

Feathers and Flight: Current Ideas

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People have a fascination with other animals, although different people seem to be attracted to different kinds. Some people love dogs; some prefer cats; some horses; some are completely fascinated by whales, or snakes, or aquarium fish. The list of preferences is as extensive as our tastes in music or food. But if we took a vote on what people prefer to know more about, two of the most popular groups would be birds and dinosaurs. Birds are not only a constant source of interest to us, but they are also one of the most successful groups of animals with backbones. Over 10,000 species of birds are alive today. In a sense, that makes them more than twice as successful as mammals, of which there are only 4,000 living species. We love to watch birds in the wild and in zoos, and to keep them as pets. Another group of animals that we have a total fascination with is known as the Dinosauria. To most people, dinosaurs and birds are as different as day and night. That is why many people are shocked when they hear modern biologists and paleontologists state that birds are in fact living dinosaurs.

Technically, under a modern biological classification, birds are part of the Dinosauria. You can correctly call them dinosaurs if you like, although it is also correct to call them birds. All birds are dinosaurs, but not all dinosaurs are birds. Think of it the same way as you do cats and dogs; all cats and dogs are mammals, but not all mammals are cats and dogs. We can refer to our pets as mammals, but we are more likely to call them cats or dogs. There is no problem with referring to our modern feathered friends as “birds” or “avians.” However, technically we should say “non-avian dinosaurs” or “non-avian theropods” if we want to refer to all dinosaurs or theropods (non-flying, meat-eating dinosaurs) other than birds. Please remember that when I say “dinosaur” or “theropod” in this article, I am using these words informally to mean “non-avian dinosaur” and “non-avian theropod”. However, when I use the technical terms “Dinosauria” and “Theropoda,” birds are included.

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Changing Ideas of Bird Origins

Bird fossils are almost as rare as the scientists who study them, because most birds are small and have fragile, hollow bones. When they die they are far more likely to be eaten or destroyed than they are to be fossilized. The popular concept of dinosaurs, on the other hand, suggests that most were enormous animals—including the largest to ever walk the Earth. Huge animals have huge bones, which are less likely to be eaten or destroyed by physical factors or bacteria, and are therefore more likely to be buried and fossilized. Our concept of the relationships of birds and dinosaurs has changed in recent years, partly because of improved techniques of analysis, but largely because of the discovery of more and better preserved fossils of birds and small dinosaurs.

Archaeopteryx (Fig. 1) is generally considered to be the first (or earliest) bird.¹ Originally discovered in 1861 in Solnhofen, Germany, *Archaeopteryx*' remarkably well-preserved fossils still provide us with some of the best informa-

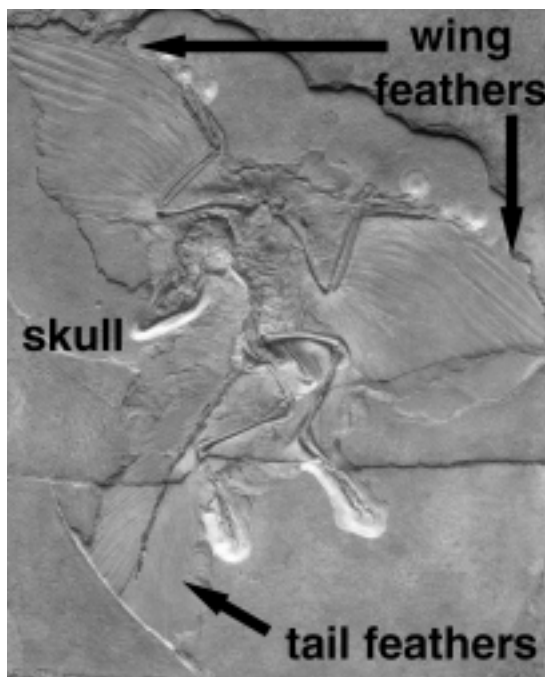


Fig. 1. The Berlin *Archaeopteryx* clearly shows a mix of dinosaur and bird characters. There are long feathers on the arms, but the fingers are clawed and separate like those of a carnivorous dinosaur. The long tail feathers are bird-like, although no bird today has such a long bony tail.

tion on the ancestry of birds. This small, chicken-sized animal was immediately recognized as a bird, but only because feathers were preserved in association with the skeleton. If the feathers had not been there, it would have been identified as a small meat-eating dinosaur from the small, sharp teeth in the jaws. The arms that support the flight feathers to form the wings still had three separate, clawed fingers. And *Archaeopteryx* has a long bony tail. All in all, this amazing little animal looks a lot like *Compsognathus*, which was celebrated for more than a century as the smallest dinosaur. Because of its combination of features, *Archaeopteryx* was recognized as the link between reptiles and birds. And by 1870, Thomas Huxley publicly announced that birds had descended from dinosaurs. This became the prevailing belief for the end of the 19th and the early part of the 20th century.

A Danish bird specialist, Gerhard Heilmann, undertook a very thorough study of bird origins, publishing his conclusions in English in 1927.² He felt that dinosaurs were anatomically the closest animals to *Archaeopteryx* and other early birds. However, he pointed out that dinosaurs were probably not the direct ancestors of birds because they lacked certain features, or characters. For example, most of us are familiar with the wishbone in chickens and turkeys that we eat. A wishbone is formed by the fusion of a pair of bones found in most vertebrates, from fish to mammals (in humans we refer to them as collarbones). But dinosaurs, according to what Heilmann knew at that time, did not have a collarbone. And if dinosaurs had lost the collarbone, how could they be ancestors of a group of animals that still had a wishbone made of collarbones? Once a bone is lost through evolution, it is virtually impossible to get it back. Therefore Heilmann concluded that birds and dinosaurs were probably “cousins” with a common ancestor. This conclusion became the prevailing hypothesis of bird origins for the next half century.

What Heilmann did not know is that a small dinosaur with a wishbone had been discovered in Mongolia in 1923. Unfortunately, the wishbone, which was almost identical in shape to that of *Archaeopteryx*, had been



misidentified as a different bone. This mistake was not corrected until almost 50 years later by a Polish scientist. Today, we know that many meat-eating dinosaurs had wishbones, including the giant tyrannosaurs. In many cases the wishbones had been collected with the skeletons, but had been misidentified as ribs or other bones.

A resurgence of interest in the question of bird origins occurred in the 1970s, and three theories prevailed. Some scientists maintained that Heilmann was correct and that birds came from a relatively primitive group of reptiles that were generally known as “thecondonts.” This group included the ancestors not only of birds, but also of crocodiles, flying reptiles, and dinosaurs. Other scientists resurrected the idea that birds are the direct descendants of dinosaurs. And others believed that birds came from primitive crocodiles. The last theory is not as unreasonable as it may sound initially, because birds are in fact more closely related to crocodiles than they are to any other living animals, and some early crocodiles were in fact small animals that may have run around on long hind legs and even climbed trees.

New dinosaur discoveries towards the end of the 20th century led to the establishment of dinosaurs as the most likely bird ancestors. This change was assisted by the introduction of a more precise method of classifying living animals and plants. Known as “cladistics” or “Phylogenetic Systematics,” large numbers of derived or specialized characters are analyzed by computer and compared (see Holtz, page 31). Meat-eating (theropod) dinosaurs were found to share with birds more than 125 unique characters that are not found in any other extinct or living animals.³ Although the majority of paleontologists came to accept that dinosaurs were the most likely ancestors of birds, some maintain that this was not possible, and most of the public is still unfamiliar with the evidence.

What if Dinosaurs Are Ancestral to Birds?

At the same time that we started to visualize birds as dinosaur descendants, a theory was be-

ing debated concerning whether or not dinosaurs were warm-blooded. This debate has not been resolved, but there is a preponderance of evidence to suggest that small theropods (meat-eating dinosaurs) did have a type of physiology similar to modern birds and mammals (see de Ricqlès, page 79). The combined ideas that birds may have come from warm-blooded dinosaurs allowed some perceptive paleontologists to predict that one day we would discover dinosaur fossils with feathers. The reasoning is simple. No matter which group of animals birds arose from, fully-formed flight feathers could not have sprouted from the arms to form wings—there must have been intermediate structures that could subsequently be adapted for flying. Feathers, therefore, must have been present in some form in the ancestors of birds.

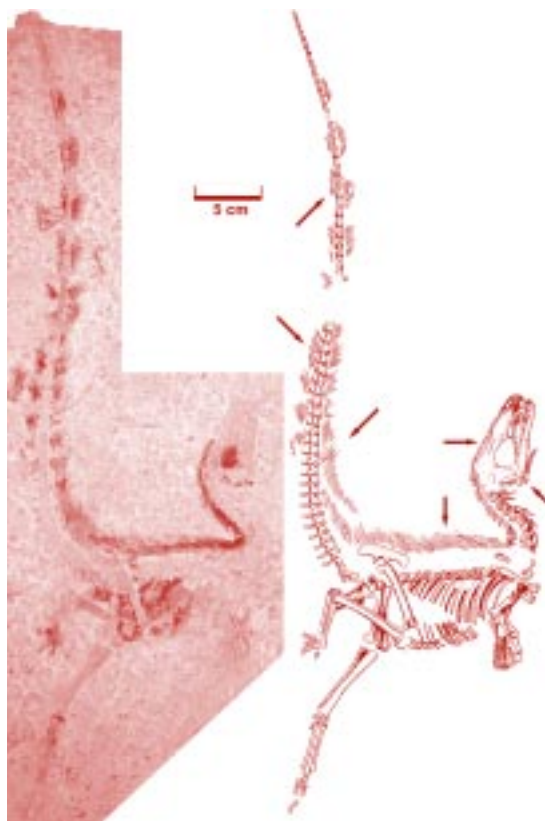
What could feathers have been used for if they were not there for flight? That answer is easy because we know that feathers, especially down, have remarkable insulation properties. If, as some scientists assumed, birds evolved from small theropods and small theropods were warm-blooded animals, it is possible that small theropods had evolved feathers as a way of staying warm. By the early 1980s, some artists had extended the idea of dinosaurs feathered for warmth to dinosaurs using feathers as ornaments. Even though many of us who worked on dinosaurs felt that these ideas were logical (and probably correct), I do not think that most of us ever expected to see fossil proof within our lifetimes. It is difficult to find the fossils of small, feathered theropods because feathers are part of the soft anatomy, which usually rots away without being fossilized. Also, small dinosaurs are much less common than large dinosaurs, whose bones are large enough to resist destruction by scavengers and decomposition.

The Feathered Dinosaurs of Asia

Even though the number of skeletal characters shared by dinosaurs and birds is the strongest evidence of their close relationship, many have resisted the idea that something like a robin could evolve from anything related to *Tyranno-*



Fig. 2. *Sinosauropteryx* is a small theropod with an extremely long tail and short arms. The fossils of this animal are well enough preserved to include simple, feather-like structures (see arrows).



saurus rex. When one prominent paleontologist was asked in 1996 what would convince him that the theory was correct, he stated that a dinosaur would have to be found with fossilized feathers. Several months later, I was in China when a Chinese newspaper reported just such a discovery. With some of my Chinese colleagues, I went to see the specimen with the expectation of seeing fossilized fungus, mineral crystals, or something else that had been misinterpreted as feathers. But it only took seconds to be convinced that the beautifully preserved, 125 million year old dinosaur really did show evidence of some kind of downy or hairy covering. Approximately the size of a large chicken, *Sinosauropteryx* (Fig. 2) seems to have been covered from the top of the head to the end of the tail by slender filaments. The filaments are stacked on top of each other, so it is difficult to see exactly what a single structure looks like. However, the evidence favors them being a simple branching structure similar to a down feather with a thick stalk at the base, and long slender filaments towards the outside (Fig. 3).

Three additional specimens of *Sinosauropteryx*, all showing the same kind of body covering, have now been recovered from the same locality in northeastern China, along with more than 1,000 fossilized birds.

The discovery of *Sinosauropteryx* focused the attention of scientists and public alike on the question of bird origins, and triggered a great deal of controversy. Controversy in science is not a bad thing of course, because it stimulates additional research. Before long, another “feathered” dinosaur was found in northeastern China. This one was named *Protarchaeopteryx*. Whereas *Sinosauropteryx* had short arms and a very long tail, *Protarchaeopteryx* had almost the opposite proportions. Its body was also covered with some simple, downy covering. However, at the end of the tail there are long stiff feathers that cannot be distinguished from the tail feathers of a mod-

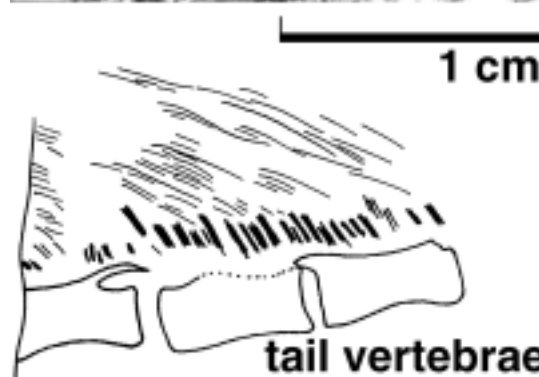


Fig. 3. Photograph and drawing of the feathers along the tail of *Sinosauropteryx*, showing the short central stalks below, and the long filamentous structures above that branch off them.



ern bird. The feathers have a stiff central shaft (Fig. 4), and the vane is formed of the Velcro-like barb and barbule arrangement characteristic of bird feathers. More specimens of this animal were reportedly found later in 1997, and I went back to China to help my colleagues, only to discover that the fossils represented yet another new species.⁴ *Caudipteryx* (Fig. 5) is similar to *Sinosauropteryx* and *Protarchaeopteryx* in having a downy body covering, and like the latter, it has long stiff feathers at the end of its short bony tail. In addition, this small dinosaur has long, stiff feathers behind its arms. Microscopically, these feathers are indistinguishable from those of modern birds.

The Chinese locality where the feathered dinosaurs are found has turned out to be one of the most remarkable and productive dinosaur sites in the world. The conditions more than 125 million years ago in northeastern China were perfect for the preservation of feathers. The bodies of the birds and feathered dinosaurs were washed into shallow lakes, where they would settle to the bottom. There they were gently buried by mud and volcanic ash under chemical conditions that seemed to prevent bacteria from decomposing the feathers.

At least three more species of Chinese theropod dinosaurs have been found with feathers in recent years. *Beipiaosaurus* is the largest feathered form found so far, and is as large as a human. It is part of a relatively strange group of theropods known as therizinosaurs. These unusual animals had relatively small skulls with leaf-shaped teeth that indicate dietary preferences for fish or possibly even plants. Their bodies were bulky, but the hands and feet were armed with strong, sharply tapering claws. Related to *Velociraptor* and *Deinonychus*, two other Chinese theropods, *Sinornithosaurus* and *Microraptor*, have also been found with preserved feathers. The Gobi Desert of Mongolia has now also produced theropod fossils with evidence of feathers. *Nomingia* is related to *Oviraptor*, but has a relatively short tail that ends in a pygostyle (sometimes called the “pope’s nose” in a roast chicken or turkey), which is a fused series of five vertebrae that

supports the tail feathers and preening gland in modern birds. *Shuvuuia* is related to *Mononykus*, and is considered by some to be a bird, and by others to be a dinosaur. Remnants of feathers were preserved with one of the specimens.

The number of specimens of feathered dinosaurs recovered since 1996 is truly amazing. Although all are theropods, they represent

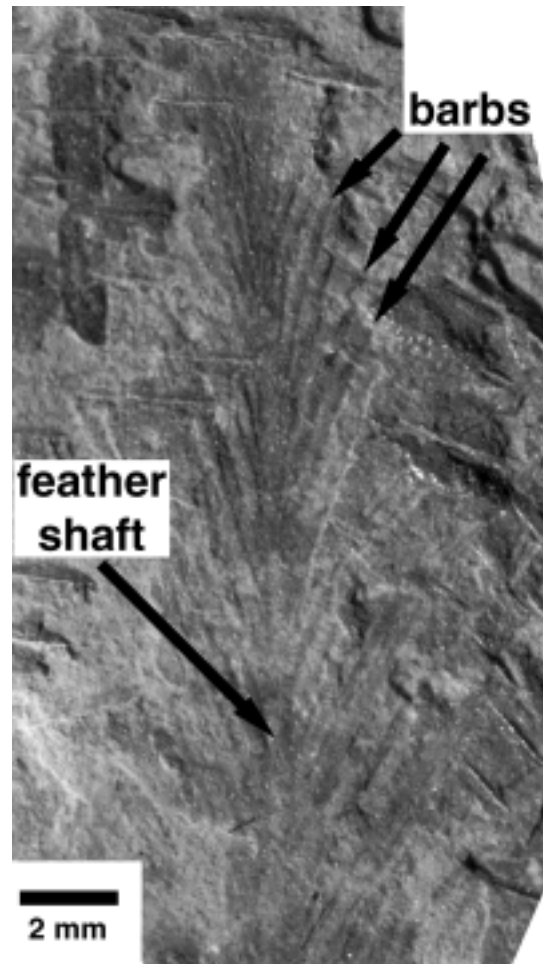


Fig. 4. Tail feather of *Protarchaeopteryx* showing the central shaft and barbs. The barbs are more or less parallel because of the smaller, Velcro-like structures called barbules that hold them together.

many different families that are as different from each other as the modern carnivore families of cats, dogs, bears, weasels, civets and hyenas. The diversity strongly suggests that feathers were present in most of the Upper Cretaceous dinosaurs of the Northern Hemisphere. For example, even though feathers have never been seen on any specimen of *Oviraptor* from the Gobi Desert, nor on *Deinonychus* from Montana, the fossils of close relatives of these animals were well enough preserved to

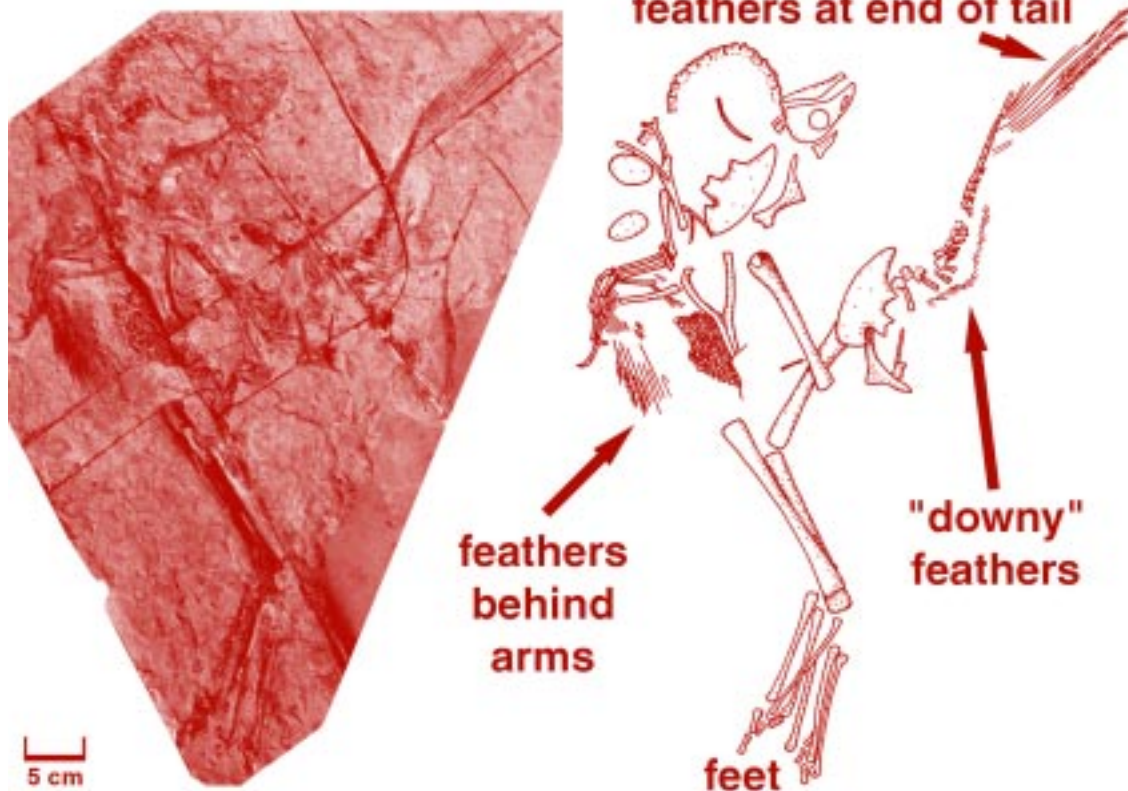


have feathers. *Caudipteryx* is closely related to *Oviraptor*, and *Sinornithosaurus* to *Deinonychus*, which suggest that feathers may have covered these animals too. In fact, looking at the distribution of feathers amongst theropod dinosaurs even opens up the possibility that a giant animal like *Tyrannosaurus rex* may have had feathers on its body at some stage of its life! Feathers are unlikely to have covered its body at maturity, however, as six-ton terrestrial animals do not need insulation.

“feathers.”⁶ In this animal, the body appears to have been covered by simple-branching, down-like feathers. They were not very long, but would have been perfect for insulating the body. Covering the body with insulation strongly supports the idea that small theropods were warm-blooded, or at least had a much more active metabolism than lizards and crocodiles do.

Small endothermic animals generally have more problems than large ones in keeping their

Fig. 5. *Caudipteryx* is a small dinosaur from northeastern China that has long bird-like feathers behind its arms and at the end of the tail, and simpler, downy feathers over much of the rest of its body.



The Evolution of Feathers

Scientists have been speculating about the origin of feathers for almost a century and a half. Some agree that they were probably derived from reptilian scales, but even this idea is under debate. The driving evolutionary mechanism has been even more elusive. The discovery of feathered dinosaurs has provided a framework within which feather evolution must fit,⁵ although there is still considerable latitude for scientific speculation and debate. *Sinosauropteryx* is the most primitive theropod dinosaur that we know of with evidence of

body temperatures constant. This relates to size scaling differences. To use a simple example, let's assume that *Sinosauropteryx* could fold up into a cube that was one meter by one meter by one meter. Its body surface area, through which heat is lost, is proportional to one meter squared. The volume and mass of the same animal would scale with one meter cubed, and this would be proportional to the amount of heat produced within the body. In this animal the amount of heat lost through the skin (surface area) compared to the amount of heat produced would be proportional to $1^2/1^3$, which is



the same as 1/1. An animal double the length would have a heat loss to heat production ratio of $2^2/2^3$, which is $4/8$ ($= 1/2$). In other words, doubling the size of the animal reduces heat loss to about half the rate. Taking this ratio to an extreme, let's assume that *Tyrannosaurus rex* is 30 times the length of *Sinosauropteryx*. The heat loss ratio of this giant would be $30^2/30^3$, equivalent to $900/27,000$ ($= 1/300$). As a very rough estimate then, *Tyrannosaurus rex* lost body heat at a rate of about $1/300^{\text{th}}$ that of *Sinosauropteryx*. To use a living example, heat loss is the reason a shrew has to eat its own body weight in food every day, while an elephant eats only a fraction of its body weight.

Fluctuations in body temperature are generally not a problem in large animals, but can be problematic in small ones like *Sinosauropteryx*. And this is probably why feathers have only been found on small dinosaurs. But insulation works in two ways; it can keep an animal warm, or if that animal is cold, the insulation can prevent it from warming up. It would make no sense for a cold-blooded animal to be insulated, because it relies on external sources like the sun to warm up. An ice cube insulated by down takes much longer to melt on a hot day than an ice cube exposed directly to the sun. Similarly, a cold-blooded insulated animal would need to stay warm, because once it did cool down, it would take much more effort to warm up again.

Protarchaeopteryx and *Caudipteryx* show us the next stages in the evolution of feathers. Long, stiff, complex feathers that are indistinguishable from the contour and flight feathers of modern birds appeared at the end of the tail and behind the forearms. Initially, these may have developed as a way of displaying to potential mates and rivals. Dinosaurs in general were very visual animals that developed a tremendous array of crests, frills, horns, plates, spikes and scales for display. Most of these features are only preserved in the skeletons. Once feathers were present on dinosaurs, however, they seem to have been quick in utilizing them for display. Although such a display hypothesis is only one possible interpretation, it does make good sense. Feathers are lightweight, strong, colorful, and replaceable, making them better

than most of the display structures developed from bone. Spreading out a fan of tail feathers or lifting the arms was probably as effective for theropods to attract mates as it is in modern birds.

Nests of *Oviraptor* and related forms have been found in Mongolia and China⁷. In a half dozen cases, adults have been found fossilized on top of the nests. The eggs were laid in a circle, two at a time, as the mother stood on one spot and turned her body. At the same time as she rotated and laid eggs, she used her hands to scoop sand onto the eggs. We can infer this because in one of the specimens, the hands are stretched out beside the nest and are at a lower level than the eggs. However, the feet in the space are level with the top of the eggs. The result was a mound nest with the eggs laid in a spiral as many as three layers deep. The mother dinosaur remained on the nest, with her feet in the center where there were no eggs. Her chest covered some of the eggs, and her tail covered others. But in all cases, the arms are wrapped around the outside of the nest. The eggs between the body and the outspread arms appear to have been unprotected. However, if the *Oviraptor* had long feathers projecting behind the arms like its close relative *Caudipteryx*, then the feathers would have protected those eggs⁸. This idea has led some scientists to speculate that the elongate feathers behind the forearms and hands may have evolved, perhaps in conjunction with the display function, as a way of protecting the eggs in a nest.

Once long, stiff complex feathers were present behind the arms and at the end of the tail, they probably gave these small theropods an aerodynamic advantage over their rivals. Perhaps they flapped their arms as they jumped across logs or ditches, and that simple action gave them just enough speed or control to escape a predator or capture a prey item. Selection would then favor lengthening those feathers in subsequent generations, and would also control the development of new ways to utilize the arms. Ultimately the descendants would have become airborne for at least short distances, and a whole new world would have opened up to these dinosaurs. It was not a



simple or easy transition because it involved the development of complex rearrangements of bones, joints, muscles and many other things. But many of the changes that led to the sophisticated flight apparatus of modern birds are documented in the fossil record.

The Origin of Flight

There has been a lot of speculation over whether the active flight of birds developed in tree-climbing dinosaurs, or ground-running species. Many animals have taken to the air, including insects, fish, amphibians, reptiles and mammals. Some of these animals are active fliers that are able to stay in the air for prolonged periods of time by actively generating thrust. This category includes most insects, flying reptiles (pterosaurs), bats and, of course, birds. But there is also a diverse assemblage of gliding animals, which includes flying frogs that use the membranes between their toes for parachuting, lizards (and even snakes!) that extend their ribs to form gliding membranes, and flying squirrels that have membranes stretched between their arms and legs. Some paleontologists believe that birds started flight by jumping out of trees, just as most of these gliders do⁹. Others argue that the complex arm movements of a bird must have started in a ground-running dinosaur, and that flight began from the ground up.¹⁰ Good arguments support both ideas, although the long-legged, small, feathered theropods of China were mostly ground-dwellers and therefore support the “ground up” theory. Without knowing the precise point at which active flight began, it is perhaps impossible to know the answer. Perhaps the correct answer was even a combination of both the “ground up” and “trees down” theories. Even though we may never know which theory is correct, the lively debate has motivated scientists to study and better understand the mechanisms involved in the evolution of active flight.

Are Dinosaurs Extinct?

In spite of the large amount of public debate that has gone on in recent years concerning the origin of birds, the overwhelming evidence shows us that birds evolved directly from

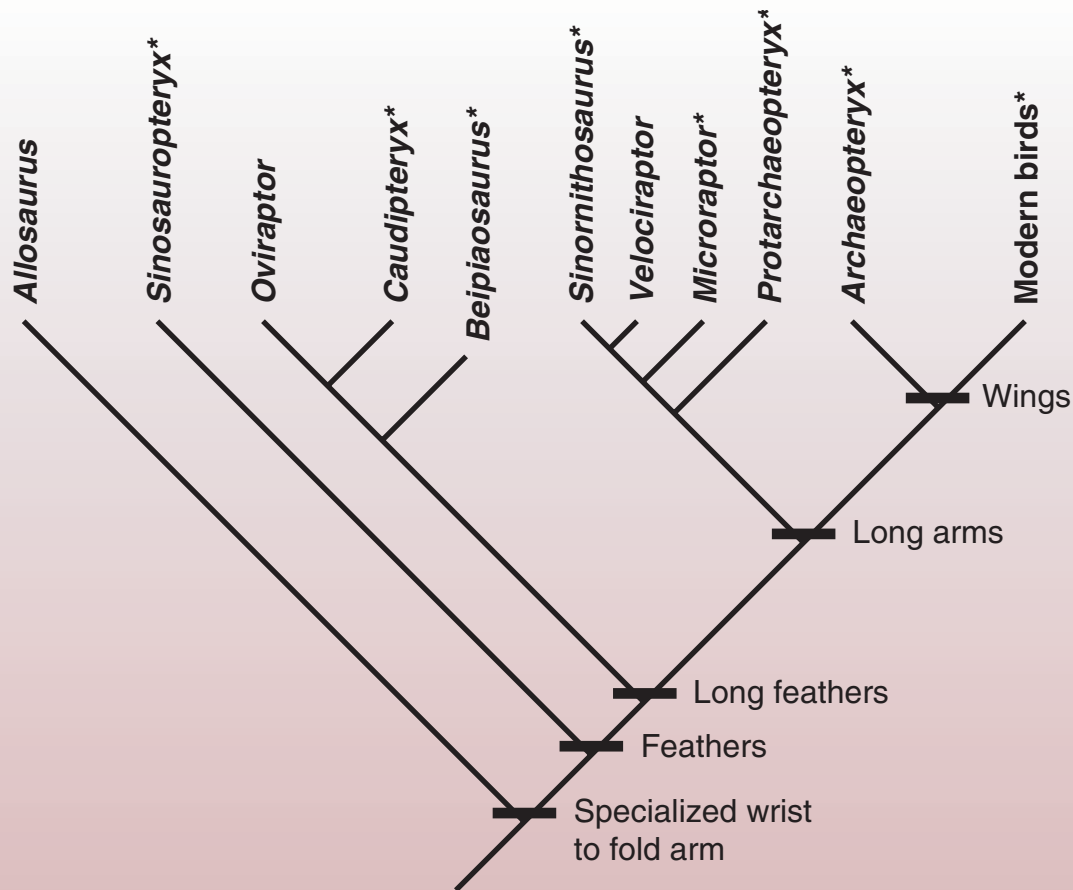
theropod dinosaurs. No other candidates exist with so many anatomical similarities and new evolutionary features (including feathers) as are shared between birds and dinosaurs. Under a modern biological and paleontological classification, birds are a subset of the Dinosauria. This means that they can be referred to as living dinosaurs, and that dinosaurs are not extinct. In a sense, dinosaurs are still more successful than mammals because there are more than twice as many living species. Birds are very specialized dinosaurs, which we will continue to call birds. But knowing that this one lineage of dinosaurs did survive the great extinction event of 65 million years ago does give dinosaurs a new edge of respectability. As the dominant land animals for more than 140 million years, dinosaurs were long considered to be one of the most magnificent failures in the history of the planet. We can still marvel about why so many dinosaur lineages disappeared at the end of the Cretaceous, but that must now be tempered with the idea that dinosaurs are still successful animals.

Somehow knowing that birds are living representatives of the Dinosauria also gives birds a new respectability. I have never been able to look at a robin in quite the same way as I did before knowing that its bloodlines merged with those of *Tyrannosaurus rex* and *Velociraptor*!

Summary

Feathers are not unique to birds. Fossilized feathers have been found in at least seven species of non-avian theropod dinosaurs (*Beipiaosaurus*, *Caudipteryx*, *Microaptor*, *Protarchaeopteryx*, *Shuvuuia*, *Sinosauropteryx*, *Sinornithosaurus*). Because these animals represent a great diversity of different families (Fig. 6), we can infer that many, many other species of dinosaurs had feathers when they were alive.

The first function of feathers was not for flight, but for insulation in small, warm-blooded, non-avian dinosaurs. It is possible that initially the insulation was restricted to the small, temperature vulnerable young. Because evidence suggests that all dinosaurs hatched from eggs, none of which were more than half a meter (18 inches) long, no newborn dinosaur



babies would have been longer than a meter (3 ft). Insulation would not have been necessary in the adults of large species, but may have been retained in the adults of small species. Once feathers were present in dinosaurs, they were adapted into many other functions. Long stiff feathers at the end of the tail and behind the arms may have been used initially for displaying to potential mates, and/or for protection of eggs in the nest. The presence of these long feathers gave some of these dinosaurs aerodynamic properties that could be used in prey capture and escape from enemies. This selective advantage would have been emphasized by lengthening the feathers and arms until active flight was possible. Flight requires many other modifications in anatomy, physiology and behavior, all of which would have been changing at the same time as the wings developed.

Active flight is what separates birds from their non-avian theropod ancestors. However,

because there is a continuous series of evolutionary steps between birds and their ancestors, it is difficult to know exactly when active flight began. Paleontologists therefore often arbitrarily consider *Archaeopteryx* as the division between non-avian theropods and birds, because this animal has been proclaimed the “first bird” since 1861. Using this scheme, any animal that shares a common ancestor with *Archaeopteryx* and modern birds would be considered as a bird. Theropods more primitive than this common ancestor would not be considered as birds, even if they had feathers and rudimentary wings.

Under a modern biological and paleontological classification, birds are a subset of the Dinosauria. Thus, dinosaurs are not extinct, and are still one of the most successful groups of vertebrates. In spite of the fact that birds are dinosaurs, they are also a very specialized group that we can continue to call birds.

Fig. 6. Cladogram showing the interrelationships of the feathered dinosaurs and modern birds, along with the stages at which certain avian characters were acquired. *Allosaurus* is included as an example of a famous dinosaur that we do not believe had feathers.



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