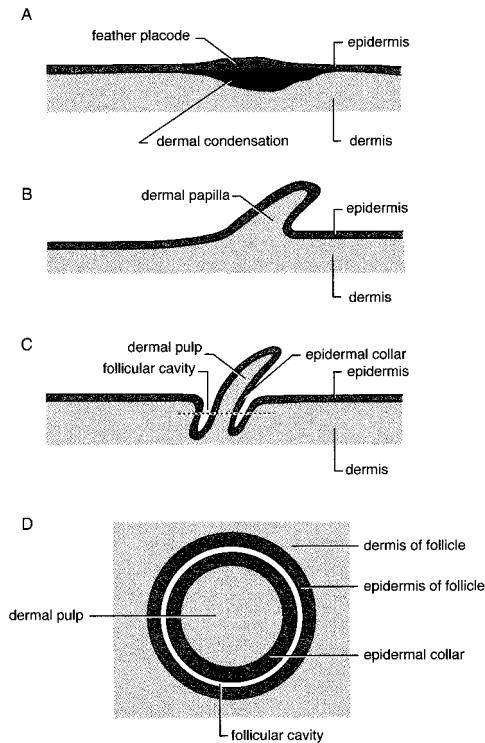


FIGURE 3. SCHEMATIC DIAGRAM OF THE INITIAL DEVELOPMENT OF A FEATHER FOLLICLE

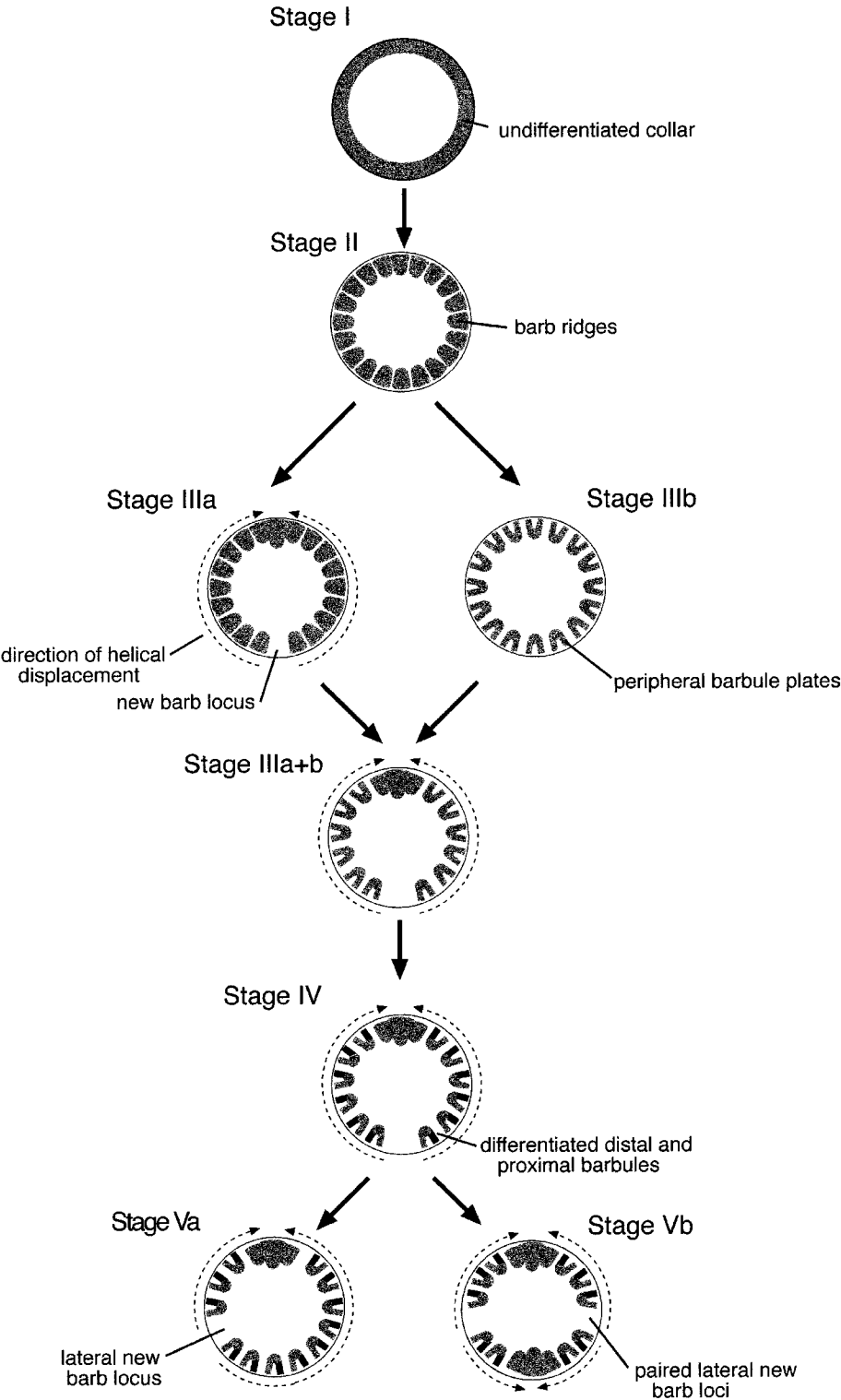
(A) Development of the epidermal feather placode and dermal condensation. (B) Development of a short bud or feather papilla. (C) Formation of the feather follicle through the invagination of a cylinder of epidermal tissue around the base of the feather papilla. (D) Cross section of the feather follicle through the horizontal plane indicated by the dotted line in C. The invaginated tubular feather follicle is characterized by 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 or ramogenic zone), and the dermal pulp (tissue at the center of the follicle). The tubular feather germ grows by proliferation and differentiation of keratinocytes in the follicle collar. Summarized from Lucas and Stettenheim (1972) and Prum (1999).

layer of the follicle, called the follicle collar, which generates the tubular feather germ. After the origin of the follicle came the differentiation of the follicle collar into barb ridges that generate the barbs (Stage II). The model proposes two alternative stages next—the ori-

gin of helical growth (Stage IIIa), or the origin of barbule plate differentiation (Stage IIIb). The model cannot differentiate between the two alternative orders for these events (i.e., IIIa before IIIb, or IIIb before IIIa), but following the evolution of both of these developmental novelties came the capacity to grow both kinds of branched structure typical of modern feathers (Stage IIIa + b). The origin of differentiated distal and proximal barbule plates followed next (Stage IV). Finally, additional developmental mechanisms evolved and created further diversity in feather structure (Stage Va–f).

This hypothesized series of five developmental novelties predicts an explicit transition series in the morphologies of the feathers grown from these follicles (Figure 5; Prum 1999). Stage I follicles would produce an unbranched, hollow, tubular feather. The model predicts the keratinaceous composition and essentially tubular geometry of the primitive feather, but does not predict the shape, size, stiffness, or other structural qualities. A Stage II follicle would grow a tuft of barbs fused basally to a single calamus. A Stage IIIa follicle would grow a feather with a rachis (formed by the initial fusion of feather barbs on the anterior side of the follicle) and a series of fused barbs. Stage IIIb follicles would produce a tuft of barbs with branched barbules. Stage IIIa + b follicles would grow the first bipinnate (double-branched) feathers with a rachis, barbs, and barbules. In the absence of differentiated barbules, a Stage IIIa + b feather would be open pennaceous. Stage IV follicles would grow a pennaceous feather with a closed, coherent vane created by the interactions of the differentiated hooks and grooves on the distal and proximal barbules of neighboring barbs. Only after Stage IV could subsequent novelties in Stages Va–f yield additional feather diversity, including an asymmetrical vane (Stage Va) and the after-shaft (Stage Vb).

The justification for the order of the evolution of the developmental novelties in the model comes from the observed causal hierarchy within feather growth mechanisms (Prum 1999). For example, a feather with filamentous barbs (Stage II) is hypothesized to have evolved before the origin of the rachis



(Stage IIIa) because the rachis of a pennaceous feather is initially created, or specified, by the fusion of barb ridges (Lillie and Wang 1941; Lucas and Stettenheim 1972; Prum 1999). Likewise, barbs (Stage II) are hypothesized to evolve before barbules (Stage IIIb) because barbules develop within layers of the preexisting barb ridges (Prum 1999). A bipinnate feather with a rachis, barbs, and barbules (Stage IIIa + b) is hypothesized to have evolved before the differentiated barbules (Stage IV) because prior to the origin of the rachis, barbules could not have had distal or proximal orientation relative to the feather vane. Prum (1999) describes developmental justifications for additional stages.

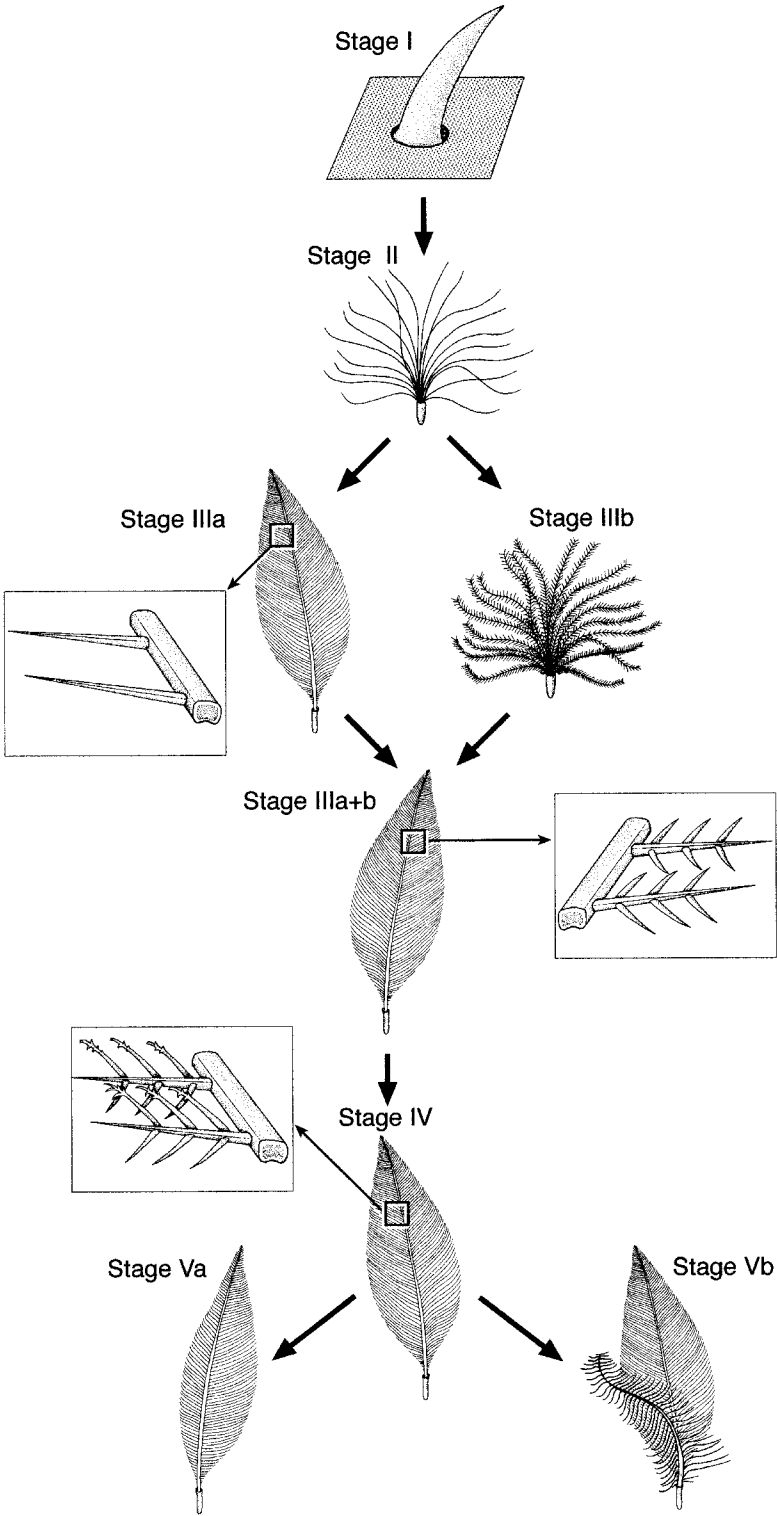
Although Prum's (1999) model is based on developmental evidence, it is explicitly *not* based on Haeckelian ontogenetic recapitulation or von Baer's Law—the notion that ontogenetically antecedent events are phylogenetically primitive. Several stages of the model are congruent with a recapitulationist scenario, but they are not justified on that basis (Prum 1999). Thus, plumulaceous feathers are hypothesized to be primitive to pennaceous feathers not because the first feathers of extant birds are typically plumulaceous, but because the simplest differentiated follicle collar would have grown a plumulaceous feather (Prum 1999). There are also several stages of the model that directly conflict with von Baer's Law (Prum 1999). For example, in the development of the first feathers in an

avian embryo, differentiated barb ridges originate in the inner epidermal layer of the feather germ during the short bud stage before the origin of the follicle, whereas in the model the follicle originates (Stage I) before the barb ridges (Stage II). The initiation of barb ridges before the follicle must be a derived alteration of the primitive ontogeny, however, because the barbs would be unable to continue to grow without the organization provided by the follicle. In a second example, the barbules differentiate and keratinize before the ramus within any horizontal section of a barb ridge. A feather with keratinized barbules that lacked barb rami would simply disintegrate, however. Barbules keratinize before the ramus because they are peripheral to the ramus within the barb ridge, and a fully keratinized ramus would block the diffusion of necessary nutrients from the central dermal pulp out to the developing barbule keratinocytes.

Important support for the plausibility of the developmental model of the evolutionary history of feathers comes from extant feather diversity (Prum 1999). All the primitive feather morphologies proposed by the model exist among extant avian feathers. For example, the basic structure of the Stage I feather is present in every known feather in the tubular cylindrical calamus at its base and the cylindrical feather sheath that surrounds it. Specialized tubular feathers that are identical to the predictions of Stage I grow from the

FIGURE 4. DEVELOPMENTAL MODEL OF THE ORIGIN AND DIVERSIFICATION OF FEATHER FOLLICLES

An hypothesized transition series of evolutionary novelties in feather development, depicted as a series of cross sections of the follicle collar—the innermost layer of epidermal tissue in the feather follicle that generates or develops into the feather (Figure 3D) from Prum (1999). The model is based entirely on the hierarchical details of feather development, and is independent of functional or phylogenetic assumptions. Each diagram is oriented with the anterior surface of the follicle 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 + IIIb—Origin of follicle capable of both 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 after-feather of the follicle. See Prum (1999) for details of additional stages in the evolution of feather diversity (Stages Vc–f).



central crown patch of male African peafowl (*Afropavo congensis*, Phasianidae) and from the entire crown of the Bornean bristlehead (*Pityriasis gymnocephala*, Corvoidea). Additional modern examples of morphologies like Stages II and III can be found among various extant avian plumages (Prum 1999). For example, certain display plumes in egrets (*Egretta*, Ardeidae) and birds of paradise (*Paradisaea*, Paradisaeidae) correspond well to Stage II morphology. Other open pennaceous contour feathers and semiplumes are congruent with the predicted Stage IIIa + b morphology. These modern feathers demonstrate that the developmental configurations and morphologies predicted by the model are among the known products of feather follicles. Thus we know that feather follicles can function in the ways proposed by the model. These extant feathers are secondarily derived or simplified, however, and their existence does not constitute evidence that primitive feathers actually had these predicted morphologies. For these inferences, paleontological data are required to document plesiomorphic feather morphologies (see below).

Brush's (2000, 2001) approach to the origin of feathers is similar to Prum's (1999) in that it also draws on observable details of feather development from extant birds. After recognizing their distinctness from scales, Brush (2000, 2001) hypothesized that feathers are essentially cylindrical structures, and

that the follicle and feather keratins are the fundamental feather novelties. Brush (2000, 2001) then hypothesized that the first "proto-feather" was an elongate tubular filament. He referred to this initial tubular structure as "barb-like," and envisioned the evolution of branched feather structure as the duplication of these barb-like structures. This hypothesis confuses the identities of an entire feather and an individual barb. A simple tubular feather would be homologous with an entire modern feather, the whole product of growth from a follicle. The hollow center of the first feather is a consequence of the tubular organization of the follicle and comes from the dermis at the center of the follicle and feather germ. In contrast, barbs are differentiated portions of the tubular feather germ. The evolution of a branched feather morphology came not from the duplication of an initial tubular structure, but from the differentiation, proliferation, and organization of cells within this epidermal tube into barb ridges.

The historical transition series of Brush's (2000) feather phylogram is extensively congruent with Prum's (1999) hypothesis. Prum, however, provided a more explicit developmental justification of the stages, and also an explicit distinction between the evolution of initial structural feather diversity and the classes of extant feathers, many of which are likely to have evolved through secondary simplification of more complex forms.

FIGURE 5. DEVELOPMENTAL MODEL OF THE ORIGIN AND DIVERSIFICATION OF FEATHERS

A predicted transition series of feather follicles based on the hypothesized series of evolutionary novelties in feather developmental mechanisms (Figure 4) from Prum (1999). Stage I—Origin of an undifferentiated tubular collar yields the first feather, a hollow cylinder. Stage II—Origin of a collar with differentiated barb ridges results in a mature feather with a tuft of unbranched barbs and a basal calamus emerging from a superficial sheath. Stage IIIa—Origin of helical displacement of barb ridges and the new barb locus results in a pinnate feather with an indeterminate number of unbranched barbs fused to a central rachis. Stage IIIb—Origin of peripheral barbule plates within barb ridges yields a feather with numerous branched barbs attached to a basal calamus. Stages IIIa + IIIb—Origin of a feather with both a rachis and barbs with barbules creates a bipinnate, open pennaceous structure. Stage IV—Origin of differentiated proximal and distal barbules creates the first closed pennaceous vane. Distal barbules grew terminally hooked pennulae to attach to the simpler, grooved proximal barbules of the adjacent barb (Figure 1B). Stage Va—Lateral displacement of the new barb locus leads 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 yields 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 Prum (1999) for details of additional stages in the evolution of feather diversity.

PALEONTOLOGICAL DISCOVERY OF NONAVIAN DINOSAUR FEATHERS

Over the last ten years, the discovery and description of the paleofauna from the Early Cretaceous of the Yixian Formation of Liaoning Province, northeastern China, have contributed numerous breakthroughs in vertebrate paleontology (Stokstad 2001a). Among the most exciting and revolutionary finds have been previously unknown radiation of early birds and small theropod dinosaurs. The exceptional taphonomic conditions preserved integumentary structures of many of these birds and some nonavian theropod dinosaur specimens. These recently discovered theropod integumentary structures provide the first new morphological evidence about the origin and evolution of feathers since the description of *Archaeopteryx* in 1861. Recent analyses have confirmed the diversity of their structure, and have documented several novel morphological features that they share uniquely with avian feathers (Ji et al. 2001; Xu et al. 2001). In combination with the independent data supporting birds as a lineage of theropod dinosaurs (Gauthier 1986; Holtz 1994; Sereno 1997; Padian and Chiappe 1998; Sereno 1999), the new paleontological evidence strongly supports the conclusion that the novel integumentary structures of these theropods are homologous with feathers and constitute primitive feather morphologies (Ji et al. 2001; Xu et al. 2001). Furthermore, the morphologies of these dinosaur feathers are congruent with the predicted stages of the developmental model of the origin of feathers (Ji et al. 2001; Sues 2001; Xu et al. 2001).

The first nonavian theropod described from the Yixian Formation was *Sinosauropteryx*, which was described by Chen et al. (1998) as having small (5–6 mm) “protofeathers” along its back and on its face and belly. Chen et al. (1998) presented a phylogenetic analysis that indicated that *Sinosauropteryx* was a basal coelurosaur, implying a deeply dinosaurian origin for feathers. Though the homology of these structures with feathers was initially rejected by some (Gibbons 1997; Feduccia 1999), the structures are cylindrical and emerge from the skin in a manner that is nearly unique to feathers and thus are likely to have grown from cylindrical follicles (A H Brush and R O

Prum, personal observation). The appendages of *Sinosauropteryx* may have been diverse: some appendages are unbranched, but others may have been a simple tube with a branched distal tuft (Brush and Prum, personal observation).

Ji et al. (1998) later described two theropods with fully pennaceous feathers on the forelimbs and tail—*Caudipteryx* and *Protarchaeopteryx*—and declared them “feathered dinosaurs.” The obvious rachis and herringbone pattern of barbs have been universally accepted as vaned feathers. The phylogenetic analysis in the original description included only a single additional nonavian dinosaur (*Velociraptor*), however, and *Caudipteryx* and *Protarchaeopteryx* were placed as the successive sister groups to birds (Ji et al. 1998). This topology left the possibility open that *Caudipteryx* and *Protarchaeopteryx* could be secondarily flightless birds. Accepting the evidence of feathers, critics of the dinosaurian origin of birds claimed that this was the case (Feduccia 1999; Jones et al. 2000b; Martin and Czerkas 2000). Subsequently, independent phylogenetic analyses have placed *Caudipteryx* within the oviraptoroid theropods (Sereno 1999; Zhou 2000; Zhou and Wang 2000; Zhou et al. 2000; Holtz 2001; Norell et al. 2001).

Filamentous integumental appendages have also been described from the head of the alvarezsaurid *Shuvuuia deserti* from a Late Cretaceous deposit in the Gobi Desert of Mongolia (Schweitzer et al. 1999; Schweitzer 2001). Schweitzer et al. (1999; Schweitzer 2001) used immunological methods and electron microscopy to infer that the filamentous structures preserved on the head of *Shuvuuia* were composed of β -keratin. The alvarezsaurids, including *Mononychus* and *Shuvuuia*, have been alternatively hypothesized to be an early lineage of birds (Chiappe et al. 1996, 1998), or the sister group to the ornithomimid theropods (Sereno 1999, 2001). The results of Schweitzer et al. (1999) support the hypothesis that the filamentous structures from *Shuvuuia* are integumentary appendages, since β -keratins are only expressed in the integument of reptiles (including birds). Regardless of whether the alvarezsaurids are an early avian lineage or are most closely related to ornithomimids,

these data substantiate the conclusion that the filamentous structures are homologous with feathers. The initial placement of the alvarezsaurids within birds may have been an artifact of the relatively small samples of non-avian theropods included in the analyses (e.g., Chiappe et al. 1996, 1998). We prefer the hypothesis that is based on more inclusive phylogenetic analyses that places alvarezsaurids with the ornithomimids. Although these analyses are new and need to be repeated, Schweitzer et al. (1999; Schweitzer 2001) provide unique biochemical, immunological data in support of the origin of feathers in theropod dinosaurs.

Since the description of *Caudipteryx* and *Protarchaeopteryx*, filamentous integumentary structures have been discovered on additional nonavian theropod specimens from the Yixian Formation, including long filamentous appendages from the back of the ulna of a large basal therizinosaur, *Beipiaosaurus* (Xu et al. 1999a), and covering large portions of the body of three basal dromaeosaurs—*Sinornithosaurus* (Xu et al. 1999b), *Microraptor* (Xu et al. 2000), and two unknown taxa closely related to *Sinornithosaurus* (Ji et al. 2001; Norell et al. 2002). The integumentary appendages of these taxa consist of filamentous structures between 25–190 mm long.

The original descriptions of *Sinosauropteryx*, *Sinornithosaurus*, and *Beipiaosaurus* did not describe these integumentary appendages in substantial detail or justify explicitly in what way they could be homologous with feathers. With the controversy over the phylogenetic relationships of the undoubtedly feathered *Caudipteryx* and *Protarchaeopteryx* (Dalton 2000), confirmation of the preavian theropod origin of feathers required demonstration of feather-like structure in the integumentary appendages of clearly nonavian theropods.

This critical evidence has come from the integumentary structures of two Liaoning theropods classified as basal dromaeosaurs. In the original description of *Microraptor*, Xu et al. (2000) proposed explicitly that the appendages of *Microraptor* were branched in structure like a rachis and barbs. Subsequently, Xu et al. (2001) presented an analysis of the integumentary appendages of the type

specimen of *Sinornithosaurus* that strongly supported their homology with feathers. They documented that these integumentary appendages varied in structure over different parts of the body. Furthermore, the *Sinornithosaurus* integumentary appendages were composed of multiple filaments and exhibit two forms of branched structure: a basal tuft and serial branching off a central shaft. Xu et al. (2001) concluded that *Sinornithosaurus* provided little direct evidence for the presence of a rachis. They inferred the presence of a rachis in one appendage which continued to add new filaments throughout its length without increasing in width. Among all known vertebrate integumentary appendages, the three features documented in the appendages of *Sinornithosaurus*—multiple filaments, basal branching, and serial branching—are unique to avian feathers (Lucas and Stettenheim 1972; Bereiter-Hahn et al. 1986; Xu et al. 2001). No other vertebrate integumentary appendages are composed of multiple filamentous structures. The hair of chinchillas (Chinchillidae) appears tufted, but actually grows from multiple independent roots that develop within a single follicle (Nowak and Paradiso 1983; Grau 1994). Furthermore, the basally tufted and the serial branched morphologies of *Sinornithosaurus* are identical in general structure to certain avian downs and to barbuleless pennaceous feathers. These uniquely shared morphological features constitute the type of special similarity and correspondence of parts that characterize morphological homologs (Patterson 1982; Pinna 1991), and their identification provides strong confirmation of the homology of these theropod integumentary structures and avian feathers. In combination with the independent phylogenetic evidence that dromaeosaurs and birds are sister groups, the homology with feathers is strongly supported.

Ji et al. (2001) later described the morphology and distribution of the integumentary appendages of a basal dromaeosaur that is probably referable to *Sinornithosaurus* and is indisputably nonavian. This extraordinary specimen exhibits abundant filamentous integumentary appendages over the entire surface of its body except for the lower legs

and feet. As in *Sinornithosaurus* (Xu et al. 2001), these appendages are diverse in morphology. The specimen has at least three types of feathers, including simple tufts, longer feathers with branches, and indisputably vaned feathers with an obvious herringbone pattern of parallel filaments preserved in the same pattern as the barbs in a pennaceous feather. Again, among all vertebrate integumentary appendages, these three classes of branched structures are unique to feathers.

Most recently, Norell et al. (2002) described the integumentary appendages of another specimen of basal dromaeosaur from the Yixian Formation that may be distinct from *Sinornithosaurus*. The specimen shows abundant integumentary appendages over the body, but the appendages of the tail, legs, and wings are particularly well preserved. The specimen has 19 cm long appendages that extend from the tip of its tail and 13 cm long appendages on the legs. Although most of its integumentary appendages are not well preserved, the appendages of the legs and forelimbs clearly demonstrate the rachis and barbs characteristic of a pennaceous vane. In a few places, the appendage vanes exhibit gaps that indicate the presence of differentiated distal and proximal barbules that normally interlock to create the closed pennaceous structure. This specimen provides definitive evidence of the presence of modern feathers in a nonavian dinosaur.

These paleontological discoveries and phylogenetic analyses essentially demonstrate the origin of feathers in nonavian terrestrial theropod dinosaurs (Padian 1998, 2001; Sereno 1999; Sues 2001; Prum 2002). Feathers originated and diversified in structure within the coelurosaurian theropod dinosaurs before the origin of birds or the origin of flight (Figure 6). Integumental appendages that share unique, derived features with avian feathers are now known from eight different nonavian theropod taxa: *Sinosauropteryx*, *Shuvuuia*, *Beipiaosaurus*, *Caudipteryx*, *Protarchaeopteryx*, *Sinornithosaurus*, *Microaptor*, and two unnamed basal dromaeosaurs from the Yixian Formation. All but the fragmentary *Protarchaeopteryx* have been or can be provisionally included in a phylogenetic hypotheses for the theropods.

Feathers are not preserved in *Compsognathus longipes* (Ostrom 1978), but since *Sinosauropteryx* is likely closely related to *Compsognathus*, it is difficult to conclude whether they were absent or not. By parsimoniously superimposing these data on one recent phylogenetic hypothesis for the theropods (Sereno 1999), it is possible to reconstruct an historical hypothesis for the origin and diversification of the feathers within theropods (Figure 6). Feathers originated in a lineage of coelurosaurian theropod dinosaurs including both *Sinosauropteryx* and birds, but excluding allosauroids, ceratosaurids, and coelophysids. Subsequently, feathers with primary branched structure (i.e., tufted), and possibly a rachis, evolved in a lineage that included the common ancestor of alvarezsaurids, ornithomimids, therizinosaurids, tyrannosaurids, oviraptorosaurids, troodontids, dromaeosaurs, and birds; branched structure may have already evolved if the feathers of *Sinosauropteryx* ultimately reveal genuine branched structure. The rachis, barbules, and the closed pennaceous vane had all evolved within or before a lineage that included the oviraptorosaurids, troodontids, dromaeosaurs, and birds. Flight and asymmetrical remiges and rectrices evolved within the exclusive common ancestor of the birds.

These new paleontological finds also permit us to understand some of the early events in the evolution of plumage, or the distribution of feathers on the body. Both *Caudipteryx* (Chen et al. 1998; Gatesy 2001) and an unnamed basal dromaeosaur (Norell et al. 2002) exhibit a tuft of long pennaceous feathers on the tip of the tail. Furthermore, a diversity of Yixian theropods have long feathers attached to the ulna and manus. These observations indicate that aspects of the distribution and pennaceous structure of the "remiges" and "rectrices" in birds evolved in a coelurosaurian ancestor long before the origin of flight in birds.

Although it has long been recognized that birds are a lineage of theropod dinosaurs, the discovery of "dinosaur feathers" (i.e., nonavian theropod feathers) has irreversibly changed our understanding of the evolution of feathers and birds. Birds are no longer synonymous with the possession of feathers, and

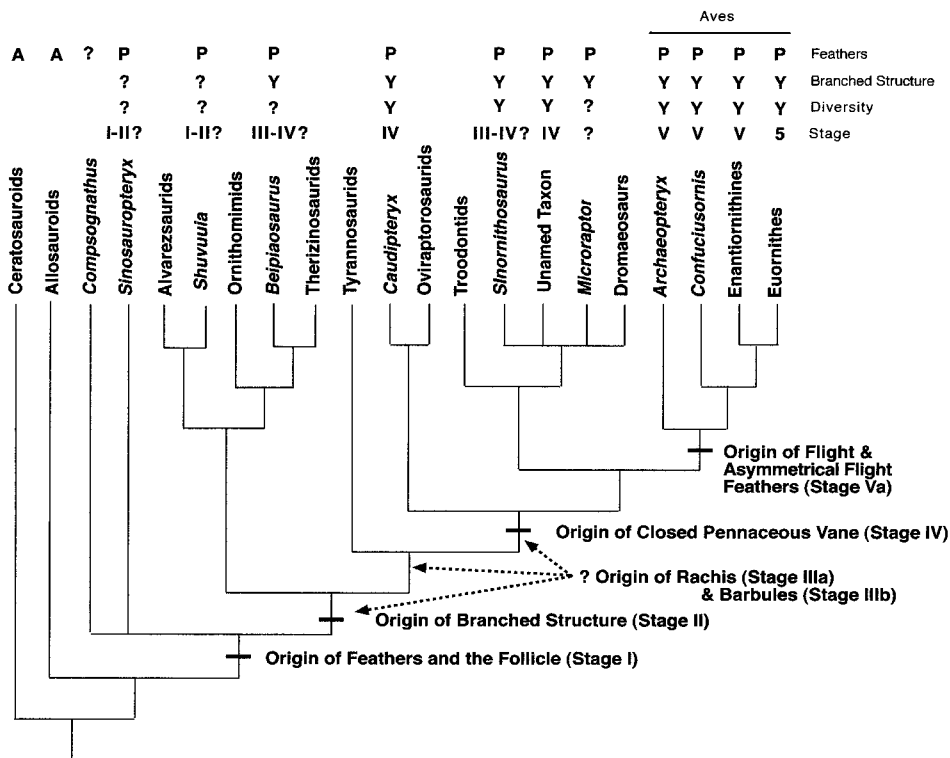


FIGURE 6. PHYLOGENETIC HYPOTHESIS FOR THE ORIGIN AND DIVERSIFICATION OF FEATHERS

This historical hypothesis for the origin and diversification of feathers is based on recent paleontological discoveries and a proposed phylogeny of the theropod dinosaurs (Sereno 1999). Details of fossil evidence of feathers is displayed at the top: presence (P) or absence (A) of feathers, presence of feather branched structure (Y), presence of feather diversity (Y), and the most advanced stage of the developmental model of feather evolution exhibited by that taxon. Fossil evidence of feathers has been reported for eight nonavian theropods. *Sinosauropteryx*, *Shuvuuia*, *Beipiaosaurus*, *Caudipteryx*, *Sinornithosaurus*, *Microaptor*, and the unnamed dromaeosaur are depicted here as sister taxa to the clades that they have been demonstrated to belong in. The only specimen of the eighth taxon, *Protarchaeopteryx*, is too fragmentary to be phylogenetically assigned. Feathers are coded as unknown in the basal coelurosaur *Compsognathus*. The historical hypothesis for the evolution of feather and feather diversity is a parsimonious reconstruction based on the available data. Optimization of some events is equivocal because of missing data (?).

our understanding of the biology of derived coelurosaurs will certainly be changed by this new appreciation of their integument (Prum 2002).

CONGRUENCE BETWEEN PALEONTOLOGY AND THE DEVELOPMENTAL THEORY

The evidence that the filamentous integumentary structures of nonavian theropod dinosaurs are homologous with avian feathers raises the question of whether these newly described primitive feather morphologies are congruent with those predicted by the developmental model (Figure 5; Prum 1999). Xu

et al. (2001) showed that the structure of the tufted and serially branched feather morphologies found in *Sinornithosaurus* are congruent with Stage II and Stage IIIa of the developmental model. They further proposed that the shorter, cylindrical, more robust integumentary structures in *Sinosauropteryx* were congruent with the hollow tubular morphology of Stage I. Ji et al. (2001) independently concluded that the three types of feathers documented on the unnamed close relative of *Sinornithosaurus* are also congruent with Stages II, IIIa, and V of the developmental model (Prum 1999).

Xu et al. (2001) did not hypothesize the presence of barbules on the feathers of *Sinornithosaurus*, but Ji et al. (2001) proposed that the herringbone pattern of barbs preserved on the forelimb and tail feathers of the unnamed basal dromeosaur constitutes evidence of coherent vanes that were maintained by differentiated interlocking distal and proximal barbules (Stage V; Figure 5; Prum 1999). The difficulty in determining the presence of barbules in fossils is that barbules consist of a linear series of individual keratinocytes that are too small to be preserved in normal fossils. There is no direct evidence of barbules on the feathers of *Archaeopteryx* (or any other fossil bird as far as we know), but their existence has been inferred from the conformation of the barbs into a coherent, closed vane. But the absence of a closed pennaceous vane may be the result of the absence of barbules (Stage IIIa), the presence of plesiomorphic barbules that lack the differentiated interlocking morphology (Stage IIIa + b), or the complete separation of the barbs of a closed pennaceous vane during preservation (Stage IV). Thus, the coherent vanes in the feathers of *Caudipteryx*, *Protarchaeopteryx*, and the unnamed basal dromeosaur do provide evidence for the presence of differentiated barbules that is identical to the evidence used to support their presence in early bird feathers. We therefore conclude that the feathers of the forelimbs and tails in *Caudipteryx*, *Protarchaeopteryx*, and the two unnamed basal dromaeosaurs had differentiated distal and proximal barbules (Stage IV). It appears, however, that some feathers in both *Sinornithosaurus* (Xu et al. 2001) and its two unnamed close relatives (Ji et al. 2001; Norell et al. 2002) also lack closed pennaceous vanes.

As Xu et al. (2001) comment, the current paleontological evidence of theropod feathers provides some additional *phylogenetic* support for the transition series predicted by the developmental model for the origin and evolution of feathers (Figures 5 and 6). Based on the current sample, the first feather morphology to have evolved was the unbranched tubular Stage I morphology represented by *Sinosauropteryx* (Figure 6). This indicates that Stage I feathers evolved phylogenetically

prior to any other more complex morphology. Further phylogenetic congruence with the predictions of the developmental model is limited by variable preservation of the integument of available specimens of coelurosaurs, the limited sample of coelurosaurs available from the highest quality preservation sites (i.e., Liaoning and Solnhofen), and the bias that fully pennaceous feathers with a prominent rachis are likely to be preserved better than earlier stages with finer filamentous morphology. Branched feathers clearly evolved prior to the common ancestor of the therizinosaur *Beipiaosaurus* and birds (Stage II), but it is not known whether these feathers possessed a rachis (Stage IIIa) or barbules (Stage IIIb). There is tentative support, however, for the conclusion that branched and open pennaceous structure (Stages II, IIIa, IIIb; e.g., *Beipiaosaurus*) evolved before differentiated proximal and distal barbules and the closed pennaceous vane (Stage IV; e.g., *Caudipteryx*). Asymmetrically vaned feathers evolved coincident with flight in the common ancestor of birds (Stage Va).

ALTERNATIVES TO THE THEROPOD ORIGIN OF FEATHERS

There are few viable alternatives to the conclusion that feathers originated in a non-avian lineage of theropod dinosaurs. One is that feather-like branched structures evolved multiple times among reptilian integumentary appendages. Convergent filamentous integumentary appendages did evolve within the archosaurian pterosaurs (e.g., *Sordes*), but these 5 mm long appendages are not branched and are independently derived within pterosaurs (Wellnhofer 1996). There are additional reports of similar hair-like structures in additional pterosaurs from inner Mongolia, China (Wang et al. 2002). Also, tantalizing references to long filamentous integumentary appendages on the tail of a specimen of psittacosaur (an ornithischian dinosaur) from the Yixian have also been published (Stokstad 2001b; Steghaus-Kovac 2002). Although they need to be studied in greater depth, the absence of detailed similarities shared between these appendages and avian feathers (e.g., branched or tubular structure) and their distant phylogenetic positions indi-

cate that these structures are entirely convergent with theropod feathers. Convergent evolution, however, is highly unlikely to explain the detailed similarities between the theropod integumentary structures and avian feathers, given the numerous shared derived similarities (i.e., synapomorphies) of these feather-bearing theropod dinosaurs and birds (Gauthier 1986; Holtz 1994; Sereno 1997, 1999). Diverse feathers including fully pennaceous vanes have now been documented precisely in the dromeosaur lineage that is hypothesized to be most closely related to birds, and in the specimens within that clade that are closest in age to the oldest indisputable bird, *Archaeopteryx*. Thus, the paleontological and phylogenetic data leave vanishingly little room for two convergent origins of feathers in two lineages that are hypothesized to be immediate sister groups. Yet, hair-like appendages from other nontheropod lineages of archosaurs do indicate that there was probably an inherent potential for the evolution of diverse integumentary appendages within all archosaurs.

Second, it has been proposed that these filamentous, nonvanded structures are not integumentary appendages but some type of fibrous connective tissue such as collagen or ossified tendons. This hypothesis is simply contradicted by the abundance of the structures, their obvious preserved relationship to the integument, their distribution all over the body, and their undeniable resemblance to feathers preserved on avian specimens in the same deposits. In many species, these structures vary in size over the body in the same way as modern avian feathers. Thus, *Beipiaosaurus* has an array of 70 mm filamentous structures coming off the trailing edge of the ulna, an unlikely position for any connective tissue or tendinous structures and identical in position to avian remiges (Xu et al. 1999a). *Sinornithosaurus* exhibits a tufted filamentous structure 35 mm on the tip of its snout—a genuinely unlikely location for an ossified tendon (Xu et al. 2001)! The integumentary appendages of the unnamed relative of *Sinornithosaurus* have a structural variation and distribution over the body that is remarkably reminiscent of avian plumage (Ji et al. 2001). The integumentary appendages of these non-

avian theropods are also preserved in essentially identical form to many contour feathers on indisputably avian fossil preserved in the same deposits, such as *Confuciusornis sanctus*, *Eoenantiornis buhleri*, *Changchengornis hendaozoiensis* (Chiappe et al. 1999), and *Protopteryx fengningensis* (Zhang and Zhou 2000). It is difficult to argue that the filamentous structures of these nonavian theropods are entirely different in nature from feathers, even though they were accidentally preserved exactly as avian feathers were in the same fossil deposits. There is also the immunological evidence that the filamentous appendages of the alvarezsaurid *Shuvuuia* are composed of β -keratin which is exclusively expressed in the integument of reptiles (Schweitzer et al. 1999). Lastly, the indisputable evidence of the herringbone pattern of barbs and the rachis in appendages of basal dromeosaurs confirms that these structures are not collagenous or fibrous connective tissues (Ji et al. 2001; Norell et al. 2002).

Third, various critics have disingenuously stated that these fossils are too young to possess feathers with ancestral morphologies (e.g., Feduccia 1999). Such statements ignore the fundamental fact that a feature phylogenetically generally distributed within a clade (i.e., feathers in higher coelurosaurian dinosaurs) must have evolved prior to another feature that is more restricted to a single, monophyletic group within that clade (i.e., flight in birds). Just as modern monotremes lay eggs, lineages may retain many primitive features present in their ancient ancestors. There is no reason why these younger theropod fossils cannot preserve a morphology that is phylogenetically primitive to an older avian fossil. Moreover, if *Sinosauropteryx* is a compsognathid, then these integumentary appendages would presumably have been present in *Compsognathus* (contra Ostrom 1978), which is contemporaneous with *Archaeopteryx*.

Fourth, it is possible to hypothesize that all these feathered theropods are actually flightless birds, as critics have argued with *Caudipteryx* and *Protarchaeopteryx* (Feduccia 1999; Jones et al. 2000b; Martin and Czerkas 2000). If all these feathered taxa were birds, then feathers could still have a single, exclusively avian origin. Such a phylogenetic hypothesis

would be wildly unparsimonious. Given the numerous primitive and derived features that these nonavian theropod taxa share with other theropods (Sereno 1999; Xu et al. 1999b, 2000; Zhou and Wang 2000; Zhou et al. 2000), their placement within the birds would only further contribute to an indisputable relationship between birds and theropod dinosaurs. It becomes increasingly difficult to argue that various birds and dinosaurs can be mistaken for each other, but that these groups have no phylogenetic relationship to one another.

Rejection of the theropod origin of feathers is often accompanied by rejection of cladistic analysis in general and the theropod ancestry of birds in particular (e.g., Feduccia 1999; Dodson 2000). Although we will not review the debate on the theropod ancestry of birds here, we can reiterate that there is no other explicit alternative hypothesis that has any data to support it (Prum 2002). No critics of the theropod origin of birds have ever presented an explicit alternative hypothesis of avian ancestry (Feduccia 1999; Dodson 2000). It is insufficient to simplistically dismiss numerous phylogenetic reconstructions of independent researchers supporting the theropod origin of dinosaurs as "garbage in, garbage out" (Stokstad 2000), and then maintain that there is no available solution to the question. To reject the theropod origin of birds, one must demonstrate explicitly that some other taxon is more closely related to birds than are theropods. Critics of the theropod origin of birds have not even attempted to do so. In contrast, Feduccia (1999) proposed the highest possible standard of evidence for the theropod ancestry hypothesis in his challenge to paleontologists to find feathers on a dromaeosaur—the lineage of theropods frequently hypothesized to be phylogenetically most closely related to birds. In only a couple of years, fossil integumentary appendages with several features uniquely shared with avian feathers have now been found in three different taxa from exactly this lineage (Xu et al. 1999b; Xu et al. 2000; Ji et al. 2001; Xu et al. 2001; Norell et al. 2002). With the apparent richness of the Yixian Formation (Stokstad 2000), it is unlikely that these discoveries will end soon.

THE APPENDAGES OF *LONGISQUAMA*

One proposed alternative to theropod origin of feathers—the appendages of *Longisquama*—requires special attention. The small Triassic reptile *Longisquama insignis* was described by Sharov (1970). *Longisquama* is notable for its extremely long, lamellar integumentary appendages along its spine that have been hypothesized to be used in gliding (e.g., Feduccia 1999). Sharov (cited as personal communication by Regal 1975) maintained that *Longisquama*'s dorsal appendages were unbranched. Feduccia (1985:76) also stated that the dorsal appendages of *Longisquama* "are not incipient feathers" and that while inspecting the specimens, "I could see no indication that the elongate scales were particularly feather like." Feduccia (1985:76) concluded that there "is simply no evidence that they in fact are [feather-like structures]." He later confirmed, "No doubt . . . that the scales of *Longisquama* were not transmuted into feathers" (Feduccia 1999:133).

Despite this unanimity of opinion over three decades, Jones et al. (2000a)—an "iconoclastic band" (Stokstad 2000) of authors including Feduccia himself—recently proposed that the long dorsal appendages of *Longisquama* were branched structures with a rachis and barbs composed of keratinaceous filaments, and that these structures are homologous with avian feathers. Subsequently, the appendages of *Longisquama* have been cited as providing morphological support for the elongate scale hypothesis of the origin of feathers (Maderson and Alibardi 2000). This proposal has received rapid, strong criticism (Reisz and Sues 2000; Prum 2001; Unwin and Benton 2001), and nearly complete rejection by paleontologists and ornithologists familiar with the material (Stokstad 2000). Based on a detailed analysis of the fossils, Reisz and Sues (2000) concluded that conditions of deposition of the fossil were inappropriately interpreted and that many of the proposed feather-like features were artifacts of preservation. Various authors have noted that the characters used to identify *Longisquama* as an archosaur—the antorbital and mandibular fenestrae—are poorly preserved at best and are quite possibly artifactual; it is uncertain whether *Longis-*

quama is even an archosaur (Stokstad 2000; Unwin and Benton 2001). Prum (2001) compared the appendages of *Longisquama* to feathers and argued that the proposed branched structure was illusory (Sharov, as cited by Regal 1975; Feduccia 1985, 1999), that the *Longisquama* appendages consisted of a continuous membranous lamina, and that many of the documented details of the proposed branched structure were inconsistent with the known mechanisms of feather growth. In an energetic but largely semantic rebuttal, Jones et al. (2001) maintained that the antorbital fenestra was visible on the previously unillustrated counterslab, that the feather-like branched structures were "observable facts" (apparently previously invisible to both Sharov and Feduccia), and that the questions raised about possible artifacts of deposition, "strain credulity."

The homology of the *Longisquama* appendages with avian feathers is highly disputed. Authors on both sides of the debate are currently preparing additional analyses for publication (P F A Maderson, R Reisz, H-D Sues, personal communication). Given the problematic and controversial evidence itself, the hypothesis that these *Longisquama* appendages are homologous with feathers has substantial additional obstacles. First, this hypothesis would imply either: (1) that feathers are uniquely shared by *Longisquama* and birds, and that birds are unrelated to theropod dinosaurs; or (2) that feathers are primitive to most archosaurs and have been lost many times. Alternative (1) would require the rejection of numerous derived morphological characters from every part of the body (including most recently pennaceous feathers from the integument) that are shared by birds and lineages of theropod dinosaurs on the basis of these disputed impressions. Alternative (2)—one origin and numerous losses of feathers—is extremely unparsimonious and completely unlikely. An additional problem with the hypothesized homology between the appendages of *Longisquama* and avian feathers is the implied scenario for the evolution of avian flight. Feduccia (1999) and others maintain that *Longisquama*'s appendages were used for gliding flight. So the hypotheses of homology between *Longisquama*'s appendages and avian

feathers implies that feathers first originated along the spine for aerial gliding, and then spread over the body to create the wings and tail (resulting in the evolution of a second novel flying structure while maintaining continuous gliding or flying ability); the original spinal flying structures were then reduced to become indistinguishable from standard contour feathers. Thus, the direct implication of Jones et al. (2000a) is that *Longisquama*'s "bizarre and unique solution to the problem of gliding" (Feduccia 1999:95) is actually ancestral to avian flight. This unusual scenario has yet to be defended.

Given the congruence among the phylogenetic support for the relationship between birds and theropod dinosaurs (e.g., Sereno 1999), the fossil evidence of feathers within lineages of nonavian theropods, and the predictions of primitive feather morphology made by the developmental model, the alternative hypothesis that the appendages of *Longisquama* are homologous with feathers is poorly supported.

THE TUBULAR NATURE OF FEATHERS

An important implication of the developmental model of the origin of feathers is the recognition of the essentially tubular (or hollow cylindrical) nature of feathers. The cylindrical follicle and feather germ are general features that characterize all feathers, therefore they should be considered the defining features of feathers. Prum (1999) defined a feather as a elongate, cylindrical or tubular epidermal appendage that grows from an invaginated feather follicle. A feather follicle differs from a hair follicle in that the follicular invagination is not merely a depression in the epidermis but a circular trough that encircles a persistent dermal papilla.

The inherently tubular nature of feathers is manifest in numerous details of feather development and morphology. All feathers originate and grow as tubes of epidermis. The tubular nature of feathers can be observed directly in the growing cylindrical pin feather, the sheath, and the basal calamus characteristic of all known feathers. The familiar planar structure of a pennaceous feather is only realized after the tubular feather emerges from its superficial sheath. The hypothesis that pla-

nar, pennaceous feathers are primitive fails to explain this most general and fundamental feature of feathers.

Developmental and genetic perturbations of feather structure further demonstrate the tubular nature of feathers. Strong (1902a) documented the case of a developmental anomaly in the contour feathers of a hybrid dove in response to temporary food deprivation during molt. In the middle of each contour feather, the barbs suddenly failed to differentiate and the entire feather temporarily reverted to a cylindrical, calamus-like form in the middle of the feather vane. When food was resumed, the barb ridges differentiated again, forming a normal vane. The effect was of a nearly normal pennaceous feather with an anomalous cylindrical calamus in the middle of the vane. Similar anomalies were described by Riddle (1908). Genetic support for the essentially cylindrical nature of feathers comes from the recessive feather mutation Porcupine (*pc*), that has been described in pigeons (Cole and Hawkins 1930), chickens (Waters 1967; Somes 1990), and Japanese quail (Fulton et al. 1982; Cheng and Brush 1984). The Porcupine mutation produces incomplete differentiation and morphogenesis of the barbs, and results in brittle tubular, quill-like feathers composed of a mass of anastomosing barbs that cannot unfold into the typical planar form. Both of these cases demonstrate that perturbations in feather development reveal the essentially cylindrical, tubular nature of feathers.

Hypothesized primitive feathers are frequently referred to as "protofeathers" (e.g., Brush 2000; Maderson and Alibardi 2000). Given the enormous structural diversity of extant feathers, it is arbitrary to attempt to distinguish "real" feathers from the various theoretically antecedent "protofeathers" on morphological grounds. In order to emphasize the fundamental importance of the cylindrical, tubular organization of the follicle as the inherent feather novelty, we think it is preferable to recognize all of the diverse structures that likely grow from feather follicles as feathers, and we recommend that the term "protofeather" be abandoned. Primitive structures that are entirely homologous with feathers should be called feathers.

HOMOLOGY OF FEATHERS AND SCALES

Since the mid-19th century, feathers have frequently been broadly homologized with scales (reviewed in Lucas and Stettenheim 1972). Although feathers and scales share some morphological, developmental, and molecular features, problems with this hypothesis have been known for more than a century (Davies 1889; see discussion above of scale-based theories of feather origins). A number of fundamental and important differences between feathers and scales led Brush (1993, 1996) to question their homology. Previous simplistic conceptualizations of the homology of feathers and scales (with the intellectual goal of evolutionarily transforming one into the other) have unnecessarily obscured the complex, hierarchical relationship between these structures. Further, it has prevented the appropriate recognition of the evolutionary novelties of feathers that require explanation.

Feathers and scales are integumentary appendages that are created by local proliferation, differentiation, and keratinization of epidermal cells (Lucas and Stettenheim 1972; Sawyer et al. 1986). Detailed scrutiny of the development of scales and feathers indicates that there are actually few features shared between the structures (Sawyer et al. 1986). Feathers and scales are appendages produced by local proliferation of epidermal and dermal cells that creates a folding or protuberance on the skin. All feathers and reptilian scales are created by epidermal keratinocytes, but the type of keratin and its distribution in these structures vary extensively (Baden and Maderson 1970; Maderson 1972; Brush 1985; Sawyer et al. 1986; Brush 1993; Maderson and Alibardi 2000; Sawyer et al. 2000). Feathers and the scutate scales of birds (those on the upper, or dorsal, surface of the legs and feet) begin development with a morphologically distinct placode—an epidermal thickening above a condensation of dermal cells. In contrast, avian reticulate scales (those on the lower surfaces of the toes) and all reptilian scales examined to date lack a morphologically definable placode (e.g., Maderson and Alibardi 2000). Avian reticulate scale rudiments share temporal and spatial patterns of expression of several feather-placode specific

genes, however (Chuong et al. 1996; Widelitz et al. 1999). Subsequent to placode formation, numerous events in feather development constitute a series of unique developmental mechanisms which have no homolog in any other avian or reptilian scales (Brush 1993, 1996, 2000; Prum 1999). The differentiation of barb ridges from one another, the tubular invagination around the dermal papilla that creates the follicle, and the subsequent developmental mechanisms within the follicle collar, the barb ridges, and the tubular feather germ, all of which determine feather form, are all unique to feathers.

How *are* feathers homologous with scales? The presence of a derived, morphologically distinct placode is only shared by feathers and avian scutellate scales (Maderson and Alibardi 2000). The patterns of gene expression specific to feather and avian scutate scale placodes are also shared with avian reticulate scales, however (Chuong et al. 1996; Widelitz et al. 1999). Thus, a molecularly defined placode is shared by all avian scales and feathers regardless of the presence of the morphological characteristics of a feather placode. These developmental features support the homology of avian scales and feathers at the level of the placode. Although scutate scales have been hypothesized to be secondarily simplified feathers (Davies 1889), it is more parsimonious to hypothesize that simpler scutate appendages with a morphological placode preceded the origin of feathers, and that these scutate structures were retained on the anterior surfaces of the legs in modern birds.

A series of classical (Sengel 1976) and modern developmental experiments (Chuong and Widelitz 1998; Chuong et al. 2000) have documented many commonalities in the signaling mechanisms of mesenchyme-epithelium interactions during the development of chick feathers and scales. Developmental experiments have even "transformed" early scutate and reticulate scales into feather short buds in response to various chemicals (Dhouailly et al. 1980; Zou and Niswander 1996; Widelitz et al. 2000). These experiments have reinforced the notion that there is detailed molecular support for the traditional, broad hypothesis of homology between feathers and scales (e.g., Dyck 1985; Maderson and Alibardi 2000).

While these experiments contribute important and fundamental details about the mechanisms of mesenchyme-epithelium signaling in vertebrates, these data do not suggest that feathers and scales are broadly homologous (i.e., beyond the level of the placode). The transformations between these structures are purely unidirectional; undifferentiated scale structures can be induced to produce feathers on them, but feather placodes or germs have yet to be induced to grow into scales (M P Harris, personal communication). This asymmetry is congruent with the hypothesis that feather and scale placodes are homologous and that postplacode mechanisms of feather morphogenesis are all derived.

In conclusion, the morphological and molecular developmental details shared by avian feather and scales support homology between these structures at the level of the placode. The morphology and development of all subsequent structures within the feather are evolutionary novelties that have no homologs in avian or reptilian scales.

FUNCTIONAL EXPLANATIONS RECONSIDERED

Explicit attempts to reconstruct the evolutionary history of feathers based on natural selection for specific functions have failed to identify an unequivocal, plesiomorphic function of feathers or to accurately predict a transition series of ancestral feather morphologies. We submit that primarily functional approaches to reconstruct the evolutionary history of feathers have hindered rather than advanced our understanding of the origin of feathers. With the development of phylogenetic methods, it has been established that phylogenetic pattern should be determined before the analysis of evolutionary process (e.g., Lauder and Rose 1996). Obviously, it is difficult to explain *why* or *how* some event has occurred in evolutionary history without actually knowing *what* has occurred. But this is exactly what functional theories of feather origins attempt to do.

Functional explanations of the origin of feathers have received so much attention because the question itself is so compelling, and not because the answers are particularly satisfying. The function of ancestral feathers

and the evolutionary mechanisms by which they diversified remain fascinating and difficult questions. With the startling discovery of primitive feathers in nonavian dinosaurs, we now have the first data that allow us to reevaluate proposed functional explanations. What does the first view of *what* happened imply about *why* and *how* feathers evolved?

A prominent and oft repeated functional hypothesis for the origin of feathers is that they evolved by natural selection for flight (Steiner 1917; Heilmann 1926; Parkes 1966; Feduccia 1985, 1993, 1999). Recent confirmation of filamentous and pennaceous feathers on nonavian theropod dinosaurs documents that feathers originated in terrestrial coelurosaurian theropods before the origin of birds and before the origin of flight. Consequently, aerodynamic hypotheses for the initial function of feathers have been falsified. It has been repeatedly and strenuously proposed that the exquisite adaptation of avian flight feathers for their aerodynamic function implies that feathers must have originated through selection for flight (e.g., Feduccia 1999), but given the evidence of pennaceous feathers on the forelimbs and tails of primarily flightless theropod dinosaurs, this argument is simply false. Concluding that feathers evolved for flight is like maintaining that digits evolved for playing the piano. Only the most derived and complex feather morphology could yield a feather with advanced aerodynamic function (Prum 1999), and only after the evolution of a bipinnate, closed pennaceous vane with differentiated distal and proximal barbules (Stage IV) could there have been selection for an asymmetrical vane with aerodynamic properties (Prum 1999). The occurrence of fully pennaceous feathers on terrestrial nonavian theropods completely confirms this conclusion.

The falsification of the aerodynamic hypothesis further corroborates Prum's (1999) conclusion that elongate aerodynamic scales were developmentally implausible because the surfaces of planar scales and feather vanes are not homologous. Given how branched flight feathers grow, an evolutionary transformation between these two analogous planar appendages would have had to proceed through intermediary cylindrical and filamentous morphol-

ogies that could not have maintained a consistently planar structure or aerodynamic function (Prum 1999). The only feather novelty attributable to natural selection for aerodynamic function is the evolution of the asymmetrical feather vane (Stage Va: Figure 5), the origin of which exactly co-occurs with the origin of flight and birds (Figures 6).

Recently, another aerodynamic hypothesis for the origin of feathers has been proposed. Based on the microanatomy and functional morphology of feather movement, Homberger and de Silva (2000) proposed that feathers evolved to produce smooth, adjustable body contours for "body lift-gliding." As with traditional aerodynamic hypotheses, this suggestion is falsified by evidence of the origin and diversification of feathers within a terrestrial, nongliding lineage of theropod dinosaurs. The feather movement mechanism of Homberger and de Silva (2000) requires a calamus for the attachment of feather erector and depressor muscles, however, and a tubular calamus would be available by Stage I of the developmental model (Figure 5; Prum 1999). Thus the developmental model could provide an extremely early potential origin for the feather movement system, as proposed by Homberger and de Silva (2000).

Prum (1999) concluded that numerous other proposed initial functions of plesiomorphic feathers are developmentally plausible because the simplest possible feathers could have performed these functions. These hypotheses include thermal insulation (Davies 1889; Ewart 1921), thermal shielding (Regal 1975), communication (Mayr 1960), water repellency (Dyck 1985), tactile organs (Broman 1941), and defense (Prum 1999). Each hypothesis constitutes a physically plausible selective advantage of the earliest feather, a hollow tubular filament. Of course, the width, length, and rigidity of the first feathers remain unknown. Based on our current knowledge of the biology and natural history of coelurosaurian theropods, it would be entirely speculative to maintain that any of these plausible functions actually was *the* selective function that led to the fixation of the first feathers. In fact, the possibility of gathering morphological or behavioral information from fossil representatives of the actual lineages in which

this event occurred is essentially impossible, and we can rationally abandon hope of identifying a singular functional explanation.

There is, however, an important fundamental commonality among these plausible functional hypotheses that is congruent with the developmental theory of the origin of feathers (Prum 1999) and that provides a more fundamental explanation of the origin of feathers. Any selection for a substantial integumentary appendage that emerges from the skin or extends out of the skin would essentially constitute selection for the evolution of a tubular follicle, the initial event (Stage I) in the evolution of feathers (Figure 4). The invaginated feather follicle creates the opportunity for the continuous proliferation and growth of a tubular epidermal appendage up and out of the follicle without demanding equivalent growth of the dermis within the appendage as required by a simple scale (Figure 3D; Prum 1999). The feather germ is nourished by the central dermal pulp, but the pulp does not grow continuously in volume with the feather germ. Rather, pulp caps continuously seal off the top of the dermal pulp and limit its growth while the pulp provides nutrition for continued epidermal growth (Lucas and Stettenheim 1972). The association between the follicle and indeterminate epidermal growth is corroborated by the convergent evolution of a follicle and extensive or indeterminate growth in mammalian hair. Whatever it was, the initial functional advantage of the earliest feathers constituted natural selection for an emergent appendage that then fostered the evolution of the feather follicle (Stage I). Although the original functional advantage of the first feathers remains a mystery, the ultimate explanation for the origin of the feather must have involved selection for epidermal appendages that emerged from the skin.

It has frequently been assumed that an evolutionary novelty such as feathers must have evolved for an important reason. For example, both Regal (1975) and Feduccia (1999) found Mayr's (1960) hypothesis that feathers evolved by selection for display to be unsatisfying. Implicit in these criticisms (and in most functional theories) was the notion that a functionally important key innovation cannot

be explained by an inconsequential mechanism (e.g., mate choice), and must have required strong direct natural selection for a current function. Actually, the origin and diversification of feathers was likely characterized by a diversity of selective forces at different stages (Brush 1993). Furthermore, strong natural selection for a specific function can lead directly to functional and developmental integration of a trait within the phenotype that can limit subsequent evolvability (Wagner and Schwenk 2000). Accordingly, if early feathers were under strong natural selection for a specific function, such selection could very well have constrained them from continuing to evolve and diversify in form. It is important to recognize that diverse sources of natural or sexual selection were likely involved in the evolution of various stages in feather diversity. By focusing too intensely on singular functional explanations, functional theories of the origin of feathers have obscured the fact that the history of feather evolution is characterized by a continued diversification and novelty in development, form, and function that cannot be explained by natural selection for a single function. The most notable features of the evolutionary history of feathers are the repeated origins of the developmental novelties that created their increasing hierarchical complexity in form, and provided the opportunities for the evolution of diversity in function.

FEATHERS AS EVOLUTIONARY NOVELTIES

Recent developments in phylogenetics and molecular developmental biology have stimulated reconsideration of the concept of evolutionary novelty (Nitecki 1990; Müller and Wagner 1991; Raff 1996; Wagner 2001). Müller and Wagner (1991) defined a morphological novelty as a structure that is neither homologous to any ancestral structure nor homonomous (i.e., serially homologous) with any other structure in that organism.

Many features of feathers and feather development meet this definition and qualify as evolutionary novelties. The follicle, the differentiated sheath and feather germ, differentiated barb ridges, barb rami, barbules, differentiated pennulae of the proximal and distal bar-

bules, and the rachis are all evolutionary novelties, as are the derived mechanisms by which these novel structures develop. At a molecular level, the derived 10 kilodalton ϕ -keratins of feathers are also novel (see below). The morphologically distinct placode present in the initial development of feathers and avian scutellate scales is also apparently an evolutionary novelty, though it may be an extreme in a continuum of changes in cell proliferation and density during epidermal appendage development. If the morphological placode and the anterior-posterior axis of feather primordia were independently evolved from other avian and reptilian integumental appendages, then feathers may be entirely novel structures (but see *HOMOLOGY OF FEATHERS AND SCALES* above).

An explicit, process-independent definition of evolutionary novelty (Müller and Wagner 1991) permits us to examine which of the hypothesized mechanisms for the origin of evolutionary novelties may have been involved in the evolution of feathers. Müller and Wagner (1991) propose three modes for generating novelties: hierarchical organization, interactivity and dissociability, and equilibria and thresholds. As documented by both Brush (1993, 1996, 2000, 2001) and Prum (1999), feather development is extraordinarily hierarchical. This hierarchy incorporates both nestedness of morphological modules and the complex interactions among modules. Thus, the tubular epidermal feather germ includes both the peripheral sheath and the developing feather. The developing feather is composed of a series of barb ridges that develop into many pairs of barbule plates and the ramus. The fusion of barb ridges early in the development of a pennaceous feather determines the identity of the rachis ridge, which becomes a major morphological component of the feather. The presence of helical growth and the rachis define the proximal and distal sides of the barb ridge, and permit the differentiation of these modules into the morphologies that create the closed pennaceous vane. The origin and differentiation of hierarchically nested morphological modules in the feather have resulted in numerous evolutionary novelties in structure and development, and consti-

tute the basis of the extraordinary diversity of extant feathers.

Other novelties within feathers are hierarchical duplications and alterations of these processes. For example, the development of an afterfeather—a second posteriorly oriented vane growing out of the same follicle and attached to the same calamus (Figures 1 and 2)—occurs as a consequence of a second opposing, posteriorly oriented direction of helical growth (Lillie and Juhn 1938; Lucas and Stettenheim 1972). As a consequence of duplication and redirection, the same mechanisms that produce the main vane of the feather result in the division of the posterior new barb locus into two laterally displaced new barb loci, the creation of a second rachis ridge (the hyporachis), and ultimately an entire second vane growing simultaneously from a single follicle.

Interactivity and dissociability refer to the ability of components to create new structures through changes in the interactions among tissues, or modules, which create the interconnectedness of ontogenetic networks. Most novelties in feather development arise as a result of such interactions and dissociations. For example, the interactions of barb ridges through fusion initiate the formation of the rachis ridge and, ultimately, determine a fundamental feature of feather morphology. Further, dissociation of the development of the proximal and distal barbule plates and the independent specification of barbule cell shape within them provided the opportunity for differentiation of barbules and the evolution of the coherent, closed vane of pennaceous contour and flight feathers.

Equilibrial and threshold effects are involved in feather morphogenesis at cellular and molecular levels. Experimental analyses have determined that chemical threshold responses to expression gradients are involved in the specification of the patterns of feather follicle location during early development (Chuong et al. 1990; Chuong 1993; Chuong and Widelitz 1998; Jung et al. 1998; Widelitz et al. 1999; Chuong et al. 2000). The molecular understanding of feather morphogenesis beyond the placode stage is still in its infancy, however, and other examples of the effects of and responses to molecular gradients on other

aspects of feather morphogenesis have yet to be elucidated.

Raff (1996) recognized an additional mechanism for the origin of evolutionary novelties: duplication and divergence. Duplication and divergence have played fundamental roles in the evolution of feather structure and diversity. The duplication of keratin genes is one example at a molecular level (Brush 1978, 1993). At the morphological level, the duplication of numerous feather follicles over the body surface and subsequent divergence in morphology of different feathers have contributed greatly to the origin and maintenance of feather novelties.

Recently, Wagner and colleagues (Wagner 2000; Wagner et al. 2000; Chiu and Wagner 2001) proposed that research on the origin of evolutionary novelties should be distinct from research on standard microevolutionary change, and should be restructured to ask fundamentally different questions that focus directly on the mechanisms of the origin of qualitative innovations. This view underscores why the traditional neo-Darwinian approaches to the origin of feathers, as exemplified by Bock (1965) and Feduccia (1985, 1993, 1999), have failed. By emphasizing the reconstruction of a series of functionally and microevolutionarily plausible intermediate transitional states, neo-Darwinian approaches to the origin of feathers have failed to appropriately recognize the novel features of feather development and morphology, and have thus failed to adequately explain their origins. This failure reveals an inherent weakness of neo-Darwinian attempts to synthesize micro and macroevolution. In contrast, the developmental theory of the origin of feathers focuses directly on the explanation of the actual developmental novelties involved in the origin and diversification of feathers (Prum 1999). Restructuring the inquiry to focus directly on the explanation of the origin of the evolutionary novelties of feathers yields a conceptually more appropriate and productive approach.

Why are feathers so complex? Why have feathers been able to diversify and innovate so extensively? Pending further details on the molecular mechanisms of feather development (see below), the explanation appears to

come from the innovative structure of the tubular feather follicle and germ, and their unique potential for interactions between the peripheral epidermis of the developing feather germ and the central dermal papilla (Figures 3D and 4). There are essentially two basic kinds of epithelial appendages: those that develop from an outgrowth (e.g., scales and claws), and those that develop from ingrowth (e.g., glands and hair) (Chuong 1998). A few appendages, like hair, horn, and feathers, are distinct in having evolved both mechanisms. Hair starts with an invagination and then proliferates from the bottom. In contrast, a feather starts with an outgrowth (the first feather papilla or short bud), and then develops its evolutionarily novel ingrowth (the cylindrical follicle). This unique combination of events creates a tubular juxtaposition of epithelial and mesenchymal layers. The tubular organization of the feather follicle and germ fostered the formation and proliferation of numerous hierarchically arranged developmental modules, such as the barb ridges within the entire feather germ and the barbules plates and ramus within the barb ridges. This hierarchical, modular organization apparently fosters the development of distinct, polarized molecular concentration gradients and asymmetries at multiple levels within different modules. The tubular epidermal feather tissue can be differentiated into barb ridges which themselves have the potential to differentiate along the peripheral-medial, lateral, and proximo-distal axes into the ramus and a series of barbules. The evolution of the tubular epidermal feather germ provided a platform for the evolution of an array of subsequent developmental evolutionary novelties that has generated the diversity in feather morphology. Interestingly, it is actually the *constraints*, or limitations, on the possible developmental processes permitted within this tubular architecture that created the hierarchy in these mechanisms and permitted the identification of the developmental model of the origin of feathers.

Brush (2000, 2001) emphasized the rapidity and the inevitability of the evolution of structural diversity in feathers subsequent to the initial origin of the follicle. Although observable mechanisms of feather morphogenesis are impressive, there are no data yet

supporting the conclusion that these features evolved rapidly or were in any sense inevitable. Although the fossil record has suddenly produced an unexpected treasure of specimens relevant to this question, the possibility of getting sufficient temporal samples to accurately judge the speed of feather evolution remains remote. Further, historical contingency may have played an important role in the evolution of the developmental and structural complexity of feathers that insights into the molecular mechanisms of feather morphogenesis may reveal.

EVOLUTION OF FEATHER KERATINS

Like other amniote epidermal appendages, feathers are composed of keratin—an intermediate filament protein produced by epidermal cells that forms a hard, flexible, and insoluble polymer. Keratins are extremely diverse in molecular structure, and two main groups are recognized: the α -keratins are characterized by an α -helical structure, and β -keratins by a β -pleated sheet organization. It is still debated whether the quite distinct α -keratins and β -keratins are historically related or entirely convergent in structure and function. There are few sequence similarities and significant molecular differences. The α -keratins are found in the epidermis of all amniotes, whereas the β -keratins are found exclusively in the epidermis of reptiles, including birds. The α -keratins compose all the skin and integumentary appendages of mammals. The α -keratins also compose the soft skin and interscale areas of reptiles and birds, but the integumentary appendages of reptiles and birds can be composed of both α -keratins and β -keratins. All β -keratins are smaller than the α -keratins, and are produced by a family of closely related genes. Their basic chemistry is similar, as is their capacity to form filaments, although the mechanisms differ. The β -keratin genes occur as low, tandem repeats throughout the genome.

Feathers are composed of a subclass of β -keratins that are referred to as feather keratins, or ϕ -keratins (Brush 1978, 1985, 1993; Sawyer et al. 2000). Avian scutate scales, beak, and claw are composed of another subclass of filament, forming ϕ -keratins that are slightly larger. The feather ϕ -keratins are a family of

smaller (10.4 kd) molecules than the 13.5 kd scutate scale, beak, and claw family of ϕ -keratins. In contrast, avian reticulate scales (on the plantar surfaces of the foot) are composed of nonfeather type β -keratins that are molecularly similar to those of other reptiles. Long thought to be restricted entirely to birds, recent reports show that alligator claw keratin is a 14 kd filament molecularly related to the avian scutate scale, claw, and beak ϕ -keratins (Sawyer et al. 2000). Thus, ϕ -keratins are now known to be broadly distributed within archosaurs. Based on outgroup comparison to alligator claw ϕ -keratin, the longer 13.5 kd filament length of the scutate scale, claw, and beak ϕ -keratins is likely primitive. Evolution within the two gene families is typified by gene duplication and subsequent deletion (Brush 1993).

Various hypotheses about the evolutionary origin of ϕ -keratins and the shorter feather ϕ -keratins have been proposed (reviewed in Brush 1993). In summary, current data indicate that the ϕ -keratins originated in an archosaurian ancestor shared by birds and crocodylians. Subsequently, the ϕ -keratins diversified into a longer (13.5 kd) filament class that is currently expressed in avian scutate scales, claw, and beak, and a shorter (10.5 kd) class that is expressed exclusively in feathers.

Brush (1993, 1996, 2000, 2001) has hypothesized that the first feather was composed of 10.5 kd filament feather ϕ -keratin. Prum (1999) countered that if this protein evolved by natural selection for some novel function, the morphological novelty of the feather probably preceded the current molecular novelty. Only after there was a novel structure would there likely be opportunity for some novel function.

MOLECULAR BASIS OF FEATHER DEVELOPMENT AND EVOLUTION

An important future goal in the study of the origin and evolution of feathers is the elucidation of the molecular mechanisms of feather morphogenesis. Feather development has been a classic model system for the study of epithelium-mesenchyme interactions for many decades (Sengel 1976). Molecular work on feather development has also accelerated (reviewed in Chuong and Widellitz

1998; Chuong et al. 2000). Nearly all of this research has focused upon the very earliest stages of development—the determination of the spatial distribution of feather placodes within the pterylae, the establishment of an anterior-posterior axis within the feather placode, and the elongation of feather buds. These data do contribute to support for the homology of feather and scale placodes (e.g., Chuong et al. 1996; Wideltz et al. 1999), but they do not yet contribute to our understanding of the development of the many *evolutionarily novel* features of feathers.

The bias toward the study of early feather development reflects the fact that feathers have been studied as a model system of general mechanisms of mesenchyme-epithelium interactions rather than as complex assemblages of evolutionary novelties. With a few preliminary exceptions (Nohno et al. 1995; Ting-Berreth and Chuong 1996; Morgan et al. 1998), little research has been done on the molecular mechanisms of the morphogenesis of barb ridges, the differentiation within a barb ridge among the barbule plates and the ramus, the differentiation of the cells of the proximal and distal barbule plates, the formation of the rachis, the mechanism of helical growth, and the duplication of helical growth within the follicle in the formation of the afterfeather. An essential and exciting future direction in the investigation of the evolution of feathers will be to describe the novel molecular developmental mechanisms that have contributed to the origin of feather structure and diversity.

CONCLUSIONS

The origin and diversification of feathers have been intractable questions in evolutionary biology for more than a century. Progress on these issues has been hampered by conceptual problems and the lack of fossils of primitive feathers. Both of these limitations have been overcome by the recent proposal

of a developmental theory of the origin of feathers, and discoveries of primitive feather fossils from nonavian theropod dinosaurs. The developmental theory provides a heuristic model of the evolution and diversification of feathers that is entirely congruent with the known details of feather development (Prum 1999). The discovery of primitive fossil feathers documents that feathers evolved and diversified in nonavian theropod dinosaurs before the origin of birds and before the origin of flight (Chen et al. 1998; Ji et al. 1998; Xu et al. 1999a, 1999b, 2000, 2001; Ji et al. 2001). These primitive feathers are morphologically and phylogenetically congruent with the predictions of the developmental theory (Ji et al. 2001; Sues 2001; Xu et al. 2001). The broad homology of feathers and scales has been nearly universally and uncritically accepted, but it is not strongly supported (Brush 1993, 1996). Scales-based theories of feather evolution have failed to explain the origin of many feather novelties. Feathers and scales are homologous at the level of the placode, but all subsequent stages of feather morphology are derived, evolutionary novelties. The hypothesis that feathers evolved by natural selection for flight is falsified, but numerous other proposed initial functions of feathers remain plausible. More specifically, feathers likely originated by selection for the growth of an integumentary appendage that emerged from the skin, without continuous investment in the dermis, resulting in the evolution of the novel tubular feather follicle. The tubular feather follicle and feather germ led to subsequent evolution of numerous additional morphological and developmental novelties. This complexity appears to have exploited an inherent capacity of the innovative tubular form of the feather follicle and feather germ. Future research on the evolution of feather keratin and the molecular mechanisms of feather morphogenesis will provide additional insights into the innovative nature of feathers.

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