The Thecodont and Theropod Hypotheses On the Origin of Birds

Since the advent of the theory of evolution the origin of birds has been a thriving topic in science. Many ideas and hypotheses have been presented, but only two stand today: that birds are descendents of ancient thecodont stem reptiles, and that birds are the direct descendents of a group of dinosaurs known as the coelurosaurs. Both hypotheses pose many interesting and insightful ideas based on information obtained from the fossil record. There is not enough evidence at this time to determine which hypothesis, if either, is right. Only more hard work by scientists will tell. Until then we have only speculation, but speculation based in observed evidence. The origin of birds is one of the great mysteries in biology. Birds are dramatically different from all other living creatures. Feathers, toothless beaks, hollow bones, perching feet, wishbones, deep breastbones, and stump-like tailbones are only part of the combination of features that no other living animal has in common with them (Padian and Chiappe 1998). Scientists have speculated on the evolutionary history of birds since shortly after Charles Darwin established his theory of evolution in On the Origin of Species (Padian and Chiappe 1998). One year later, in 1860, a solitary fossil feather of a bird was found dating back 150 million years. The next year a skeleton of an animal that had bird-like wings and feathers, but a very unbirdlike long, bony tail and toothed jaw, turned up in the same region. These finds became the first two specimens of Archaeopteryx lithographica, the most archaic known member of the birds, and sparked the immense interest in the evolution of birds and the search for their ancestors (Padian and Chiappe 1998).

Two major hypotheses are current. The first hypothesis, and most widely accepted, states that birds are the direct descendents of theropods (Feduccia 1996). Theropods are a diverse group of bipedal saurischian dinosaurs (see cladogram). They include the largest terrestrial carnivores ever to have walked the earth. Several characters typify a theropod: hollow bones, three main fingers on the manus (hand), and three main (weight-bearing) toes on the...
pes (foot). Most theropods had sharp, recurved teeth useful for tearing flesh, and claws were present on the ends of all of the fingers and toes (Hutchinson 2000). It is thought that birds are descendents of the group of theropods known as the coeluroosaur or maniraptora. (There is debate as to whether these two groups should be one, so for the sake of this paper, I will refer to them as coelurosaurs.) This group can be typified by such species as Velociraptor and Deinonychus (Hutchinson 2000). The other hypothesis is that birds arose much earlier than dinosaurs from a group known to be the ancestors of theropods: the thecodonts (Dingus and Rowe 1998). Thecodonts were small, agile reptiles with long tails and short forelimbs, thought to include the ancestral stock of all other archosaurs, including birds, all dinosaurs, pterosaurs (extinct flying reptiles), and crocodilians (Anonymous 2000).

The Theropod Hypothesis

The theropod hypothesis puts the entry of birds into the evolutionary arena after the line of descent had continued from thecodonts to the saurischian dinosaurs and their subsequent split into distinctive lineages (Feduccia 1996). Thomas Huxley (1868) originated this hypothesis with his comparison of the species Compsognathus with modern day birds: Sure there is nothing very wild or illegitimate in the hypothesis that the phylum of the class Aves has its foot in the dinosaurian reptiles—that these, passing through a series of such modifications as are exhibited in one of their phases by Compsognathus, has given rise to birds. (1868, p 74) The fact that Archaeopteryx was often mistaken for Compsognathus further highlights the degree of resemblance (Dingus and Rowe 1998). Other paleontologists also saw the resemblance, and the idea of a close connection between birds and dinosaurs found a wide following (Dingus and Rowe 1998). Most of the recent debate on bird origins has centered on the new version of Huxley’s dinosaurian hypothesis, initiated and since advocated by John H. Ostrom (Feduccia 1996). His hypothesis is that birds are not only descended directly from dinosaurs, as proposed by Huxley, but are descendents from small coelurosaurian dinosaurs similar to Deinonychus, the lightly built, early Cretaceous coelurosaur that he discovered in 1964 (Ostrom 1969). In Deinonychus Ostrom (1969) saw remarkable similarities to Archaeopteryx. He saw these similarities in the:

1. Semilunate carpal (wrist bone)
Padian and Chiappe (1998) go on to say that it was on the basis of these remarkable similarities, shared only between birds and theropods, that Ostrom concluded birds are the direct descendents of the coelurosaurs. According to Hutchinson (2000), Ostrom’s work provided the drive for a paradigm shift in paleontologists’ visions of the origin of birds and the evolution of flight.

Ostrom did not apply the cladistic method to determine that birds evolved from theropods (Padian and Chiappe 1998). But in 1980 Jacques Gauthier did an extensive analysis of birds, dinosaurs, and their reptilian ancestors. He put Ostrom’s comparisons and many other features into a cladistic framework and came to the conclusion that birds evolved from coelurosaurs. Some of the closest relatives of birds included Deinonychus that Ostrom had so vividly described (Padian and Chiappe 1998).

Some skeptics of this hypothesis argued that because many theropods lacked a clavicle they could not be the ancestors of birds since clavicles are a feature found in every bird (Padian and Chiappe 1998). But, in 1936, Charles Camp found the remains of a small Early Jurassic theropod complete with a clavicle. Recent studies have found clavicles in a broad spectrum of the theropods thought to be related to birds (Padian and Chiappe 1998).

Among the main characters that support the bird-theropod connection are the ascending process of the anklebone and the mesotarsal joint (Feduccia 1996, p 75). Debate on the homologies of this type of ankle goes back to Huxley (1870), who noted that birds and theropods share a triangular prominence in front of the distal tibia known as the ascending process of the astragalus. According to Feduccia (1996), the mesotarsal joint is present with the line of flexion between the proximal and distal tarsals. The astragalus and calcaneum are reduced and integrated with the ends of the tibia and fibula. The above features exhibit dinosaurs’ closest resemblance to birds, and the question is whether or not the resemblance
is due to homology or convergence.

Recently the gap between theropods and birds has been narrowed even further. Important avian characters, such as the furcula (wishbone), have been discovered in theropods thought to be close to birds. Typical theropod characteristics, such as an enlarged claw on digit two of the foot, have been found in early birds (Unwin 1998).

Evidence for the dinosaurian origin of birds is not confined completely to anatomy. Recent discoveries of nesting sites in Mongolia and Montana reveal that some reproductive behaviors of birds originated in nonavian dinosaurs (Padian and Chiappe 1998). These theropods did not deposit a large clutch of eggs all at once, as most other reptiles do. Instead they filled a nest more gradually, laying one or two eggs at a time, perhaps over several days, as birds do. Recently skeletons of the Cretaceous theropod Oviraptor have been found atop nests of eggs; the dinosaurs were apparently buried while protecting the eggs in a very birdlike fashion. Even the structure of the eggshells in theropods shows features seen only in bird eggs. The shells consist of two layers of calcite, one prismatic and one spongy (Padian and Chiappe 1998).

With all of this information in mind it would be easy to come to the conclusion that birds are direct descendents of coelurosauris. But there is additional information that contradicts the above ideas. What one must keep in mind is that most of this information is opinion embedded in some fact. Because the data for this type of research are so sensitive, can be viewed to support numerous ideas, and are open to many different interpretations, the data received can either be viewed as solid or as an intermediate step leading to a solid argument.

Problems with the Theropod Hypothesis

The hypothesis of theropod origins, though sound in many areas, does pose problems. A point I want to make clear is that much of this information is what is believed at this moment and that future finds may contradict these ideas or help them.

First, the timing is off (Feduccia 1996). Archaeopteryx occurred in the Late Triassic some 150 million years ago and presumably, because of its advanced feathers, birds originated much earlier. The earliest dinosaurs, Euraptor and Herrerasaurus, from the Late Triassic (150 million years ago), lack the synamorphies, similarities in bone structure, that are used to unite birds and dinosaurs. Deinonychus is from the early Cretaceous, 40 million years after Archaeopteryx, and most bird-like dinosaurs are from the Late Cretaceous, some 75 million years after the appearance of the first bird. This time difference provides evidence that birds and dinosaurs appear similar because of convergent evolution, but it may also be because at some point they shared a common ancestor, such as the thecodonts.

The idea that the timing is off has recently been contradicted. Zhao and Xu (1998) reported the discovery of a therizinosaur (coelurosaur) from the Early Jurassic. This discovery extends the age range of these animals previously known only from the Cretaceous, back another 94 million years to about 240 million years. This is the oldest known coelurosaur
theropod, which therefore minimizes the divergence time for members of the group. Most importantly, it contradicts the idea that the non-avian Coelurosauria occurred too late in the fossil record to give rise to birds. The presence of a non-avian coelurosaurian in the Early Jurassic indicated that by the Late Jurassic (150 million years ago) the major clades of the group could have already diverged, well before Archaeopteryx appears in the fossil record. (Zhao and Xu 1998).

Second, the ancestors of birds would have to be suited to flight, but dinosaurs 1) are large, and 2) had shortened forelimbs, representing the worst possible morphological arrangement for the evolution of flight (Feduccia 1996, p 90). However, the coelurosaurs were small and had bone structures that could have easily evolved into structures suitable for flight.

Many of the arguments against the theropod hypothesis come down to slight differences in the physical appearance of the fossils. Tarsitano and Hecht (1980) believed that the pattern of digital reduction differs in birds and dinosaurs and that therefore they could only be related at the level of ancestral thecodonts, the other hypothesis. Paleontological evidence favors the view that the dinosaur hand is a derived amniote condition, characterized by the reduction of two digits, 4 and 5, leaving 1-2-3, and therefore it is a different hand than that of the bird manus, which is 2-3-4. Also, in most species of bird fossils the middle finger is crossed over the outer finger in a strange style of preservation not found in any known theropod (Feduccia 1996, p 70).

Another dramatic character is the footed or booted pelvis. This character is seen in a number of theropods and superficially resembles the condition in Archaeopteryx (Feduccia 1996). However, the footed pelvis is also known among thecodonts, again pointing to the likelihood that the thecodont hypothesis is correct. In Archaeopteryx, and a number of Early Cretaceous intermediate birds, the pubes meet distally to form a hypo-pubic cup. The typical theropod pubes has a prominent, hooked-back pubic foot or boot, which is a massive bony structure resembling an inverted anvil. Because the pube extended vertically downward, it would not have been suited for the practices of tree climbing associated with Archaeopteryx and other early birds. It would have been maladaptive and a hindrance (Feduccia 1996). The organization of the theropod pelvis in the Late Cretaceous illustrates the possibility that dinosaurs and birds are examples of convergent evolution.

According to Dingus and Rowe (1998), another challenge to the hypothesis came from Sanker Chatterjee (1991), with the discovery of a fossil for which he coined the name Protoavis texenis. It was collected from Late Triassic rock, predating Archaeopteryx by 75 million years, and pushing the origin of birds back to the earliest stages of dinosaur evolution. Chatterjee maintains that Protoavis is on the direct path from dinosaurs to birds, and that Archaeopteryx and other theropods represent an unrelated side path on the map of avian evolution. The scientific community has been skeptical about Chatterjee’s findings, and will need more evidence before the idea is seriously considered (Dingus and Rowe 1998).

The theropod hypothesis ultimately either rests on the homology of the supposed shared, derived character similarities between birds and dinosaurs or falls on the proposition that the
characters in birds and dinosaurs acquired a similar appearance through convergence (Feduccia 1996).

The Thecodont Hypothesis

The other hypothesis states that birds arose from the thecodons in the Middle Triassic some 230 million years ago. Before the discovery of Deinonychus, most paleontologists agreed that birds descended from thecodonts, which died out 100 million years before Deinonychus roamed the earth (Dingus and Rowe 1998). Modern crocodiles, dinosaurs, and pterosaurs are also thought to have evolved from the thecodonts. This view of avian origins sprouted over a century before the name Deinonychus was coined. Dingus and Rowe (1998) say that the thecodont hypothesis has been advocated ever since by a sizable constituency of paleontologists and is the view championed by most ornithologists.

Robert Bloom found the first solid evidence to support the thecodont hypothesis (Feduccia 1996). In 1913, Bloom described from the rich Lower Triassic (230 million years old) deposits of South Africa the thecodont Euparkeria, which he believed was ancestral not only to birds but to the ruling reptiles. In Euparkeria, a small, 230 million year old thecodont, still quadrupedal but tending toward bipedality, there appeared to be all the necessary anatomical qualifications (small build and long arms suited for flight) for the ancestor of birds (Feduccia 1996). Dingus and Rowe (1998) say that Euparkeria has long reigned as the most important discovery of the twentieth century in terms of archosaur evolution and the origin of birds.

Gerhard Heilmann was a major advocate of the thecodont hypothesis (1926). He meticulously considered how Archaeopteryx could have arisen from Euparkeria, and flight from small bipedal thecodonts. His argument worked equally well to validate the theropod hypothesis, but in the end he argued for the early thecodontian ancestry:

It would seem a rather obvious conclusion that it is amongst the coelurosaurians that we are to look for the bird ancestor. And yet, this would be too rash, for the very fact that clavicles are wanting would in itself be sufficient to prove that these saurians could not possibly be the ancestors of birds.... We have therefore reasons to hope that in a group of reptiles closely related to the coelurosaurians we shall be able to find an animal wholly without the shortcomings here indicated for bird ancestors.... such a group is possibly the pseudosuchians [thecodonts].... All our requirements of a bird ancestor are met in the pseudosuchians, and nothing in their structure militates against the view that one of them might have been the ancestors of birds. (1926, p 183-185)

Recer (2000) states that the fossils of a small, lizard-like, flying reptile with a complex set of feathers, Longisquama insignis, supports the thecodont hypothesis. He believes that the feathered reptile lived 220 million years ago, providing evidence that feathered animals evolved millions of years before the appearance of the dinosaurs. The fossil of L. insignis is thought to be a thecodont. Archaeopteryx appeared some 75 million years after L. insignis. In the scientific community as a whole, there is still dispute over the legitimacy of L. insignis and whether or not it can be used as viable evidence.
Jones et al. (2000) say that feathers form from the circular epidermal collar of a follicle. The invaginated base of the follicle houses a dermal papilla. This organization is the defining developmental and morphological characteristic of feathers. They then go on to say that the preservation of a follicular, calamus-like base in L. insignis’ appendages is consistent only with the developmental pattern heretofore known in the avian feather.

As a result of observing the specimen, Jones et al. (2000) are suggesting that the combination of shared, specialized morphological characters of avian feathers unlikely to have evolved more than once. The interpretation is that the pinnate appendages of L. insignis are nonavian feathers, probably homologous to those of birds.

Appenzeller (1999) adds more evidence to further the thecodonts-bird relationship. He came to the conclusion that many predatory dinosaurs had some kind of plumage. He made this observation from recent finds in China of stunningly preserved fossils found with fibrous down or feathers as unmistakable as a pigeon’s. This proliferation is one that dramatically underscores the proposed evolutionary link between dinosaurs and birds (Appenzeller 1999). It means feathers had to evolve before dinosaurs, linking birds to a more distant relative, such as the thecodonts.

The thecodont hypothesis, unlike the theropod hypothesis, is not as widely accepted because there is relatively little known about thecodonts in general. Yet, it still has its supporters as it is a plausible idea. If more fossils are found and more information collected about this unfamiliar group, the thecodont hypothesis may become accepted, as is the theropod hypothesis. Both have strong evidence that support them and both are viable explanations to the origin of birds.

Problems with the Thecdont Hypothesis

One of the problems with the thecodont hypothesis concerns the discovery of L. insignis. Jacques Gauthier says that the specimen is poorly preserved and is not enough evidence to dismiss the theropod hypothesis (Recer 2000). More on this issue comes from Stokstad (2000). He says that the problem with the L. insignis find and the conclusions scientists are making about it is not that it is presenting a rival hypothesis about bird origins; it is that it is not really presenting a hypothesis at all. Simply arguing that L. insignis is birdlike is not enough. One must be able to show that it is more closely related to birds than something else, such as theropods.

Dingus and Rowe (1998) present another problem. They go on to say that it is difficult identifying Euparkeria as a possible ancestor of birds and other archosaurs. The oldest known bird is 100 million years younger than Euparkeria, leaving a long, dark gap of pre-avian history. Paleontologists wonder what the intermediate ancestors of birds (specialized reptiles) may have looked like, how they functioned, and how they behaved.

Feduccia (1996) says that Jacques Gauthier criticizes the thecodont hypothesis because he feels that there is just not enough known about the thecodonts. They are simply an
undefinedable (lacking specific synamorphies) assemblage of Triassic archosaurs (precursors to dinosaurs), and therefore the hypothesis cannot be considered legitimate (Feduccia 1996). “From a phylogenetic perspective, ‘Thecodontia’ and Archosauria are diagnosed by the same synamorphies. Thus, these taxa are redundant, and when one says that birds evolved from ‘thecodonts’ one is simply reiterating that birds are part of Archosauria” (Gauthier 1986, p 2).

It ultimately comes down to whether or not scientists can effectively map the distinctive avian features such as bipediality and flight into one of the known lineages. If they cannot, the theropod hypothesis could be true. But if they can map birds onto one of the known thecodont lineages, it would show the theropod hypothesis to be inaccurate (Dingus and Rowe 1998). When and how this mapping will be accomplished is unknown, but once it is done we will know once and for all the origin of birds.

Discussion

These two hypotheses pose realistic views about the origin of birds, yet each has flaws, each has supporters, and each has opponents. What evidence is the most convincing? The evidence is there, and there is no telling when more will come to either support or disprove either. So which is more likely?

I feel that the more successful idea is the theropod hypothesis. Even though there is a lot of evidence against it, there is also a lot for it. When compared to the idea of thecodont origins there are certain aspects that make it more realistic. There is little known about the thecodonts in general, and until there is, there is only room for speculation. Theropods have a much more complete fossil record and can be understood more completely. Some argue that the similarities can be a result of convergent evolution, but there are just too many similarities, both in appearance and lifestyles, such as nesting habits, for that to be entirely true.

As more and more is discovered it is certain that one, if not both of the ideas will be called correct. Both being right is not that inconsistent with current scientific evidence. Most researchers agree that thecodonts are the ancestors of the dinosaurs, crocodiles, and pterosaurs. If this is correct it is not that absurd to call them very distant ancestors of birds even if they are more closely related to dinosaurs. It really comes down to the specific lines of descent and the time when the first birds appeared.

When looking at the specifics of the coelurosaurs, especially Deinonychus, resemblances are seen. The anatomy of the fossils, when compared to birds, are strikingly similar. The ankle and wrist, along with the wishbone, all share remarkable likenesses. Deinonychus was also suited for flight in both size and the way it moved. Some opponents of the theropod hypothesis say that dinosaurs are too young and too big to have given rise to birds. Thecodonts make a more likely candidate, being small and ancient. But with the recent discovery by Zhao and Xu (1998) the problem with timing was practically eliminated, showing that the theropod hypothesis is sound, and just needs more time and more discoveries to be solidified.
Even when all the problems are added up both of the hypotheses still have ample evidence to support them. What really mystifies me is the recent discovery of feathers in theropods. Their presence is an indication that feathers evolved early, perhaps even before dinosaurs, if L. insignis is legitimate, which can be argued. With this in mind one would think that birds had to evolve earlier than dinosaurs. But Appenzeller’s (2000) view that feathers in theropods underscore the bird-dinosaur relationship is not necessarily true. I see two possible answers here, the one Appenzeller discusses, and one he failed to mention. If approached from an evolutionary standpoint, feathers evolving early in history does not mean birds had to evolve early. Theropods with feathers could have given rise to birds, which would explain how they were able to have such advanced feathers so early on. That is typical of much of the information presented in this paper. If dissected long enough it could work both ways.

**Conclusion**

The argument over which hypothesis is correct, the theropod or thecodont, is a problem that cannot be solved easily. It will take time, the meticulous collection of more and more fossils, and countless hours of data analysis. Both hypotheses pose logical and substantial ideas as to the origin of birds, but until more evidence is found neither can be considered definitive. Both are, instead, in stasis, waiting for the right discovery to set them in motion. Until then these two ideas pose probable origins of birds and have been accepted for years, and, without a doubt, will go on to be accepted for years to come. I feel birds are direct descendents of dinosaurs. I do not disagree with the thecodont hypothesis; I simply feel there is more supporting the theropod hypothesis. So where do birds come from? They are a creature unlike anything living today, but very similar to creatures that roamed and ruled the earth millions of years ago. This mystery is one that has baffled scientists for years, and one that will continue to for years to come.
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