

Phylogenetic Context for the Origin of Feathers¹

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SYNOPSIS. A number of hypotheses have been suggested for the origin of birds and feathers. Although distributions of functional complexes have frequently been used to test phylogenetic hypotheses, analysis of the origin of feathers remains hampered by the incomplete fossil record of these unmineralized structures. It is also complicated by approaches that confuse the origins of birds, feathers, and flight without first demonstrating that these relate to the same historical event. Functional speculation regarding the origin of feathers usually focuses on three possible alternatives: (1) flight; (2) thermal insulation; or (3) display. Recent fossil finds of Late Cretaceous feathered dinosaurs in China have demonstrated that feathers appear to have originated in taxa that retained a significant number of primitive nonavian features. Current evidence strongly suggests that birds are theropod dinosaurs, and that the most primitive known feathers are found on non-flying animals. This further suggests that feathers did not evolve as flight structures. Thermoregulatory, display, and biomechanical support functions remain possible explanations for the origin of feathers. As the earliest function of feathers was probably not for aerial locomotion, it may be speculated that the transitional animals represented by the Chinese fossils possessed skin with the tensile properties of reptiles and combined it with the apomorphic characteristics of feathers.

INTRODUCTION

Any description of “birds,” whether technical or colloquial, will include the simple statement that birds have feathers. Historically, feathers have been considered a reliable synapomorphy for birds and the key to avian flight. Hence, the origin of birds, the origin of feathers, and the origin of flight have been regarded as closely-linked problems, with the solution of one likely to resolve the others (e.g., Heilmann, 1926).

Since the 1970s, the strict linkage between these issues has been questioned. Nineteenth-century ideas that birds were close relatives of dinosaurs were reawakened, spurred by new fossil discoveries and the application of new phylogenetic methods (Ostrom, 1976; Gauthier, 1986). These studies opened the possibility that the im-

mediate ancestor of birds was not an arboreal animal, leading to speculation that flight was not as intimately involved in the origin of birds, or of feathers, as originally thought. New discoveries of exceptionally well-preserved avian fossils (e.g., Currie, 1997; Sanz *et al.*, 1997; Forster *et al.*, 1998; Chiappe *et al.*, 1999) and feathered dinosaurs in China (Ji *et al.*, 1998; Xu *et al.*, 1999a) suggest that while feathers are characteristic of extant birds, they must have originated earlier than the group descended from the most recent common ancestor of *Archaeopteryx* and extant birds.

The purpose of this paper is to review the phylogenetic context for the origin of feathers in light of these recent developments in avian paleontology and systematics. The review is organized into three basic areas: competing hypotheses for the origin of birds and their impact on a most parsimonious origin of feathers; new discoveries from the fossil record and what they might tell us about the origin of feathers relative to the origin of birds; and how data from extant organisms bracket or limit the phy-

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logenetetic range in which feathers must have originated.

In the following discussion, we apply phylogenetically-defined taxon names where appropriate. There is some debate over the definition of Aves. Although historically the term included anything that would conventionally be called a bird, the first strictly phylogenetic definition (Gauthier, 1986) restricted Aves to the crown group including the last common ancestor of paleognaths and neognaths and all their descendants. The name *Avialae* is often used to refer to the group including living and fossil birds, including *Archaeopteryx*, and we apply that name in its original stem-based usage—extant birds and those taxa closer to them than to *Dromaeosauridae*. Not all current workers use these definitions, and proposals for a phylogenetic definition of Aves including *Archaeopteryx* have been made (*e.g.*, Sereno, 1998), but Gauthier's (1986) definition has priority. It is critical to remember that currently accepted standards of phylogenetic analysis demand a more rigorous approach than a search for ancestors. A search for avian origins is more properly described as an attempt to determine the closest sister taxa of birds. More specifically, we endeavor to determine that group which shares a most recent common ancestor with birds to the exclusion of others.

Currently accepted standards of phylogenetic analysis demand a more rigorous approach than a search for ancestors. Modern phylogenetic approaches call for the identification of sister taxa rather than real ancestors, and regard questions of the origins of groups, structures, and functions as separate, at least *a priori*. We are thus searching for the closest extinct relatives of birds, and approach the origins of birds, feathers, and flight as potentially separate problems. If subsequent phylogenetic work suggests that the first feathers were flight adaptations, than a linkage between the origins of a structure and function can be entertained—but this is a linkage to be determined on the basis of evolutionary patterns recovered from the fossils, not from initial assumptions that the function show by a

structure in living animals constrains the original function in extinct relatives.

HYPOTHESES ON THE ORIGIN OF BIRDS

There is precious little information available about the skin of Mesozoic reptiles, but we can begin to constrain the possible phylogenetic extent of dermal structures (such as feathers) with an understanding of the phylogenetic relationships of birds (Fig. 1). Thus, we present a brief review of competing hypotheses for the origin of birds. A minority of workers favor bird origins from crocodylomorphs (Whetstone and Martin, 1979, 1981; Martin, 1983) or generally defined “thecodonts” (Tarsitano, 1985, 1991; Feduccia, 1999). However, the significant majority of systematists currently consider a theropod dinosaurian origin for birds to be the most reasonable and most parsimonious explanation of all available data (Padian and Chiappe, 1998*a, b*). Individual taxa that have been considered as possibly close to the origin of birds include *Longisquama*, *Euparkeria*, *Megalancosaurus*, and *Scleromochlus*. A detailed analysis of all of the characters and arguments used to support or refute these competing hypotheses is beyond the scope of this brief review; only capsule summaries will be presented below. For a more detailed overview, the reader is referred to Padian and Chiappe (1998*a*) and to Witmer's (1991) admirably thorough and even-handed review of the hypotheses.

“Thecodont” hypothesis

Although the hypothesis of a “thecodont” ancestor for birds dates back to the early 20th Century (*e.g.*, Heilmann, 1926), it has been advocated most recently by Tarsitano (1985, 1991) and Feduccia (1999). These arguments are driven by two concerns: that theropod dinosaurs exhibit too many terrestrial and cursorial adaptations to be avian precursors, and that any characters that might be shared by birds and theropods are either convergent or functionally constrained. Thus, to find an ancestor that does not possess an unreasonable accumulation of autapomorphous or presumed homoplastic characters, one must revert to more basal “thecodont” archosauromorphs. Ultimately

this proposal is problematic, as “Thecodontia” is a paraphyletic grouping of any archosauriform not belonging to Crocodyliformes, Pterosauria, or Dinosauria (Gauthier and Padian, 1985; Fig. 1). Saying that birds are derived from “thecodonts” is akin to saying that birds are derived from some sort of non-dinosaurian, non-pterosaurian, non-crocodyliform archosauriform, which is begging the question.

Tarsitano (1985, 1991) suggested that avian ancestors must have incorporated functional preadaptations for flight, yet rejects characters uniting theropods and birds based on grounds of functional similarity. Although there may indeed be room for argument regarding some of the characters hypothesized to unite theropods and birds, no alternative hypothesis of relationships based on shared, derived characters has been advanced to support a “thecodontian” sister-group for birds. Moreover, although functional studies can highlight possible character nonindependence, rejecting a hypothesis of homology, on any basis, assumes some knowledge of the tree at the outset. If two character states are not homologous, then they were not inherited from a common ancestor; but such a conclusion assumes that the ancestral states between two taxa are known. Ultimately, the thecodont hypothesis has become what can only be termed a case of “cladistic despair”

in which a purported lack of synapomorphies between crocodylomorphs plus birds or theropods plus birds has lead to a search for ancestors based primarily on shared, but primitive characters.

Crocodylomorph hypothesis

Crocodylomorphs have been suggested as close relatives of birds. This hypothesis was based initially on features of the braincase proposed by Walker (1972) and later limited and refined by others (Whetstone and Martin, 1979, 1981; Martin, 1983). In support of the alternative thecodontian hypothesis of avian relationship, Tarsitano and Hecht (1980) rejected many of Walker’s chondrocranial characters as symplesiomorphies. It should be noted that while Walker (1985) has since withdrawn many of his suggestions of crocodylomorph-bird relationship, others maintain it as a viable hypothesis. Whetstone and Whybrow (1983) placed birds *within* Crocodylomorpha, closer to crocodyliforms than to sphenosuchians. Similarities in the teeth and cranial pneumatic air-sac system have figured prominently in these discussions.

Although Martin and colleagues draw specific comparisons between birds and sphenosuchians, the monophyly of “Sphenosuchia” is not certain (Benton and Clark, 1988). Cranial pneumaticity has been proposed as an important link between crocod-

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FIG. 1. Hypothesis of relationships of primitive birds as nested within Amniota and its closest sister taxa Seymouriamorpha and Diadectomorpha. The hypothesized relationships are based on combining the phylogenetic hypotheses of Benton (1985, 1999), Laurin (1991), Lombard and Sumida (1992), Holtz (1994, 1996), Sereno (1991, 1999), Forster *et al.* (1998), Norell *et al.* (2000), Merck (1997), Parrish (1993), and Chiappe (1997). More details on the saurian portion of the tree can be found in Brochu and Norell (2000a, b). *Longisquama*’s position on the tree reflects the fact that it is a problematic diapsid; it has never been analyzed phylogenetically and may not be an archosaur. The position of turtles within Reptilia is controversial, as indicated in this figure; see Rieppel and Reisz (1999) for a review of the literature. The column next to the taxon names indicates whether feathers (or feather precursors) are definitely present (Y), definitely absent (N), or unknown (?). Notes: 1—We indicate *Longisquama* as lacking feathers, but some (*e.g.*, Ruben and Jones, 2000) believe the long structures arising from the back are homologous with feathers; see text for discussion. 2—Whether fibrous external structures are present in a primitive ornithomimosaur is debated (Perez-Moreno *et al.*, 1994; Briggs *et al.*, 1997). 3—Some phylogenetic analyses draw Pterosauria and *Scleromochlus* close together (Sereno, 1991), but others do not (Benton, 1999). 4—Most phylogenetic analyses of Theropoda consider Coelophysoidea and Abelisauridae to form a monophyletic group (Ceratosauria; Gauthier, 1986; Sereno, 1999), but some analyses are beginning to suggest a closer relationship between abelisaurids and all other theropods (Carrano and Sampson, 1999). 5—The position of Therizinosaurioidea and Alvarezsauria on this tree is an Adams consensus of competing hypotheses. Therizinosauroids are either oviraptorosaurs (Sues, 1997; Makovicky and Sues, 1998) or close relatives of the ornithomimosaurs (Sereno, 1999). Alvarezsaurids were initially thought to be very basal birds (Perle *et al.*, 1994; Chiappe *et al.*, 1996), but the most recent analyses place them either as the sister taxon of *Archaeopteryx* and all other avialans (Chiappe *et al.*, 1999) or close to ornithomimosaurs (Sereno, 1999).

ylomorphs and birds, but cranial pneumaticity is a widespread feature among theropods (Currie, 1985; Witmer, 1997; Currie and Sao, 1996; Clark *et al.*, 1994; Larsson, 1996; Maryanska and Osmólska, 1997; Makovicky and Norell, 1998), and theropods and birds also share extensive postcranial pneumaticity (Britt *et al.*, 1998). Some of the nonpneumatic characters purportedly shared exclusively between very primitive birds and crocodylomorphs, such as similarities in the dentition, are also found in one or more dinosaurian lineages (*e.g.*, Currie, 1987; Norell and Makovicky, 1999a). In any case, simply listing features held in common between birds and crocodylomorphs, even if they are shared uniquely, is meaningless unless these features are considered in the context of all available information.

Other proposed nondinosaurian relatives

Given the difficulties of allying birds with “thecodonts” or crocodylomorphs, a number of individual genera have been suggested as putative relatives of birds. The best known of these is *Euparkeria*. Its proposal as a close avian relative is logical, given that it has been a source of much of the “thecodont” data, occurs in Triassic deposits predating *Archaeopteryx*, and is a basal, unspecialized archosauriform with few outward morphological peculiarities. This can be considered a special case of the “thecodont” hypothesis. Most recently, Welman (1995) proposed the sister-group relationship between *Euparkeria* and *Avialae*. However, the basicranial characters used by Welman (1995) to support a bird-*Euparkeria* clade have recently been challenged (Gower and Weber, 1998), and phylogenetic analysis suggests that *Euparkeria* lies outside the crown-group Archosauria in current optimal trees (Fig. 1; Sereno, 1991; Benton, 1999).

Feduccia (1999; see also Feduccia and Martin, 1998) and Ruben and Jones (2000) have suggested that the enigmatic reptile *Longisquama* from the late Triassic of Kirghizia may possess structures possibly intermediate between scales and feathers. The type material of *Longisquama* preserves, as natural molds, a plume of elon-

gate, featherlike features above the shoulder (Sharov, 1971) that have been interpreted as paired structures adapted for gliding (Haubold and Buffetaut, 1987). Based on molecular and developmental dissimilarities, Brush (1993, 1996, 2000) has argued that feathers may not be homologous to reptilian scales. If he is correct, the need for such an intermediate organism is weakened considerably and a nonavian organism with both feathers and scales becomes a more realistic and parsimonious model. Moreover, the elongate feather-like structures in *Longisquama* are preserved as impressions that are open to multiple interpretations, and one of us (C. A. Brochu, unpublished observation) believes they are solid structures forming a single midline row, and that similarities to feathers are minimal. Another argument in favor of a close relationship between *Longisquama* and birds is the purported presence of a furcula in both, but one of us (C. A. Brochu, unpublished observation) has examined part of the type specimen and is unconvinced that the U-shaped structure identified as a furcula is homologous with the clavicles of birds or other archosauromorphs. Finally, Sharov (1971) interprets its teeth as acrodont, a condition more suggestive of lepidosauromorph than archosauromorph affinities.

Different phylogenetic analyses place *Scleromochlus* from the Upper Triassic of Scotland within Archosauria (Benton, 1999), possibly as a close relative of pterosaurs (Sereno, 1991). Although Feduccia (1999) discounted an exclusive relationship between birds and *Scleromochlus* on the basis of limb morphology, he suggested that a combination of features derived from it together with *Longisquama* and the basal archosauromorph *Megalancosaurus* (see below) might provide the complex suite of features necessary for a hypothetical protobird. Unfortunately, a sister-group relationship for birds cannot be established with a hypothetical hybrid derived from a number of taxa for which no close phylogenetic relationship has been demonstrated.

Another basal archosauromorph that has received attention as a putative avian relative is *Megalancosaurus*. Feduccia and Wild (1993) proposed that the appendages

in *Megalancosaurus* were preadaptive for perching abilities, suggesting it as a possible avian ancestor. It also has a very thin scapular blade, much as in birds. Renesto (1994a) provided the most thorough description of the genus and supports an arboreal and scansorial functional interpretation. However, Padian and Chiappe (1998a) argued that the elongate neural spines and haemal arches of the tail should be interpreted as an aquatic adaptation. Renesto (1994a) anticipated this interpretation, focusing on what he believed to be similarities with extant chameleons. This led him to reconstruct the manus in a manner similar to that in *Chameleo*, although he admitted that the proposed orientation of the digits was only tentative.

Geist and Feduccia (2000) argued forcefully against Padian and Chiappe's (1998a) interpretation, interpreting *Megalancosaurus* as possessing a suite of features that suggest it as the best model for an avian precursor. They point to the digital morphology as appropriate to perching, and interpret the tail as being a relatively stiff, laterally compressed appendage useful as a rudder in gliding. Additionally, they propose that the tail was also prehensile as in certain extant primates. They note that this is an additional arboreal adaptation; and that, numerous extant primates use clinging and leaping travel in concert with parachuting strategies.

This mosaic of functional interpretations suffers from numerous flaws. (1) It is worth noting that the small Triassic reptile *Dolabrosaurus* has a tail and manual morphology similar to that in *Megalancosaurus*, and was interpreted by Berman and Reisz (1992) as aquatically adapted. This demonstrates the variety of alternative interpretations for such a morphology. We are not arguing that *Megalancosaurus* was aquatic, but functional interpretation of this taxon is ambiguous. (2) If an aquatic interpretation can be ruled out, and if the ventrally directed curvature of the tail in *Megalancosaurus* is real, such a tail would not be particularly useful as an elongate and stiffened rudder. Combining a stiff, rudder-like structure with the extreme specializations of a prehensile tail based on a primate model

proposes structures with mutually exclusive design features. (3) Using extant primates that engage in vertical clinging and leaping as a functional analog ignores the fact that no primate that employs a prehensile tail also glides or parachutes. Certain scansorial primates and scansorial rodents are known to use their elongate tails as rudders, but none engage in caudal prehension. (4) If the digital morphology of *Megalancosaurus* is considered adaptive for perching, the question as to why such adaptations are present in both the fore- and hindlimbs arises. If the ventral curvature of tail is real, then that, in concert with its extremely narrow scapulae, suggests that a more appropriate functional analog would be found in arboreal chameleons. However, the suite of functional adaptations present in chameleons is one that is fundamentally oriented to remaining arboreal as opposed to departing that niche for an aerial one. (5) *Megalancosaurus* is one of the few putative bird ancestors among basal saurians that has been included in a more global cladistic analysis or in the context of smaller taxonomic groupings. Three independent phylogenetic analyses (Renesto, 1994a; Merck, 1997; Dilkes, 1998) place *Megalancosaurus* very close to the base of Archosauromorpha (Fig. 1), but none consider it a viable close relative of birds. Although none of these analyses are as global as those of Gauthier (1986) or Padian and Chiappe (1998a) with respect to crown-group archosaurs, it must be remembered that *Megalancosaurus* is best considered together with other such drepanosaurids as *Drepanosaurus* (Pinna, 1986; Renesto, 1994b; Merck, 1997, Dilkes, 1998). When Drepanosauridae is taken as a whole, there exists no current alternative phylogenetic hypothesis of relationship that links *Megalancosaurus* and Aves in a sistergroup relationship.

One aspect shared by all of these putative bird relatives is the presence of one or a few outwardly birdlike characters. *Megalancosaurus* has grasping feet and a strap-like scapular blade, *Longisquama* has structures that resemble a furcula and feathers, and *Euparkeria* has cranial features found in birds. But we are faced with a problem—none of them shares *all* of these features.

Birds have grasping feet, thin scapular blades, furculae, feathers, and the cranial features found in *Euparkeria* (and other archosauriforms). No phylogenetic analysis has included *Longisquama*, largely because known material is not well preserved, but there is little reason *a priori* to expect a close relationship between *Longisquama* and *Megalanosaurus*, and discrete birdlike features are not *shared* between them. To use these taxa, we are forced to construct an amalgam “relative” that may bear no resemblance with any real animal, known or unknown.

However, we actually know of fossil animals that *share* large numbers of birdlike features, and which are known on the basis of phylogenetics to be close relatives of each other. The distribution of birdlike features in this group is arranged hierarchically. We call them theropod dinosaurs.

Dinosaurian hypothesis

The significant majority of systematists currently consider a theropod dinosaurian origin for birds to be the most reasonable and most parsimonious. That dinosaurs are close to the ancestry of birds was proposed as early as 1870 by T. H. Huxley. It was vaulted back into prominence by Ostrom's (1974, 1975*a, b*, 1976) documentation of detailed similarities between birds, specifically the Late Jurassic *Archaeopteryx*, and theropod dinosaurs, particularly *Deinonychus*. Ostrom's hypothesis has since been supported by a succession of phylogenetic analyses. To date, every comprehensive cladistic analysis including fossils as in-group taxa supports the hypothesis that birds are derived theropod dinosaurs (Thulborn, 1984; Gauthier, 1986; Gauthier *et al.*, 1988; Benton and Clark, 1988; Sereno, 1991, 1997, 1999; Holtz, 1994, 2000*a, b*; Novas, 1996; Chiappe *et al.*, 1998; Forster *et al.*, 1998; Makovicky and Sues, 1998; Ji *et al.*, 1998; Norell *et al.*, 2000). Although some of the above-mentioned studies disagree on minor details, the broad relationships appear stable, and a particular set of lineages—Dromaeosauridae, Troodontidae, and Oviraptorosauria—repeatedly appear close to the origin of birds (Fig. 1).

Extensive reviews of this body of work

have been published (*e.g.*, Padian and Chiappe, 1997, 1998*a*; Witmer, 1991), but we briefly discuss some details here. The most obvious similarities to a nonspecialist are in the foot and hindlimb—in all dinosaurs (including birds), the hindlimb projects ventrally from the hip and not laterally as in other reptiles; and in theropods, the foot is functionally tridactyl during locomotion, with the middle three toes supporting the animal's mass. Heilmann's (1926) initial reservations concerning theropod origins of birds were in part due to the perceived lack of a clavicle in dinosaurs. But clavicles are now known from a variety of nonavian dinosaurs, and a fused furcula is present in several nonavian theropods, including allosauroids and tyrannosaurids (Chure and Madsen, 1996; Makovicky and Currie, 1998). Gauthier (1986) and Padian and Chiappe (1997, 1998*a*) have demonstrated that the semilunate carpal of the avian and tetanuran theropod wrist are homologous (*contra* Feduccia, 1999). The caudally swept pubis and construction of the distal pubic foot unite maniraptoran theropods and birds (Norell and Makovicky, 1997, 1999*b*). Despite arguments to the contrary (Martin *et al.*, 1980; Martin and Stewart, 1985; Feduccia, 1996), McGowan (1985), Gauthier (1986), Sereno (1991), and Rieppel (1993) have demonstrated that the ascending process of the astragalus and the pretibial of birds are homologous.

One of the more contentious characters proposed for the close relation between theropods and birds is the interpretation of the digits of the manus. The hands and wrists of *Archaeopteryx* and maniraptoran theropods are extremely similar. Those who support theropod origins for birds interpret the remaining digits of theropods and primitive birds to be numbers I–III, based on the observed sequence of digit reduction and loss on current hypotheses of theropod phylogeny. Opponents of the theropod hypothesis however, regard the modern avian hand as retaining digits II–IV, based largely on developmental evidence (Burke and Feduccia, 1997). Although this debate has been cast as a dispute between paleontologists and developmental biologists, differences may be found among paleontologists (*e.g.*, Pa-

dian and Chiappe, 1998*a*, *versus* Martin, 1991) as well as among developmental biologists (*e.g.*, Hinchliffe, 1985 *versus* Shubin, 1991). Moreover, one study co-authored by a paleontologist and a developmental biologist (Gauthier and Wagner, 1998; Wagner and Gauthier, 1999) suggests that both patterns are “correct,” in that the fourth and fifth adult digits were lost during theropod phylogeny, but that a frame shift occurred at some point after the loss of the fourth adult digit, so that the digital precursors in the developing avian hand are homologous with II–IV in other amniotes. Frame shifts of this nature have been observed elsewhere within Tetrapoda (Shubin, 1991). New experimental approaches are expected to shed further light on this controversy in the future (*e.g.*, Nikbakht and McLachlan, 1999), but given the obvious difficulties of studying developmental processes in Mesozoic reptiles, the most telling data are still derived from the fossils themselves. Shubin (1994) and Padian and Chiappe (1998*a*) have provided compelling data that demonstrate the progressive loss of manual digits IV and V in the progression from basal archosaurs, through basal theropods, to derived maniraptorans.

Another putative problem with the dinosaurian origin of birds is the so-called “temporal paradox”—the first undisputed bird is Late Jurassic in age, but most hypothesized dinosaurian sister taxa make their first appearance in the Cretaceous (Hinchliffe, 1997; Hou *et al.*, 1996; Feduccia and Martin, 1998; Feduccia, 1999). This argument is flawed on both philosophical and empirical grounds, as discussed by Padian and Chiappe (1998*a, b*) and Brochu and Norell (2000*a, b*). It confuses the concepts of “sister taxon” and “ancestor”; no one is saying that birds are directly descended from dromaeosaurids or troodontids, so the absence of unambiguous dromaeosaurid or troodontid remains in the Jurassic (but see Jensen and Padian, 1989; Chure, 1994; Evans and Milner, 1995; Metcalf and Walker, 1995) means that the common ancestor of birds and nonavian theropods is in the Jurassic, with an unrecovered history for these nonavian lineages. That nonavian theropods “become more bird-

like” as one moves toward the end of the Cretaceous (*e.g.*, Feduccia 1999) simply reflects the imperfect preservation of older members of these lineages—Late Cretaceous dromaeosaurids look more birdlike than Early Cretaceous dromaeosaurids because more of the skeleton is known. And application of quantitative techniques to this problem shows that, numerically, trees in which birds are dinosaurs are favored by stratigraphy, as moving birds out of Dinosauria does not improve relative congruence and diminishes absolute congruence (Brochu and Norell, 2000*a, b*).

If birds are not dinosaurs, we would expect new fossils to bring birds unambiguously closer to another lineage. Yet, every new fossil found in recent years appears to confirm birds as sharing a sistergroup relationship with certain subsets of dinosaurs, specifically maniraptoran theropods. As the theropod origin of birds appears most parsimonious, Figure 1 provides an overview hypothesis of the phylogenetic relationships of amniotes from the base of the amniote radiation to primitive members of Aves.

PHYLOGENETIC PATTERNS VERSUS FUNCTIONAL SCENARIOS IN THE ORIGIN OF BIRDS AND FLIGHT

The cladogram shown in Fig. 1 is a statement about the origin of birds. It reveals the groups of extinct vertebrates most closely related to birds, whether we restrict the name “bird” to living feathered tetrapods or include anything with unambiguous feathers. But what about the origin of flight, or of the feathers that diagnose birds?

The immediate outgroups to Avialae are known from animals thought to have been terrestrial cursors. We cannot rule out the possibility that a dromaeosaurid could climb a tree, but none of them show obvious modifications specifically for arboreality. Some features necessary for avian flight appear among non-volant nonavian theropods (Gauthier, 1986; Gatesy, 1994; Padian and Chiappe, 1998*a*; Sereno, 1999; Garner *et al.*, 1999). From a strict reading of the cladogram, we can conclude that flight originated among small terrestrial theropods—the so-called “ground-up” model for flight origins, which has been advocated in sev-

eral incarnations by systematists for several decades (*e.g.*, Ostrom, 1976; Gauthier and Padian, 1985; Padian and Chiappe, 1998a; Burgers and Chiappe, 1999; Garner *et al.*, 1999) and dates back to the early 20th Century (Nopcsa, 1907). The ground-up scenario seems counterintuitive at first, but both phylogenetic and functional evidence are mounting to support its feasibility. Padian and Chiappe (1998a) extensively review the evidence and literature in support of this scenario, and more recent discussion can be found in Burgers and Chiappe (1999), Garner *et al.* (1999), and Earls (2000).

Cladograms are primarily statements about taxonomic hierarchy. Inferences of the origins of certain features, including functions and behaviors, are secondary. From this perspective, arguments against birds as derived dinosaurs confuse a primary hypothesis of relationship (birds as members of Dinosauria) and a secondary hypothesis of evolutionary process (bird flight evolving from ground-dwelling precursors), which may or may not be attached to a given cladogram.

The ground-up hypothesis appears counterintuitive at first—gliding would seem to be a natural intermediate step between simple jumping and flying, and gliding usually requires jumping or falling from an elevated perch. The most vocal critics of the dinosaurian hypothesis argue explicitly for the so-called “trees-down” model for the origin of flight (*e.g.*, Feduccia, 1999; Geist and Feduccia, 2000). According to this, the precursors of birds were small scansorial diapsids that leapt from one elevated point, such as a branch, to another. Selective pressure for an increased length of leap would have led to a gliding stage, followed by active flapping flight. But none of the putative dinosaurian outgroups to Avialae were demonstrably arboreal, and many were probably restricted to a life on the ground. Theropod dinosaurs are seen to exhibit too many terrestrial and cursorial adaptations to be avian precursors. Hence, because the cladogram does not fit a preconceived notion of what must have happened, something must be wrong with the cladogram. This line of reasoning, which effectively

uses prior knowledge of what happened to determine what happened, is circular.

The cursorial hypothesis, in its modern incarnation, is the simplest model for the origin of flight in the context of the preferred phylogenetic hypothesis. But is it a necessary corollary, as implied by some authors? We can infer the mechanism for the origin of flight from a phylogenetic tree, but this will always be a secondary inference. A strict reading of current cladograms does not necessarily reject a trees-down model of flight origins—the fossil record is incomplete, and one can always posit an unpreserved arboreal dinosaurian relative of birds. Additionally, rejection of a ground-up model for flight origins need not imply rejection of the dinosaurian hypothesis (Gauthier and Padian, 1985; Padian and Chiappe, 1998a), and some authors who derive birds from theropods explicitly prefer a trees-down model for flight origins (*e.g.*, Chatterjee, 1999). The origin of a group, the origin of a structure, and the origin of a behavior or function are fundamentally different questions, and a cladogram primarily addresses the first. Some authors find legitimate reason to prefer a less-parsimonious scenario for a give cladogram on the basis of some sort of external evidence (*e.g.*, Zaher and Rieppel, 1999).

One could argue that nonavian maniraptorans could climb, or that small arboreal theropods are yet to be discovered. Such a model would be much less parsimonious than the cursorial model, at least from the perspective of present phylogenetic understanding. It would require stages in the origin of flight not preserved in our current sample of extinct nonavian dinosaurs. The arboreal model is thus less parsimonious, but is not strictly falsified by the cladogram in Figure 1; an arboreal nonavian theropod may await discovery somewhere. The statement by Geist and Feduccia (2000) that clastic analyses posit that “avian flight *necessarily* developed within a terrestrial context” (our emphasis) reflects a misunderstanding of how cladograms are constructed and what they can actually falsify.

A point often missed by critics of the dinosaurian hypothesis is that none of the terminal taxa on the tree are directly ancestral

to birds. They belong to less and less inclusive groups, and the nodes uniting birds with them increasingly approximate animals ancestral to birds as we approach Avialae, but though birds are the direct descendants of theropod dinosaurs, they are not the direct descendants of dromaeosaurids, troodontids, allosauroids, or any other specific theropod terminal taxon on Figure 1. Attempts to “rule out” such animals as bird ancestors on biomechanical or physiological grounds (e.g., Geist and Feduccia, 2000) are *non sequitur*, since such animals are not bird ancestors in the first place.

FOSSIL FEATHERS

The cladogram in Figure 1 shows us what the fossil record currently says about the origin of birds—Aves is a very derived clade within Dinosauria. It also shows that a cursorial model of flight origins is favored by phylogeny, though as discussed above, one need not force the adoption of a cursorial model with the acceptance of a dinosaurian origin of birds. But what about the origin of feathers?

We can predict the character states for an incompletely-known taxon by referring to the conditions in better-known relatives. Given two well-characterized organisms, soft-tissue features and behaviors for fossils closer to one or the other can be reconstructed based on the optimized ancestral states for the clade as a whole (Witmer, 1995). However, this operation needs at least two anchor taxa—otherwise, one cannot constrain the smallest monophyletic group that a character may diagnose. As feathers occur in only one extant group (Aves), our capacity to predict the distribution of feathers in fossil nonavian reptiles is limited.

We can confidently predict that the extinct diving bird *Hesperornis* had feathers, as we know that the genus is ultimately descended from the last common ancestor of *Archaeopteryx* and extant birds. *Archaeopteryx* has well-developed primary flight feathers, and feathers in some form must have existed long before *Archaeopteryx*, but as long as *Archaeopteryx* is the basal-most animal known with feathers, we cannot plot the origin of the first feathers on

any cladogram. Most dinosaur skin impressions in the fossil record are from ornithischians and sauropodomorphs (Osborn, 1912; Sternberg, 1925; Horner, 1984; Martill, 1991; Czerkas, 1997), and imply unfeathered, scaly skin in these animals, but we would be forced to regard virtually any nonavian theropod as ambiguous with respect to feathers in the absence of fossil evidence.

Phylogenies also make predictions about future discoveries. As the plumage of *Archaeopteryx* includes full asymmetrical flight feathers on the forelimbs, it can be presumed that feathers had a long, unsampled history from the earliest examples to the derived forms seen in Avialae (Feduccia, 1999). Even without a phylogenetic bracket, a phylogenetic hypothesis lets us constrain the groups in which we might expect to find primitive feathers—we may not be able to rigorously constrain the smallest monophyletic group unambiguously sharing them, but we can at least reduce our speculations to the few clades immediately outside *Archaeopteryx* plus all other birds. If birds are more closely related to *Euparkeria* or Crocodylomorpha, we would predict the discovery of new fossil taxa closing the morphological gap between them and birds. On the other hand, the dinosaurian hypothesis would predict the continued discovery of new taxa corroborating current phylogenetic views. The dinosaurian hypothesis predicts feathers, or something like feathers, in derived nonavian maniraptorans and perhaps other theropod groups, while alternative hypotheses would place them on an as yet undiscovered arboreal nondinosaurian archosaur. A lower bound cannot be placed on the tree in this manner, but it gives us a place to start.

For years, *Archaeopteryx* was the earliest evidence of true feathers. All other fossil feathers postdated the Jurassic, and until recently, all were on unquestioned birds (e.g., Sanz *et al.*, 1997). Skin impressions have been published for very basal theropods, such as *Carnotaurus*, which had scaly, unfeathered skin (Bonaparte *et al.*, 1990). On this basis, we can optimize featherless skin for the earliest theropods (Fig. 1).

Dramatic finds from the Late Cretaceous

(approximately 120 million years old) Sihetun locality of the western part of Liaoning Province in the People's Republic of China are beginning to change this picture. Some fossils from this locality are members of Avialae (Hou *et al.*, 1996; Zhou and Hou, 1998; Chiappe *et al.*, 1999) and add to our understanding of early bird diversity and phylogeny, but others appear not to have achieved the structural grade of organization traditionally associated with birds. These include *Sinosauropteryx*, *Caudipteryx*, *Protarchaeopteryx*, *Beipiaosaurus*, and *Sinornithosaurus*. These are essentially feathered theropod dinosaurs.

The first announced was *Sinosauropteryx* (Ji and Ji, 1996; Chen *et al.*, 1998; Ji *et al.*, 1998), which preserves a halo of filamentous structures, the longest of which are 30 mm long. They are feather-like in that they are hollow and “resemble most closely the plumules of modern birds, having relatively short quills and long, filamentous barbs” (Chen *et al.*, 1998; p. 151). Currie (1997) also observed that the fibers are constructed of a central rachis and simple branching barbs. This morphology is consistent with the most parsimonious model available for the earliest protofeather (Brush, 2000). The structures cover the head, neck, tail, and parts of both the pectoral and pelvic limbs.

This fossil has significant phylogenetic implications, as *Sinosauropteryx* is probably a close relative of *Compsognathus*, a diminutive theropod from the Late Jurassic of Europe. *Compsognathus* is regarded as a relatively basal coelurosaur in different phylogenetic analyses (Gauthier, 1986; Holtz, 1996, 2000a, b; Sereno, 1999; Norell *et al.*, 2000). If these structures are feather precursors, we can assume that a filamentous covering of some sort was present in the last common ancestor of Avialae and *Compsognathus* (Fig. 1). Regardless of the position of these two closely related taxa, an obvious consequence is the effective removal of feathers as a synapomorphy of Aves. This is indicated by the thick line on the cladogram in Figure 1. This further predicts its presence, whether preserved or not, in any other theropod lineage descended from this ancestor, including dromaeosaurids, troodontids, oviraptorosaurs, and (de-

pending on the analysis) perhaps even ornithomimosaurs and tyrannosaurids. As more basal theropods appear to lack feathers, we can constrain the origin of feather precursors to a range of nodes at the base of Coelurosauria.

Does this mean that *Tyrannosaurus* was a feathered animal, as suggested in several popular accounts (*e.g.*, Appenzeller, 1999)? Possibly. More specifically, it means that, assuming Tyrannosauridae is ultimately descended from the last common ancestor of *Sinosauropteryx* and Avialae, it had filamentous dermal structures ancestrally. This is a prediction, not a conclusion. It is entirely possible that these structures were secondarily lost. Based on this same phylogenetic reasoning, we would predict the presence of fur on all whales—secondary loss is certainly not impossible. In the absence of definitive evidence, our phylogenetic prediction is the presence of feathers or something like them in tyrannosaurids.

Ruben and Jones (2000) have challenged the interpretations of these structures as feathers, suggesting instead that they are degraded internal collagenous structures along the midline. In fact, these structures are not restricted to the midline—they occur on the appendages (Chen *et al.* 1998) and do not follow the midline of the skull. The skull of *Sinosauropteryx* is not preserved in perfect anatomical orientation, but is rotated to the animal's right by a few degrees. The bedding plane—and hence the halo of fibers we see—intersects the left dorsolateral surface of the skull. We agree that testing these structures for the presence of keratin and absence of collagen would be informative; this kind of testing was performed for similar fibers from the alvarezsaurid *Shuvuuia*, demonstrating the presence of beta keratin and the absence of alpha keratin (Schweitzer *et al.*, 1999)—a pattern most consistent with feathers. But for now, we see little reason from external morphology to interpret the structures on *Sinosauropteryx* as internal midline structures.

Beipiaosaurus and *Sinornithosaurus* bear short fibers similar to those on *Sinosauropteryx*, but the structures on *Caudipteryx* and *Protarchaeopteryx* are unambiguous feath-

ers, with a central rachis and barbs. Unlike the primary feathers of *Archaeopteryx*, which are asymmetrical (like those of flying birds), the feathers of these animals are symmetrical. Preliminary analyses of *Caudipteryx* and *Protarchaeopteryx* placed these taxa outside the clade including *Archaeopteryx* and modern birds (Ji et al., 1998), but taxon sampling was limited. More complete analyses indicate that *Caudipteryx* is a close relative of oviraptorosaurs or possibly within Oviraptorosauria (Barsbold et al., 2000; Sereno, 1999; Norell et al., 2000). *Caudipteryx* includes a well-developed feather tail plume, which may be a general feature for oviraptorosaurs, based on the recent discovery of an oviraptorosaurian pygostyle (Barsbold et al., 2000). *Protarchaeopteryx* may be an avialian in the strictest sense, but still not descended from the last common ancestor of *Archaeopteryx* and living birds. *Beipiaosaurus* is a therezinosauroid, a bizarre group of theropods currently thought to be closely related either to Oviraptoridae (Sues, 1997; Makovicky and Sues, 1998) or Ornithomimosauria (Sereno, 1999); and *Sinornithosaurus* is a dromaeosaurid (Xu et al., 1999b).

The external dermal structures of *Protarchaeopteryx* and *Caudipteryx* are certainly feathers, but questions have been raised about whether these are dinosaurs at all, along with suggestions that they might be secondarily flightless birds (Geist and Feduccia, 2000; Ruben and Jones, 2000). These arguments are directed toward a preliminary analysis with modest taxon and character sampling, and only address the unambiguous synapomorphies for Avialae exclusive of *Caudipteryx* and *Protarchaeopteryx*. More comprehensive analyses strongly place these animals outside Avialae (Sereno, 1999; Norell et al., 2000). Data supporting the hypothesis that *Caudipteryx* and *Protarchaeopteryx* are birds have not been published, and it must be analyzed in the context of all other anatomical information.

Another potential problem is the purported preservation of unfeathered skin in very derived theropods. Czerkas (1997) reported unfeathered skin in a tyrannosaurid, but illustrations were not provided. Possible

external fibers were reported for a primitive ornithomimosaur by Perez-Moreno et al. (1994), but Briggs et al. (1997) disputed this claim; further work is needed on this specimen to resolve the issue, as it is not clear what the surface of this animal's skin would have been like. Other reports appear problematic at first, but are actually uninformative in the context of the present issue. In some of these cases, skin is not preserved at all, even though internal soft structures are present (Dal Sasso and Signore, 1998). In others, there are indications of wrinkled, unscaled skin over parts of the body (Kellner, 1996). The absence of dermal fibers in these specimens could mean one of two things—they were absent on those parts of the body preserved, or they were present and did not preserve. Feathers were not preserved in all known specimens of *Archaeopteryx*, so there is no *a priori* expectation that feathers or feather precursors must be present on a fossil if they were present on a living animal. And, if these truly represent unfeathered skin, they simply indicate reversals on the phylogeny in Figure 1.

SKIN, FEATHERS, AND FUNCTIONAL SPECULATION

In modern birds, feathers serve a vast number of functions. Primary wing feathers create the flight surface, thus allowing birds to fly. Down is one of the best insulation substances found within Animalia, and parent birds use feathers (along with their own body heat) to incubate eggs. Social signaling is very important to birds, for a variety of reasons, and combinations of plumage and call are central to this. Aquatic birds use feathers, along with the secretions of specialized oil glands, to keep their skin dry.

But what was the original function of feathers? Some workers emphasize the importance of flight in modern birds, and flight function has figured prominently in the origin of feathers literature (e.g., Heilmann, 1926; Pennycuick, 1986; Feduccia, 1999; Ruben and Jones, 2000). Others instead emphasize the thermoregulatory importance of feathers (e.g., Ostrom, 1974; Regal, 1975; Bock, 1986). But do the func-

tions of structures in the living necessarily constrain the functions in distant extinct ancestors? This is where phylogenetics steps in—if the most primitive feathers resemble flight feathers and are present on flying animals, flight is a plausible original use; otherwise, we must entertain alternative speculations.

Thus far, all known nonavian theropods were nonvolant animals. The phylogenetic distribution of probable feather precursors (Fig. 1) argues against the hypothesis that feathers were initially for flight: they seem to have appeared in bipedal ground-dwelling theropods, and any flight utility came later. The earliest precursors of feathers were clearly not flight structures—they were either short fibers (as in *Sinosauropteryx*) or symmetrical structures (as in *Protarchaeopteryx* and *Caudipteryx*). If flight was a primary driving force behind the origin of feathers, an enormous number of steps are missing from the fossil record—in fact, all of them up to *Archaeopteryx*. This does not falsify the hypothesis that feathers evolved primarily for flight, but renders it extremely unparsimonious. It requires a large number of reversals to flightlessness.

Insulation can control the thermal milieu of the body both by conserving heat and protecting the body from external sources to prevent overheating. But that feathers evolved first as insulatory structures has been disputed by those who argue against elevated metabolic rates in nonavian dinosaurs (e.g., Randolph, 1994; Ruben and Jones, 2000). A review of the literature on this debate is beyond the purview of this article, and readers should consult Padian (1997), Ruben (1995), and Horner *et al.* (1999) for more information; but if one rejects insulation as an early benefit derived from feathers, one cannot simply point to flight as the only remaining alternative; other possible functions can be considered, and the fossil record simply does not support flight as the initial purpose of feathers.

Display remains a viable primitive function; signaling could have been effected with pigmented patterning or, if primitive feathers were mobile as suggested by Hom-

berger (2000), through changes in body shape and proportion. Birds often use feathers to protect and incubate eggs, and at least some nonavian theropods are known to have exhibited very birdlike nesting behaviors (Clark *et al.*, 1999; Varricchio *et al.*, 1999). Frolich (1997) noted that feathers can provide a reasonable compromise between trauma protection and the need to reduce torque in the externalmost region of the body wall during cursorial locomotion; since most nonavian theropods lack the stiffening structures seen in the trunk of living volant birds, one might speculate that feathers had an early structural support function. Various uses in food capture have also been proposed (Ostrom, 1974; Thulborn and Hamley, 1985). These are speculations; we have no direct evidence for display behavior in nonavian theropods, and feathers were not preserved with the nesting theropods.

CONCLUSIONS

Current phylogenetic work strongly indicates that birds are members of Dinosauria. It also supports a ground-up model for the origin of flight and suggests that the earliest function of feathers was not locomotory. Alternative scenarios—deriving flight from arboreal ancestors or early flight utility in feathers—are not falsified, but they are extremely unparsimonious. Future discoveries may overturn the currently-accepted evolutionary pattern and point toward a different scenario for the origins of feathers and flight, but over the past decade, every discovery made in Mesozoic units around the world bolsters the dinosaurian nature of birds and the non-volant origin of feathers.

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