ANATOMY

WHICH CAME FIRST, THE FEATHER OR THE BIRD?

A long-cherished view of how and why feathers evolved has now been overturned

By Richard O. Prum and Alan H. Brush

Illustration by Kazuhiko Sano

FEATHERS EVOLVED in carnivorous, bipedal dinosaurs before the origin of birds. The creatures depicted here are reconstructions of fossils found in northern China that show clear traces of feathers. The large dinosaur eating a lizard is *Sinornithosaurus;* to its right is *Sinosauropteryx;* and the small dinosaur on the tree limb is *Microraptor.*

HAIR, SCALES, FUR, FEATHERS. OF ALL THE BODY COVERINGS NATURE has designed, feathers are the most various and the most mysterious. How did these incredibly strong, wonderfully lightweight, amazingly intricate appendages evolve? Where did they come from? Only in around the past two decades have we begun to answer this question. Several lines of research have converged on a remarkable conclusion: the feather evolved in dinosaurs before the appearance of birds.

The origin of feathers is a specific instance of the much more general question of the origin of evolutionary novelties—structures that have no clear antecedents in ancestral animals and no clear related structures (homologues) in contemporary relatives. Although evolutionary theory provides a robust explanation for the appearance of minor variations in the size and shape of creatures and their component parts, it does not yet give as much guidance for understanding the emergence of entirely new structures, including digits, limbs, eyes and feathers.

Progress in solving the particularly puzzling origin of feathers has also been hampered by what now appear to be false leads, such as the assumption that the primitive feather evolved by elongation and division of the reptilian scale, and speculations that feathers evolved for a specific function, such as flight. A lack of primitive fossil feathers hindered progress as well. For many years the earliest bird fossil has been *Archaeopteryx lithographica,* which lived in the Late Jurassic period (about 148 million years ago). But *Archaeopteryx* offers no new insights on how feathers evolved, because its own feathers are nearly indistinguishable from those of today's birds.

Contributions from several fields have put these traditional problems to rest. First, biologists have begun to find fresh evidence for the idea that developmental processes—the complex mechanisms by which an individual organism grows to its full size and form—can be a window into the evolution of a species' anatomy. This idea has been reborn as the field of evolutionary developmental biology, or "evo-devo." It has given us a powerful tool for probing the origin of feathers. Second, paleontologists have unearthed a trove of feathered dinosaurs in China. These animals have a diversity of primitive feathers that are not as highly evolved as those of today's birds or even *Archaeopteryx.* They are critical clues to the structure, function and evolution of modern birds' intricate appendages.

Together these advances have produced an extremely detailed and revolutionary picture: feathers originated and diversified in carnivorous, bipedal theropod dinosaurs before the origin of birds or the origin of flight.

THE TOTALLY TUBULAR FEATHER

THIS SURPRISING PICTURE was pieced together thanks in large measure to a new appreciation of exactly what a feather is and how it develops in modern birds. Like hair, nails and scales, feathers are integumentary appendages—skin organs that form by controlled proliferation of cells in the epidermis, or outer skin layer, that produce the keratin proteins. A typical feather features a main shaft, called the rachis [*see box on opposite page*]. Fused to the rachis are a series of branches, or barbs. In a fractal-like reflection of the branched rachis and barbs, the barbs themselves are also branched: a series of paired filaments called barbules are fused to the main shaft of the barb, the ramus. At the base of the feather, the rachis expands to form the hollow tubular calamus, or quill, which inserts into a follicle in the skin. A bird's feathers are replaced periodically during its life through molt—the growth of new feathers from the same follicles.

Variations in the shape and microscopic structure of the barbs,

IN BRIEF

Dinosaur fossils found in China have feathers that are more primitive than those of modern birds or even of the oldest known bird fossil.

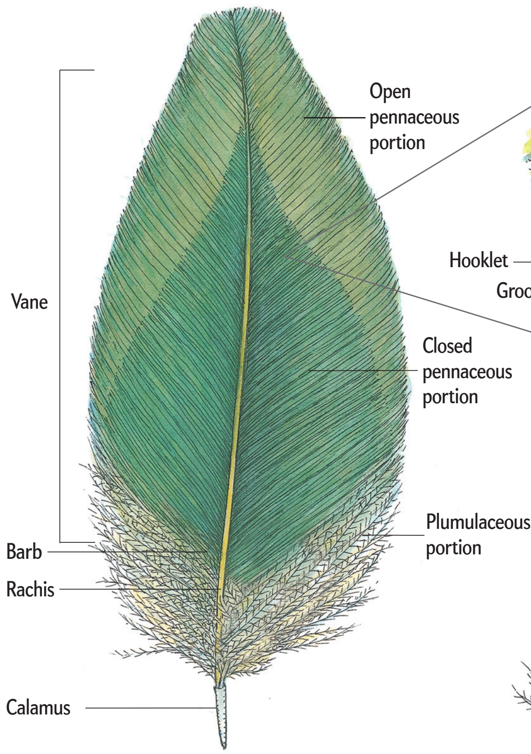
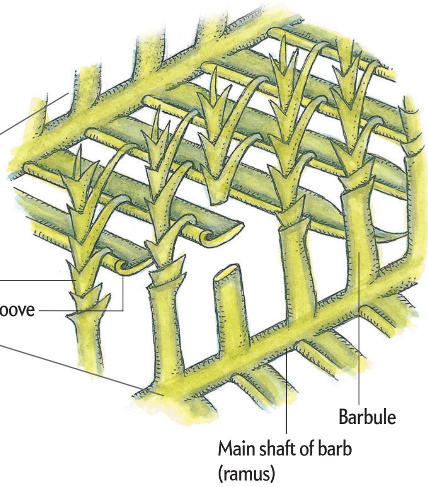
The Chinese fossils provide evidence that feathers originated and diversified in bipedal, carnivorous dinosaurs before the origin of birds or flight. Variations in shape and microscopic structure determine the functions of different types of feathers, such as flight and insulation.

Feathers probably evolved in stages, beginning with a simple tubular feather, with each stage evolving in a particular group of dinosaurs.

VARIATIONS

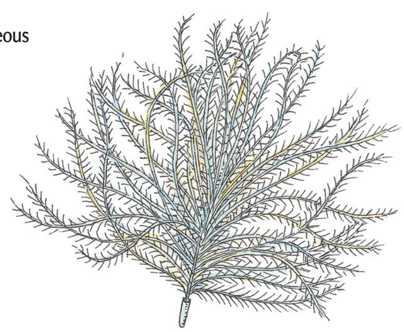
The Nature of Feathers

Feathers display an amazing diversity and serve almost as wide a range of functions, from courtship to camouflage to flight. Variations in the shapes of a feather's components—the barbs, barbules and rachis—create this diversity. Most feathers, however, fall into two basic types. The pennaceous is the iconic feather of a quill pen or a bird's wing. The plumulaceous, or downy, feather has soft, tangled plumes that provide lightweight insulation.

Pennaceous Feather

Paired barbs fused to the central rachis create the defining vane of a pennaceous feather. In the closed pennaceous portion of the vane, tiny hooklets on one barbule interlock with grooves in the neighboring barbule (*detail* and *middle micrograph*) to form a tight, coherent surface. In the open pennaceous portion, the barbules do not hook together. Closed pennaceous feathers are essential for avian flight.



Plumulaceous (Downy) Feather

A plumulaceous feather has no vane. It is characterized by a rudimentary rachis and a jumbled tuft of barbs with elongated barbules.

Open pennaceous vane

Closed pennaceous vane

Plumulaceous (downy) feather

Downy Feather
Fluffy structure provides insulation.

Contour Feather
Planar vane helps to form the outline of the body.

Flight Feather
Asymmetrical vane creates aerodynamic forces.

Pinfeathers
Newly emerged, incompletely developed feathers are visible on these toucan chicks.

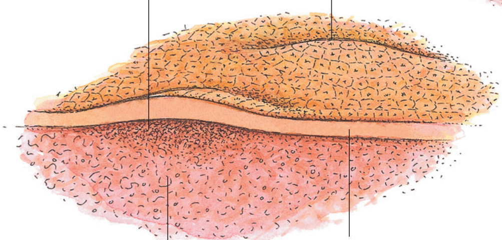
TIM LEE QUINN (*feather micrographs*); TINA WEST (*feather photographs*); ZSSD *Corbis* (*baby toucans*)

Illustrations by Patricia J. Wynne

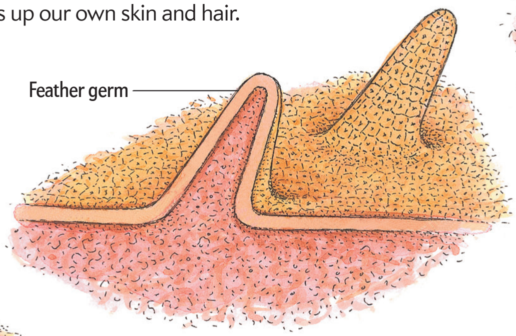
STAGES

How Feathers Grow

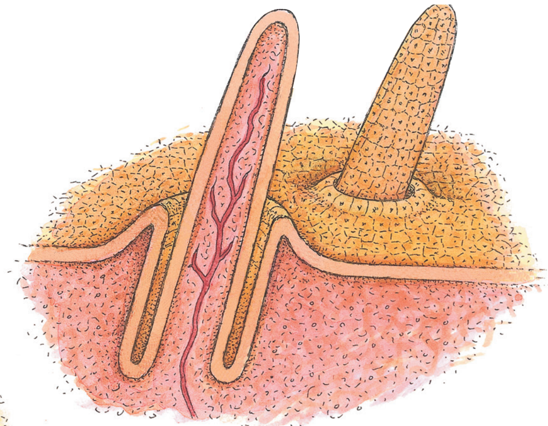
As in hair, nails and scales, feathers grow by proliferation and differentiation of keratinocytes. These keratin-producing cells in the epidermis, or outer skin layer, achieve their purpose in life when they die, leaving behind a mass of deposited keratin. Keratins are filaments of proteins that polymerize to form solid structures. Feathers are made of beta-keratins, which are unique to reptiles and birds. The outer covering of the growing feather, called the sheath, is made of the softer alpha-keratin, which is found in all vertebrates and makes up our own skin and hair.



Feather growth begins with the placode, a thickening of the epidermis over a condensation of cells in the dermis.

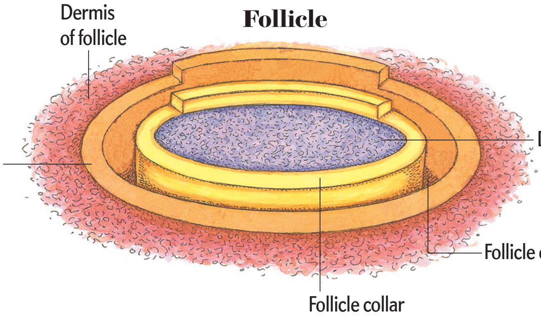


The placode then forms a unique elongated tube, the feather germ.



Proliferation of cells in a ring around the feather germ creates the follicle (*detail below*), the organ that generates the feather. At the base of the follicle, in the follicle collar, the continuing production of keratinoctyes forces older cells up and out, eventually forming the entire, tubular feather.

Follicle



barbules and rachis create an astounding range of feathers. But despite this diversity, most feathers fall into two structural classes. A typical pennaceous feather has a prominent rachis and barbs that create a planar vane. The barbs in the vane are locked together by pairs of specialized barbules. The barbules that extend toward the tip of the feather have a series of tiny hooklets that interlock with grooves in the neighboring barbules. Pennaceous feathers cover the bodies of birds, and their tightly closed vanes create the aerodynamic surfaces of the wings and tail. In dramatic contrast to pennaceous feathers, a plumulaceous, or downy, feather has only a rudimentary rachis and a jumbled tuft of barbs with long barbules. The long, tangled barbules give these feathers their marvelous properties of lightweight thermal insulation and comfortable loft. Feathers can have a pennaceous vane and a plumulaceous base.

In essence, all feathers are variations on a tube produced by proliferating epidermis with the nourishing dermal pulp in the center. And even though a feather is branched like a tree, it grows from its base like a hair. How do feathers accomplish this?

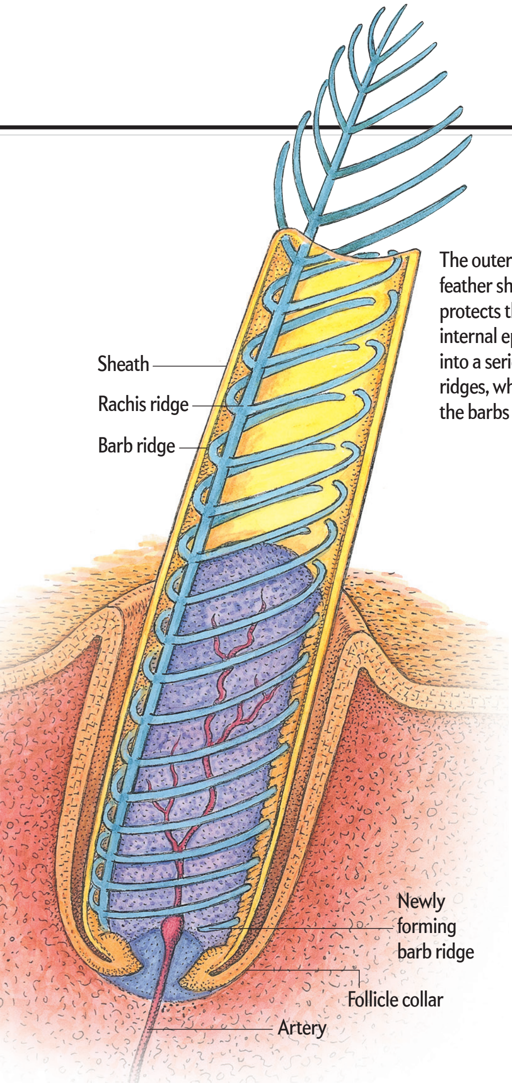
Feather growth begins with a thickening of the epidermis called the placode, which elongates into a tube—the feather germ [*see box above*]. Proliferation of cells in a ring around the feather germ creates a cylindrical depression, the follicle, at its base. The growth of keratin cells, or keratinocytes, in the epidermis of the follicle—the follicle "collar"—forces older cells up and out, eventually generating the entire feather in an elaborate choreography that is one of the wonders of nature.

As part of that choreography, the follicle collar divides into a series of longitudinal ridges—barb ridges—that create the separate barbs. In a pennaceous feather, the barbs grow helically around the tubular feather germ and fuse on one side to form the rachis. Simultaneously, new barb ridges form on the other side of the tube. In a plumulaceous feather, barb ridges grow straight without any helical movement. In both types of feather, the barbules that extend from the barb ramus grow from a single layer of cells, called the barbule plate, on the periphery of the barb ridge.

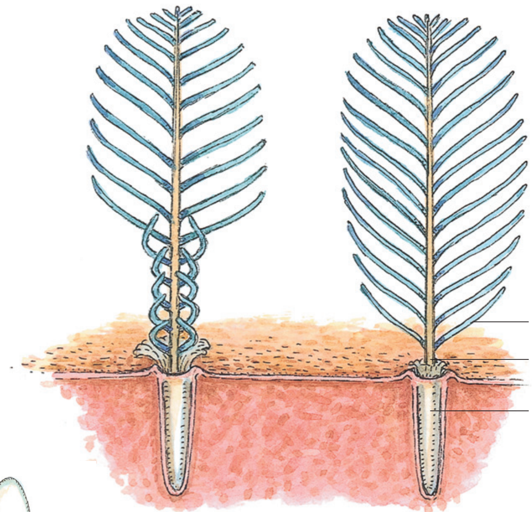
EVO-DEVO COMES TO THE FEATHER

TOGETHER WITH VARIOUS COLLEAGUES, we think the process of feather development can be mined to reveal the probable nature of the primitive structures that were the evolutionary precursors of feathers. Our developmental theory proposes that feathers evolved through a series of transitional stages, each marked by a developmental evolutionary novelty, a new mechanism of growth. Advances at one stage provided the basis for the next innovation [*see box on pages 82 and 83*].

In 1999 we proposed the following evolutionary scheme. Stage 1 was the tubular elongation of the placode from a feather germ and follicle. This yielded the first feather—an unbranched, hollow cylin-

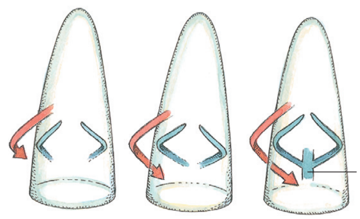


The outermost epidermal layer becomes the feather sheath, a temporary structure that protects the growing feather. Meanwhile the internal epidermal layer becomes partitioned into a series of compartments, called barb ridges, which subsequently grow to become the barbs of the feather.



As growth proceeds, the feather emerges from its superficial sheath. The feather then unfurls to obtain its planar shape. When the feather reaches its final size, the follicle collar forms the calamus, a simple tube at the base of the feather.

Helical Growth



In a pennaceous feather, the barb ridges grow helically around the collar until they fuse to form the rachis ridge. Subsequent barb ridges fuse to the rachis ridge. In a plumulaceous feather (*not shown*), barb ridges do not grow helically, and a simple rachis forms at the base of the feather.

der. Then, in stage 2, the follicle collar, a ring of epidermal tissue, differentiated (specialized): the inner layer became the longitudinal barb ridges, and the outer layer became a protective sheath. This stage produced a tuft of barbs fused to the hollow cylinder, or calamus.

The model has two alternatives for the next stage—either the origin of helical growth of barb ridges and formation of the rachis (stage 3a) or the origin of the barbules (3b). The ambiguity about which came first arises because feather development does not indicate clearly which event occurred before the other. A stage 3a follicle would produce a feather with a rachis and a series of simple barbs. A stage 3b follicle would generate a tuft of barbs with branched barbules. Regardless of which stage came first, the evolution of both these features, stage 3a+b, would yield the first double-branched feathers, exhibiting a rachis, barbs and barbules. Because barbules were still undifferentiated at this stage, a feather would be open pennaceous—that is, its vane would not form a tight, coherent surface in which the barbules are locked together.

In stage 4 the capacity to grow differentiated barbules evolved. This advance enabled a stage 4 follicle to produce hooklets at the ends of barbules that could attach to the grooved barbules of the adjacent barbs and create a pennaceous feather with a closed vane. Only after stage 4 could additional feather variations evolve, including the many specializations seen at stage 5, such as the asymmetrical vane of a flight feather.

THE SUPPORTING CAST

INSPIRATION FOR THE THEORY came from the hierarchical nature of feather development itself. The model hypothesizes, for example, that a simple tubular feather preceded the evolution of barbs because barbs are created by the differentiation of the tube into barb ridges. Likewise, a plumulaceous tuft of barbs evolved before the pennaceous feather with a rachis because the rachis is formed by the fusion of barb ridges. Similar logic underlies each of the hypothesized stages of the developmental model.

Support for the theory comes in part from the diversity of feathers among modern birds, which sport feathers representing every stage of the model. Obviously, these feathers are recent, evolutionarily derived simplifications that merely revert back to the stages that arise during evolution because complex feather diversity (through stage 5) must have evolved before *Archaeopteryx*. These modern feathers demonstrate that all the hypothesized stages are within the developmental capacity of feather follicles. Thus, the developmental theory of feather evolution does not require any purely theoretical structures to explain the origin of all feather diversity.

Support also comes from exciting molecular findings that have confirmed the first three stages of the evo-devo model. Technological advances allow us to peer inside cells and identify whether specific genes are expressed (turned on so that they can give rise to the products they encode). Several laboratories have combined these methods with experimental techniques that investigate the functions of the proteins made when their genes are expressed during feather development. Matthew Harris, now at Harvard Medical School, John F. Fallon of the University of Wisconsin–Madison and one of us (Prum) have studied two important pattern formation genes—*sonic hedgehog* (*Shh*) and *bone morphogenetic protein 2* (*Bmp2*). These genes play a crucial role in the growth of vertebrate limbs, digits, and integumentary appendages such as hair, teeth and nails. We found that Shh and Bmp2 proteins work as a modular pair of signaling molecules that, like a general-purpose electronic component, is reused repeatedly throughout feather development. The Shh protein induces cell proliferation, and the Bmp2 protein regulates the extent of proliferation and fosters cell differentiation.

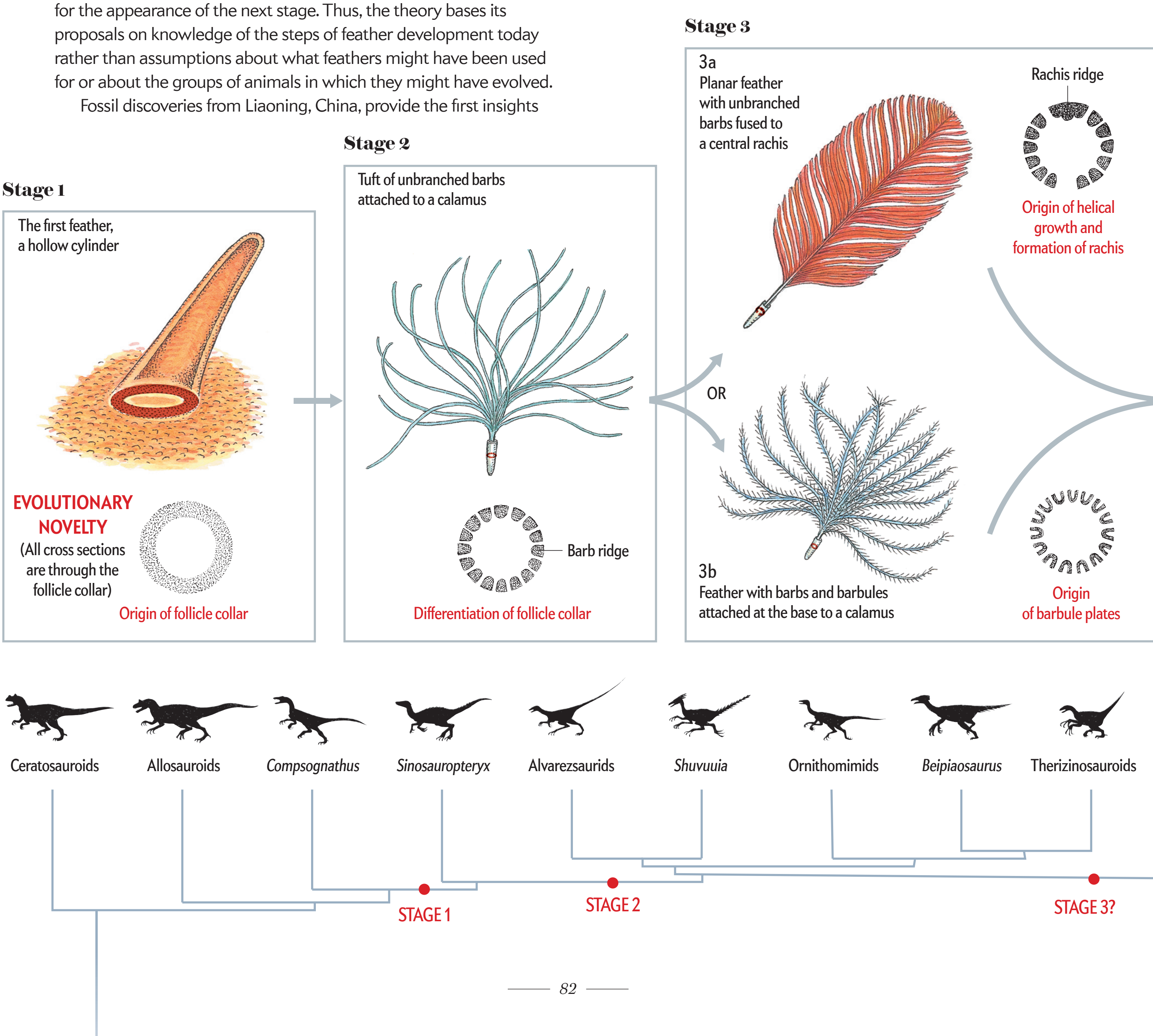
The expression of Shh and Bmp2 begins in the feather placode, where the pair of proteins is produced in a polarized anterior-posterior pattern. Next, Shh and Bmp2 are both expressed at the tip of the tubular feather germ during its initial elongation and, fol-

FINDINGS

Evo-Devo and the Feather

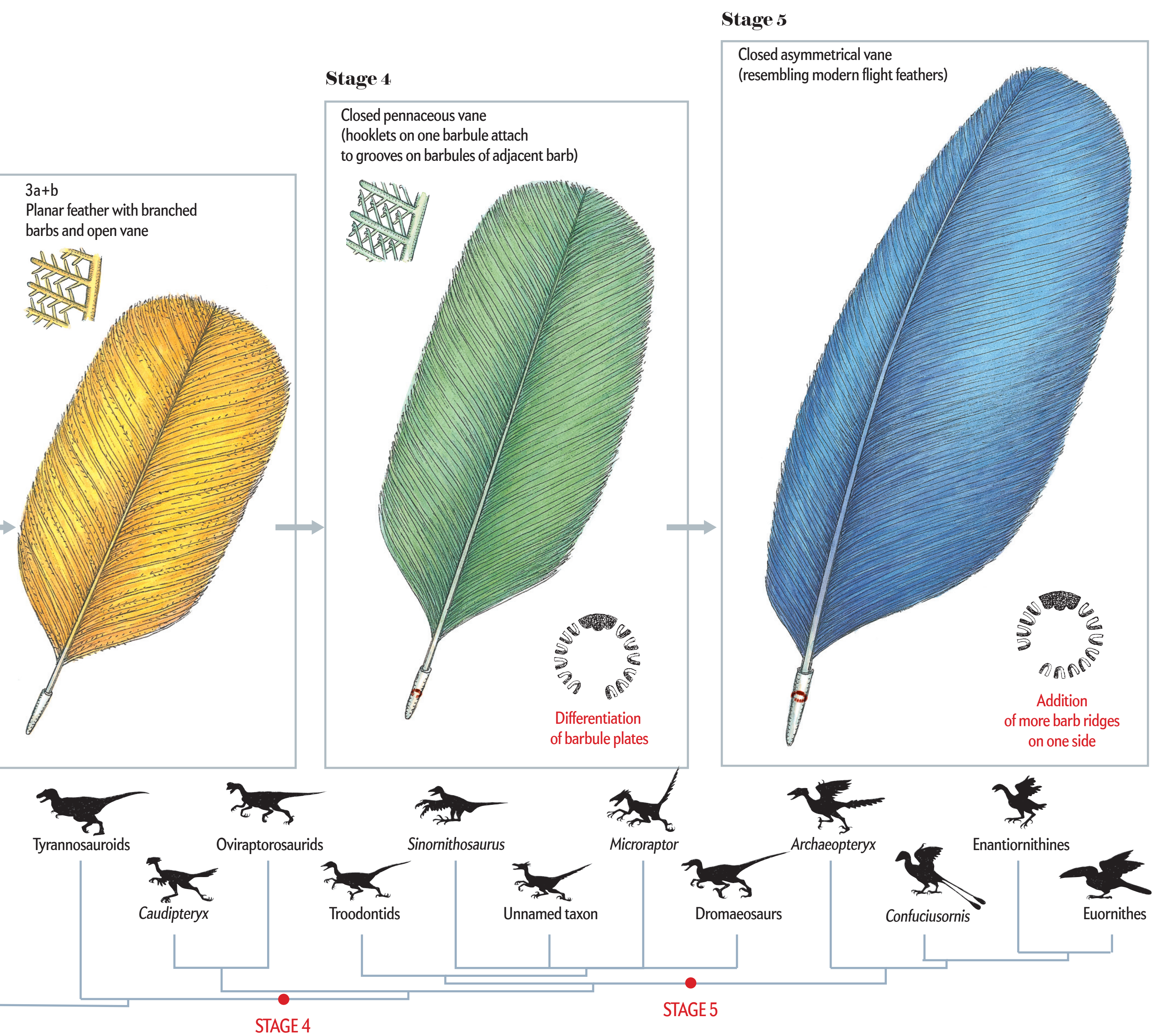
The authors' theory of feather origin grew out of the realization that the mechanisms of development can help explain the evolution of novel features—a field dubbed evo-devo. The model proposes that the unique characteristics of feathers evolved through a series of evolutionary novelties in how they grow, each of which was essential for the appearance of the next stage. Thus, the theory bases its proposals on knowledge of the steps of feather development today rather than assumptions about what feathers might have been used for or about the groups of animals in which they might have evolved.

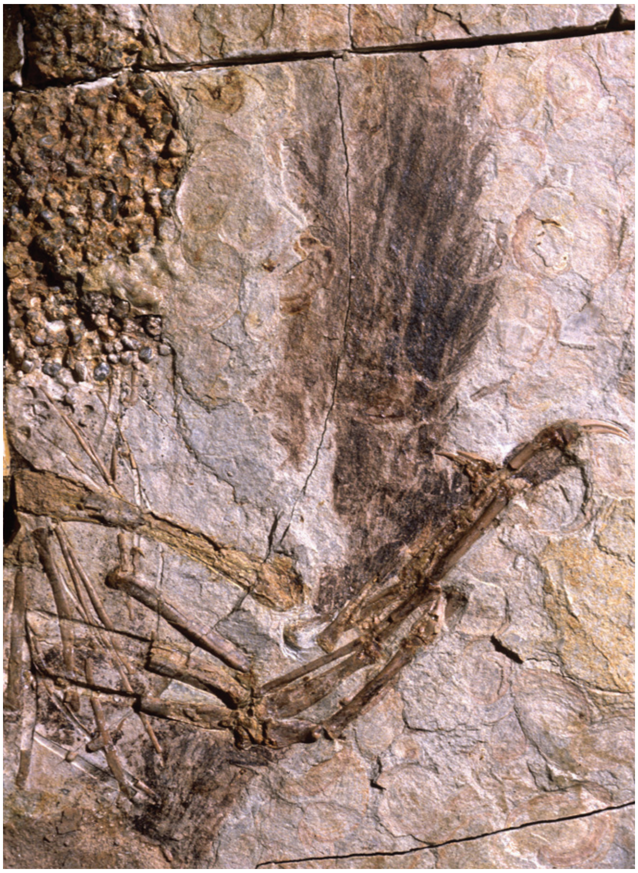
Fossil discoveries from Liaoning, China, provide the first insights into which theropod dinosaurs evolved the feathers of each hypothesized stage. Based on the similarities between the primitive feather predictions of the model and the shapes of the fossil skin appendages, the authors suggest that each stage evolved in a particular group of dinosaurs.



lowing that, in the epithelium that separates the forming barb ridges, establishing a pattern for the growth of the ridges. Then, in pennaceous feathers, the Shh and Bmp2 signaling lays down a pattern for helical growth of barb ridges and rachis formation, whereas in plumulaceous feathers the Shh and Bmp2 signals create a simpler pattern of barb growth. Each stage in the development of a feather has a distinct pattern of Shh and Bmp2 signaling. Again and again the two proteins perform critical tasks as the feather unfolds to its final form.

These molecular data confirm that feather development is composed of a series of hierarchical stages in which subsequent events are mechanistically dependent on earlier stages. For example, the evolution of longitudinal stripes in Shh-Bmp2 expression is contingent on the prior development of an elongate tubular feather germ. Likewise, the variations in Shh-Bmp2 patterning during pennaceous feather growth are contingent on the prior establishment of the longitudinal stripes. Thus, the molecular data are beautifully consistent with the scenario that feathers evolved from an elon-





SPECIMEN of *Microraptor gui* (*above*) shows asymmetrical feathers, blurring the distinction between birds and dinosaurs. Fossils found in quarries in Liaoning Province, China, such as this *Caudipteryx* forelimb (*left*), reveal feathered appendages. This dinosaur, which was roughly the size of a turkey, has excellently preserved pennaceous feathers on its tail as well as its forelimbs.

gate hollow tube (stage 1), to a downy tuft of barbs (stage 2), to a pennaceous structure (stage 3a).

THE STARS OF THE DRAMA

CONCEPTUAL THEORIES have spurred our thinking, and state-of-the-art laboratory techniques have enabled us to eavesdrop on the cell as it gives life and shape to a feather. But plain old-fashioned detective work in fossil-rich quarries in northern China has turned up the most spectacular evidence for the developmental theory. Chinese, American and Canadian paleontologists in Liaoning Province have unearthed a startling trove of fossils in the Early Cretaceous Yixian Formation (128 million to 124 million years old). Excellent conditions in the formation have preserved an array of ancient organisms, including the earliest placental mammal, the earliest flowering plant, an explosion of ancient birds and a diversity of theropod dinosaur fossils with sharp integumentary details. Various dinosaur fossils clearly show fully modern feathers and a diversity of primitive feather structures. The conclusions are inescapable: feathers originated and evolved their essentially modern structure in a lineage of terrestrial, bipedal, carnivorous dinosaurs before the appearance of birds or flight.

The first feathered dinosaur found there, in 1997, was a chicken-sized coelurosaur (*Sinosauropteryx*); it had small tubular and perhaps branched structures emerging from its skin. Next the paleontologists discovered a turkey-sized oviraptoran dinosaur (*Caudipteryx*) that had beautifully preserved, modern-looking pennaceous feathers on the tip of its tail and forelimbs. Some skeptics have claimed that *Caudipteryx* was merely an early flightless bird, but many phylogenetic analyses place it among the oviraptoran theropod dinosaurs. Subsequent discoveries at Liaoning have revealed pennaceous feathers on specimens of dromaeosaurs, the theropods that are hypothesized to be most closely related to birds but that clearly are not birds. In all, investigators found fossil feathers from more than a dozen nonavian theropod dinosaurs, among them the ostrich-sized therizinosaur *Beipiaosaurus* and a variety of dromaeosaurs, including *Microraptor* and *Sinornithosaurus*.

The heterogeneity of the feathers found on these dinosaurs is striking and provides strong direct support for the developmental theory. The most primitive feathers known—those of *Sinosauropteryx*—are the simplest tubular structures and are remarkably like the predicted stage 1 of the developmental model. *Sinosauropteryx, Sinornithosaurus* and some other nonavian theropod specimens show open tufted structures that lack a rachis and are strikingly congruent with stage 2 of the model. There are also pennaceous feathers that obviously had differentiated barbules and coherent planar vanes, as in stage 4 of the model.

These fossils open a new chapter in the history of vertebrate skin. We now know that feathers first appeared in a group of theropod dinosaurs and diversified into essentially modern structural variety within other lineages of theropods before the origin of birds. Among the numerous feather-bearing dinosaurs, birds represent one particular group that evolved the ability to fly using the feathers of its specialized forelimbs and tail. *Caudipteryx, Protopteryx* and dromaeosaurs display a prominent "fan" of feathers at the tip of the tail, indicating that even some aspects of the plumage of modern birds evolved in theropods.

MICK ELLISON *American Museum of Natural History* (*left*); XING XU (*right*)

The consequence of these amazing fossil finds has been a simultaneous redefinition of what it means to be a bird and a reconsideration of the biology and life history of the theropod dinosaurs. Birds—modern birds and the group that includes all species descended from the most recent common ancestor of *Archaeopteryx*—used to be recognized as the flying, feathered vertebrates. Now we must acknowledge that birds are a group of the feathered theropod dinosaurs that evolved the capacity of powered flight. New fossil discoveries have continued to close the gap between birds and dinosaurs and ultimately make it more difficult even to define birds. Conversely, many of the most charismatic and culturally iconic dinosaurs, such as *Tyrannosaurus* and *Velociraptor,* are very likely to have had feathered skin but were not birds.

DINOSAUR OR BIRD? THE GAP NARROWS

THE DISTINCTIONS between birds and dinosaurs continue to diminish with every new discovery. In 2003 Xing Xu and Zhonghe Zhou of the Institute of Vertebrate Paleontology and Paleoanthropology at the Chinese Academy of Sciences described some remarkable new specimens of *Microraptor gui,* a dromaeosaur in the group of theropods that are most closely related to birds. The creatures have asymmetrical feathers on both their arms and legs. In living birds, feathers with asymmetrical vanes function in flight. *Microraptor* had four wings—two on its arms and two on its legs—that apparently had an aerodynamic function. Xu and his colleagues hypothesize that *Microraptor* was an advanced glider, and because *Microraptor* is in the group that is most closely related to birds, they further propose that the two-winged powered flight of birds evolved through a similar four-winged gliding ancestor.

The debate on the origin of bird flight has focused on two competing hypotheses: flight evolved from the trees through a gliding stage, or flight evolved from the ground through a powered running stage. The trees-down theory gets some support from the discovery of a functional glider in the theropod dinosaurs most closely related to birds. Many questions remain, of course, including how *Microraptor* actually used its four wings.

For thousands of years, humans have believed that feathers and feather-powered flight were unique to birds. But we have learned that feathers evolved and diversified in theropod dinosaurs before the origin of birds and discovered that even some aspects of avian flight may not be unique to birds. Both of the historical claims to the status of the birds as a special class of vertebrates—feathers and flight—have evaporated. Although this realization may disappoint some people, the disappearance of large gaps in our knowledge about the tree of life represents a great success for evolutionary biology.

A FRESH LOOK

THANKS TO THE DIVIDENDS provided by relatively recent findings, researchers can now reassess the various earlier hypotheses about the origin of feathers. The new evidence from developmental biology is particularly damaging to the classical theory that feathers evolved from elongate scales. According to this scenario, scales evolved into feathers by first elongating, then growing fringed edges, and finally producing hooked and grooved barbules. As we have seen, however, feathers are tubes; the two planar sides of the vane—the front and the back—are created by the inside and outside of the tube only after the feather unfolds from its cylindrical sheath. In contrast, the two planar sides of a scale develop from the top and bottom of the initial epidermal outgrowth that forms the scale.

The fresh evidence also puts to rest the popular and enduring theory that feathers evolved primarily or originally for flight. Only highly evolved feather shapes—namely the asymmetrical feather with a closed vane, which did not occur until stage 5—could have been used for flight. Proposing that feathers evolved for flight now appears to be like hypothesizing that fingers evolved to play the piano. Rather feathers were "exapted" for their aerodynamic function only after the evolution of substantial developmental and structural complexity. They evolved for some other purpose and were then exploited for a different use.

Numerous other proposed early functions of feathers remain plausible, including insulation, water repellency, courtship, camouflage and defense. Even with the wealth of new paleontological data, though, it seems unlikely that we will ever gain sufficient insight into the biology and natural history of the specific lineage in which feathers evolved to distinguish among these hypotheses. Instead our theory underscores that feathers evolved by a series of developmental innovations, each of which may have evolved for a different original function. We do know, however, that feathers emerged only after a tubular feather germ and follicle formed in the skin of some species. Hence, the first feather evolved because the first tubular appendage that grew out of the skin provided some kind of survival advantage.

Creationists and other evolutionary skeptics have long pointed to feathers as a favorite example of the insufficiency of evolutionary theory. There were no transitional forms between scales and feathers, they have argued. Further, they asked why natural selection for flight would first divide an elongate scale and then evolve an elaborate new mechanism to weave it back together. Now, in an ironic about-face, feathers offer a sterling example of how we can best study the origin of an evolutionary novelty: focus on understanding those features that are truly new and examine how they form during development in modern organisms. This new paradigm in evolutionary biology is certain to penetrate many more mysteries. Let our minds take wing. SA

Richard O. Prum and **Alan H. Brush** share a passion for feather biology. Prum, who started bird-watching at the age of 10, is now William Robertson Coe Professor of Ornithology in the department of ecology and evolutionary biology at Yale University. He also serves as curator of ornithology and head curator of vertebrate zoology at the Peabody Museum of Natural History there. His research has focused on avian phylogeny, avian courtship and breeding systems, the physics of structural colors and the evolution of feathers. He has conducted field studies in Central and South America, Madagascar and New Guinea. Brush is emeritus professor of physiology and neurobiology at the University of Connecticut. He has worked on feather pigment and keratin biochemistry and the evolution of feather novelties. He was editor of *The Auk*.

MORE TO EXPLORE

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DINOSAURS!