

# The Debate on Avian Ancestry

## Phylogeny, Function, and Fossils

LAWRENCE M. WITMER



Ever since the time of Huxley (1868), the debate on the place of birds within vertebrate phylogeny has been one of the highest-profile and hotly contested of all evolutionary debates. What makes the origin of birds so contentious? Why can we not agree and then move on to other issues? Will we ever regard the problem as solved? It would seem that establishing the ancestry of birds would be a relatively simple, empirical task, but, despite abundant data, the debate rages like never before. I previously published a fairly exhaustive review of the history of the controversy (Witmer, 1991), which has been updated and expanded by Feduccia (1996, 1999b) and Padian and Chiappe (1998b). Rather than repeat the historical chronicle, this chapter seeks to explore the impact of more recent developments on the debate and also to touch on the allied debate on the origin of avian flight. At the time of completing my previous review, it is fair to say that the theropod hypothesis was the most widely held notion, and other ideas (e.g., basal archosaurs, crocodylomorphs) were on the decline. There simply was little substantial opposition to birds being dinosaurs.

In the intervening years, however, a great deal has happened. *Protoavis texensis* moved from the popular arena to the scientific arena with the publication of Sankar Chatterjee's 1991 monograph (see also Chatterjee, 1995, 1997a, 1998b, 1999; Witmer, 2001b). Alick Walker (1990) published a large monograph on *Sphenosuchus acutus* in which he renewed his support for the relationships of birds to crocodylomorphs. Relationships of the basal archosauriform *Euparkeria capensis*, previously little more than a historical footnote, resurfaced in a paper by Johann Welman (1995; but see Gower and Weber, 1998). Various conferences provided a forum for discussion of new hypotheses and perspectives, such as the 1994 meeting of the International Ornithological Congress in Vienna (Bock and Bühler, 1995) and the 1992, 1996, and 2000 meetings of the Society of

Avian Paleontology and Evolution in Frankfurt (Peters, 1995), Washington (Olson, 1999), and Beijing (Shi and Zhang, 2000), respectively. The late 1990s saw the publication of two important and high-profile reviews of early avian evolution in the science weeklies (Chiappe, 1995; Feduccia, 1995), a seminal and wide-ranging review (Padian and Chiappe, 1998b), a major symposium with subsequent volume (Gauthier and Gall, 2001), and a host of books directed toward a broader audience (Feduccia, 1996, 1999b; Chatterjee, 1997a; Dingus and Rowe, 1997; Shipman, 1997a; Paul, 2002).

Most important, however, are the many newly discovered testaments of the avian transition coming from the fossil record. For example, as documented in this volume, many new fossil birds relevant to avian origins have recently been described, primarily from Spain, China, Argentina, Madagascar, and Mongolia, and, from Germany, even new specimens of *Archaeopteryx*. Likewise, a number of new birdlike theropods have come to light, such as *Sinornithoides youngi* (Russell and Dong, 1993), *Unenlagia comahuensis* (Novas and Puerta, 1997), *Sinornithosaurus millenii* (Xu et al., 1999b), *Caudipteryx zoui* (Ji et al., 1998), *Bambiraptor feinbergi* (Burnham et al., 2000), *Nomingia gobiensis* (Barsbold et al., 2000a,b), *Sinovenator changii* (Xu et al., 2002), and *Microraptor zhaoianus* (Xu et al., 2000), as well as important new specimens of previously known taxa such as *Troodon formosus* (Currie and Zhao, 1993), *Deinonychus antirrhopus* (Witmer and Maxwell, 1996; Brinkman et al., 1998), *Velociraptor mongoliensis* (Norell and Makovicky, 1997, 1999; Norell et al., 1997), oviraptorids (Clark et al., 1999), and ornithomimosaurs (Pérez-Moreno et al., 1994; Makovicky and Norell, 1998; Norell et al., 2001), among others.

The debate heated up considerably with the publication in 1996 of Alan Feduccia's *The Origin and Evolution of Birds*. In this book, Feduccia launched a vehement attack on the prevailing consensus that birds are nested within Thero-

poda, opening the door to other studies purporting to cast doubt on the theropod relationships of birds (e.g., Burke and Feduccia, 1997; Ruben et al., 1997; Feduccia and Martin, 1998; Martin, 1998; see also Thomas and Garner, 1998). Some of the scientific points discussed by Feduccia and his colleagues will be taken up in this chapter, but it is worthwhile to examine briefly the tone the debate has taken and direction to which it has turned because they cannot help affecting the science. The initial response to the volume (e.g., Norell and Chiappe, 1996; Padian, 1997) was highly critical of Feduccia's apparent disregard for the recent cladistic analyses that argue for the theropod relationships of birds, although several later reviews were either mixed (Serenó, 1997a; Witmer, 1997b; Steadman, 1998) or highly favorable (Bock, 1997; Mayr, 1997; Ruben, 1997). The popular press was quick to provide an opportunity for the players to voice strong opinions. Among the many barbs slung back and forth to reporters were "paleobabble," "total garbage," "pure Fantasyland," "the greatest embarrassment of palaeontology of the 20th century," "absurdity," "poisoning his own discipline," "as impervious to evidence as the fundamentalists," "beyond ridiculous," "just hot air," "bombastic rhetoric and armwaving," "like taking candy from a baby," and "that's always the problem, these paleontologists just don't know birds." In order not to further the ad hominem tone of the discourse, these remarks will remain unattributed here, but the reader may consult McDonald (1996), Zalewski (1996), DiSilvestro (1997), Morell (1997), and Shipman (1997b). Clearly, the vituperative and combative turn that the debate has taken is likely to do little to advance the science—bombast is a poor substitute for evidence.

Perhaps a more important question is, Why is the origin of birds so important that professional scientists would make such strong public statements? In other words, what is the larger meaning of the debate? It is impossible to escape the fact that, as with any form of human endeavor, personalities may collide (and the media will be there with a microphone). But the *scientific* stakes really are quite high, and for at least two reasons: crownward inferences and stemward inferences. First, the origin of birds is critical if we are to gain a deeper understanding of birds themselves. Establishing the phylogenetic relationships of Aves is the logical first step in a wide variety of inferences such as the evolution of flight, feathers, metabolism, and various ecological and physiological parameters. All these attributes have a phylogenetic history, and thus we must know what came before birds in order to truly comprehend birds. If we are interested in, say, tracing the evolution of avian craniofacial kinesis, it makes a great difference whether birds are viewed as being derived from theropod dinosaurs (Chatterjee, 1991) or from crocodylomorphs (Walker, 1972).

Second, there is a sense that if we can sort out the origin of birds, we will *automatically* know a great deal about the

biology of their antecedents. For example, if birds are descended from theropod dinosaurs, then we might feel justified in reconstructing nonavian theropods with a whole suite of avian attributes, from feathers and endothermy (Paul, 1991) to reproductive biology (Varricchio et al., 1997; Clark et al., 1999) and locomotor attributes (Gatesy, 1990; Gatesy and Dial, 1996a). Indeed, there may be compelling reasons to do so, and, according to the inferential hierarchy of Witmer (1995a), these might be reasonable level II inferences. If the prevailing orthodoxy is correct, then all dinosaurs are *not* extinct, and we thus have the potential to say a lot about even the extinct clades of dinosaurs. If, however, birds have no close relationship with dinosaurs, then all of a sudden dinosaurs seem more remote, less familiar, and perhaps even less interesting. Feduccia correctly noted that the theropod hypothesis provides "a mechanism by which you can vicariously study dinosaurs by stepping into your backyard. There's a real emotional investment here" (quoted in Zalewski, 1996:24). In fact, for studies that employ the extant phylogenetic bracket approach to make inferences about extinct archosaurs (e.g., Witmer, 1995a,b, 1997a, 2001a; Rowe, 2000; Hutchinson, 2001a,b), it is particularly fortunate and useful for birds to be dinosaurs because then extant birds and crocodylians together bracket a huge diversity of archosaurs. If birds are instead more closely related to, say, crocodylomorphs, then our inferential base with regard to other archosaurs is weakened significantly. Thus, resolution of the problem is critical for studies not just of birds and theropods but really of all archosaurs.

This chapter examines a variety of issues surrounding the debate. In all cases, the goal is to discover how that particular issue relates and contributes to the *resolution* of the question of avian origins. The next section takes up the central role that *Archaeopteryx* has played in the debate, and the following section briefly examines the controversial taxon *Protoavis*. The discovery of an incredible fossil deposit in China holds great importance for understanding avian origins and is discussed here. The relationship of the origin of flight to the origin of birds, which has reemerged as a critical topic with the publication of Feduccia's 1996 book, will then be taken up. The question of alternatives to theropod dinosaurs will then be explored, followed by an assessment of the status of the theropod hypothesis itself.

## The Centrality of *Archaeopteryx* in the Debate

The first sentence of the abstract of John H. Ostrom's 1976 landmark paper states: "The question of the origin of birds can be equated with the origin of *Archaeopteryx*, the oldest known bird" (Ostrom, 1976:91). This statement reflects a very common sentiment, with, for example, Martin (1991: 485) regarding *Archaeopteryx* as occupying "the center stage" and Feduccia (1996:29) calling it an "avian Rosetta

Stone.” Certainly, virtually all the ancillary issues surrounding avian origins—from the origin of flight (Padian, 1985; Rayner, 1991; Feduccia, 1993, 1996; Herzog, 1993; Gatesy and Dial, 1996b) to feathers (Parkes, 1966; Dyck, 1985; Griffiths, 1996), endothermy (Ruben, 1995, 1996), and others—either take *Archaeopteryx* as their starting point or use it as the ruler against which particular scenarios are measured. A high-profile international meeting was devoted entirely to *Archaeopteryx*, and, as the editors of the subsequent volume noted (Hecht et al., 1985:7), it probably was “the first time that a scientific conference was devoted to a single fossil species.” Martin (1995:33) is no doubt correct in noting that “there are probably more individuals who have worked on *Archaeopteryx* than all other palaeornithologists put together.”

But *Archaeopteryx* is more than a series of scientific specimens (see Elzanowski, Chapter 6 in this volume). *Archaeopteryx* has reached iconic status, partly because of the beauty of the specimens and partly because they have been important and prominent documents in establishing the fact of organic evolution; certainly creationists have regarded *Archaeopteryx* as a serious challenge (e.g., Cousins, 1973). *Archaeopteryx* is a celebrity. A respected scientific periodical bears its name. It is the logo for museums and graces the covers of numerous books and magazines. As a fossil celebrity, *Archaeopteryx* is more similar to *Australopithecus* in inspiring a sense of respectful awe and reverence than to “pop favorites” like *Tyrannosaurus*. It is indisputable that *Archaeopteryx* has historically been the central focus of virtually all studies on the origin and early evolution of birds, and this is likely to continue for the foreseeable future.

The obvious next question is: Is this reliance—perhaps even overreliance—on *Archaeopteryx* justified and wise? The avian status of *Archaeopteryx* is often an unquestioned assumption of many analyses, and in some phylogenetic studies (e.g., Padian, 1982; Holtz, 1994; Weishampel and Jianu, 1996), *Archaeopteryx* alone stands as a proxy, in a sense, for all birds. The concern obviously is that if we have hung all our conclusions about avian evolution on a fossil that is peripheral to avian origins, then much of the research for the past century may have been misguided (Witmer, 1999). The stakes could not be higher. Looking carefully back over the history of this debate reveals a small but continuous thread of dissent (see Witmer, 1991). P. R. Lowe (1935, 1944), for example, considered *Archaeopteryx* to be too specialized to be ancestral to later birds. Moreover, he went so far as to claim that *Archaeopteryx* “represented the culminating attempt of the reptiles toward flight, that is to say, it was a flying dinosaur. This, of course, implies a belief in the diphyletic origin of feathers—a zoological transgression for which I expect no mercy” (Lowe, 1935: 408–409). Lowe (1935:409) denied any features that were “definitely avian as opposed to dinosaurian,” and he spent much of the 1944 paper attempting to refute the most bird-

like characters (e.g., the boomerang-shaped element could not be a furcula because *Hesperornis*, *Palaelodus*, and embryonic birds have unfused clavicles). Lowe’s views on avian origins were complex and somewhat idiosyncratic (Witmer, 1991) and were refuted to most people’s satisfaction by Simpson (1946) and de Beer (1954, 1956).

Although it is tempting to marginalize Lowe’s views because they were expressed so long ago, a number of modern workers have questioned the avian status of *Archaeopteryx*. For example, in a series of papers from 1975 to 1984, R. A. Thulborn moved progressively closer to the conclusion that *Archaeopteryx* was a theropod dinosaur of no particularly close relationship to birds (Thulborn, 1975, 1984; Thulborn and Hamley, 1982); his 1984 paper presented a cladogram in which tyrannosaurids, an ornithomimosaur-troodontid clade, and *Avimimus* were closer to birds than was *Archaeopteryx*. He denied virtually all characters that unite *Archaeopteryx* with true birds to the exclusion of other theropod groups, noting that furculae were present in a variety of theropods and that the presence of feathers in *Archaeopteryx* “probably signifies nothing more than a rare circumstance of preservation” (Thulborn, 1984:145). Thus, for Thulborn (1984:151), “*Archaeopteryx* is not a convincing ‘intermediate’ between reptiles and birds, nor is it an ancestral bird” because there are other theropods even more birdlike than *Archaeopteryx*. Likewise, Kurzanov (1985, 1987) was so struck by the birdlike features of the Cretaceous theropod *Avimimus portentosus* (see also Vickers-Rich, Chiappe, and Kurzanov, Chapter 3 in this volume)—not least of which was the inference of feathered forelimbs—that he regarded the supposed avian features of *Archaeopteryx* as insufficient evidence to establish it as a true bird.

A similar theme was elaborated somewhat earlier by the Mongolian paleontologist Barsbold Rinschen, who articulated a notion that has major implications for the interpretation of the avian attributes of not just *Archaeopteryx* but really all theropods. Barsbold’s (1983) concept of “ornithization” in theropod evolution suggests that various lineages of theropods independently evolved birdlike attributes but with no clade possessing the entire suite of avian apomorphies. Thus, *Archaeopteryx* is seen by Barsbold (1983) as potentially just one of several parallel, “ornithized” lineages, “aberrant” in and of itself yet otherwise showing the underlying affinity of birds and theropods. In fact, it was conceivable to Barsbold (1983) that perhaps more than one group of “ornithized” theropods crossed the line into “birds” and that neornithine birds may actually be diphyletic (reminiscent of Lowe) or even polyphyletic. It is not clear what kind of evolutionary process Barsbold envisioned that would produce the recurrent evolution of avian features, but the fact that avian features have arisen repeatedly and independently in theropod evolution now seems to be an inescapable conclusion.

The preceding discussion, of course, begs the question of just what is a bird: How do we recognize birds? How do we define them in both a scientific and a colloquial sense? The foregoing has presumed a more colloquial sense of birds, that is, a sense of “birds” being feathered vertebrates that fly or had flight in their ancestry. This idea generally works in the modern time plane but breaks down when evaluated over the fossil record of theropods because the attributes of extant birds were acquired sequentially. Thus, there is no sharp line demarcating bird and nonbird—the distinction has become entirely arbitrary. Defining taxa has emerged as a major focus for phylogenetic taxonomists, and *Archaeopteryx* in relation to the definition of “Aves” and “birds” has likewise become a central test case (see Gauthier, 1986; de Queiroz and Gauthier, 1990, 1992; Padian and Chiappe 1998b; Sereno, 1998, 1999b; Padian et al., 1999; see also Clark, Norell, and Makovicky, Chapter 2 in this volume). The issues surrounding this matter are lengthy and complex, and they have been well discussed in the references just cited.

Traditionally, *Archaeopteryx* has been regarded as both a bird and a member of Aves. For example, Richard Owen, in his 1863 description of the London specimen, “declare[d] it unequivocally to be a Bird, with rare peculiarities indicative of a distinct order in that class” (Owen, 1863:46). Likewise, Haeckel (1866, 1876), Huxley (1867), and other early taxonomists referred *Archaeopteryx* and other Mesozoic birds to Aves. All modern ornithology texts regard *Archaeopteryx* as within their purview. This traditional sense can be captured by modern phylogenetic taxonomy by defining the name “Aves” using a node-based definition: *Archaeopteryx*, Neornithes (“modern birds”), and all descendants of their most recent common ancestor (see Chiappe, 1992, 1997; Padian and Chiappe, 1998b; Sereno, 1998, 1999b; Padian et al., 1999). The colloquial term “birds” is usually applied to this same group. These definitions of Aves and birds are the ones adopted generally for this volume. However, an alternative nomenclature pioneered by Gauthier (1986) advocates a crown-group definition for Aves that encompasses just the clades of living birds: ratites, tinamous, neognaths, and all descendants of their common ancestor. Gauthier (1986) defined the term “Avialae” as more or less equivalent to the traditionally conceived Aves, yet he applied the colloquial term “birds” to Avialae. The Avialae convention has seen a fair amount of use, and with good reason (see Clark, Norell, and Makovicky, Chapter 2 in this volume). Nevertheless, at this writing, preferences seem to be tending toward the Aves convention adopted here (see Padian and Chiappe, 1998b; Sereno, 1998; and Padian et al., 1999, for justification). Interestingly, Padian et al. (1999) retained the term “Avialae” but redefined it as a stem-based taxon comprising Neornithes and all taxa closer to them than to the dromaeosaurid *Deinonychus*. Thus, if we regard the terms “Aves” and “birds” as being more or less synonymous, then *Archaeopteryx* is a

bird, because we have defined it as such, as a member of the clade Aves.

Nevertheless, nomenclature aside, given the number of birdlike theropods and theropodlike birds, what is it about *Archaeopteryx* that leads us to conclude that it is truly a bird (i.e., by definition part of Aves) and thus worthy of all the attention? Long before the recent flurry of discoveries, workers recognized that *Archaeopteryx* possessed few uniquely avian characters that, in modern parlance, would contribute to a diagnosis of Aves (see Owen, 1863; Heilmann, 1926). For example, de Beer (1954:44) listed only four “features which differ completely from the condition in reptiles and agree with that of modern birds”: (1) a retroverted pubis, (2) a furcula, (3) an opposable hallux, and (4) feathers. Of these, a pubis with at least some measure of apomorphic retroversion is now well documented for dromaeosaurids, basal troodontids, and therizinosauroids (Barsbold, 1979; Barsbold and Perle, 1979, 1980; Norell and Makovicky, 1997, 1999; Rasskin-Gutman, 1997; Xu et al., 2002), and furculae are turning out to be very widely distributed indeed among theropods (Barsbold, 1983; Bryant and Russell, 1993; Chure and Madsen, 1996; Norell et al., 1997; Dal Sasso and Signore, 1998; Ji et al., 1998; Makovicky and Currie, 1998; Norell and Makovicky, 1999; Xu et al., 1999a). Although the opposable hallux may still stand as an avian apomorphy (Gauthier, 1986; Chiappe, 1995; Feduccia, 1996; Sereno, 1997b; Forster et al., 1998), it is, of course, the presence of feathers that, since its discovery in 1861, has garnered for *Archaeopteryx* a seemingly unshakable position within Aves. However, even the uniqueness of feathers to birds was cast into doubt in 1996 with reports of non-avian theropod dinosaurs with feathers or featherlike filamentous structures from Liaoning, China (Ji and Ji, 1996, 1997 [see also Gibbons, 1996, 1997a, reporting on the work of Ji and Ji]; Currie, 1997; Chen et al., 1998; Ji et al., 1998; Xu et al., 1999a,b). Although the true identity of the filamentous structures has been called into question (Brush et al., 1997; Geist et al., 1997; Gibbons, 1997b) and has been highly controversial, the reports fueled the persistent speculation, if not expectation, that feathers might have been present in taxa outside birds (Gauthier, 1986; Paul, 1991). The startling announcement in 1998 (Ackerman, 1998; Currie, 1998; Ji et al., 1998) of nonavian dinosaurs with indisputable feathers truly has shaken the foundations of just what it takes to recognize something as a bird (Padian, 1998). The importance of feathered dinosaurs is taken up in a later section.

Without the uniqueness of opisthophy, furcula, and even feathers, is there any basis for uniting *Archaeopteryx* with birds to the exclusion of other archosaurian taxa? Definitions can be constructed to suit personal tastes, and, regardless of whether one defines Aves to exclude (Gauthier, 1986) or include (Chiappe, 1992) *Archaeopteryx*, it is rele-

vant to ask just what features suggest that *Archaeopteryx* is the outgroup to less controversial birds. As it turns out, there are many such features. In addition to the reflexed hallux, other oft cited synapomorphies (see also Elzanowski, Chapter 6 in this volume) include (1) an elongate premaxilla (Gauthier, 1986; Sereno, 1997b); (2) the breaking down of the postorbital bar (Chatterjee, 1991, 1997a; Sanz et al., 1997; Sereno, 1997b); (3) the absence of dental serrations and the presence in the teeth of a characteristic constriction (Martin et al., 1980; Gauthier, 1986; Chiappe, 1995; Chiappe et al., 1996); (4) the enlargement of the cranial cavity (Gauthier, 1986; Chatterjee, 1997a); (5) the caudal tympanic recess opening within the columellar recess (Witmer and Weishampel, 1993; Chiappe et al., 1996); (6) the presence of a caudal maxillary sinus (Witmer, 1990; Chiappe et al., 1996; Chatterjee, 1997a); (7) fewer tail vertebrae, with the prezygapophyses reduced distally (Gauthier, 1986; Chiappe, 1995; Chiappe et al., 1996; Chatterjee, 1997a; Sereno, 1997b; Forster et al., 1998); and (8) various modifications of the shoulder girdle (Gauthier, 1986; Feduccia, 1996; Chatterjee, 1997a), although some of the shoulder characters may have a broader distribution (Novas and Puerta, 1997; Forster et al., 1998; Norell and Makovicky, 1999; Xu et al., 1999b, 2002).

Some of the foregoing characters may seem a bit subtle, even trifling, but such is the nature of any phylogenetic transition as it becomes better and better known. In fact, we should *predict* that the number of characters per node should decrease (and that the characters themselves may well seem more trivial) as sampling of the fossil record improves. What is remarkable is that so many characters do affirm the avian status of *Archaeopteryx*, thus providing ample justification for the sharp focus placed on *Archaeopteryx*. Although many of the characters listed previously are far from “clean,” with homoplasy and missing data complicating the picture such that Chiappe (Chapter 20 in this volume) found only three unambiguous synapomorphies for the node *Aves*, *Archaeopteryx* is indeed avian. Moreover, it has very few autapomorphies (Gauthier, 1986; Chatterjee, 1991; Sereno, 1997b) and thus, in a strictly phylogenetic sense, may legitimately serve as a model for an avian ancestor.

However, there is a danger here. Even if *Archaeopteryx* is the best available *model* for an ancestral bird, the worry is that we might come to regard it as *truly* the first bird. Even the German common name for *Archaeopteryx*—Urvogel—carries this sense of being the very first bird. But *Archaeopteryx* had an evolutionary history, and, as with any organism, its phylogenetic heritage has an impact on not only its form and function but also our *interpretation* of its form and function. Thus, although *Archaeopteryx* may be our best and oldest evidence for, say, feathers, there is no guarantee that *Archaeopteryx* gives us any *direct* glimpse into the origin of feathers and flight because both pre-

sumably predate *Archaeopteryx* by perhaps millions of years. For example, whether or not there were trees in the Solnhofen landscape suitable for *Archaeopteryx* to perch upon (Peters and GÖrgner, 1992; Feduccia, 1993, 1996; Padian and Chiappe, 1998a,b) bears little relevance for the arboreal versus cursorial origin of flight. On the one hand, the presence of Solnhofen trees would not automatically mean that *Archaeopteryx* either used them or evolved from an arboreal ancestor. On the other hand, the absence of Solnhofen trees would not dictate that flight arose in a terrestrial context, because *Archaeopteryx* could well have evolved from fully arboreal ancestors and apomorphically became terrestrial or just visited Solnhofen seasonally. We can never know these things. The point here is that we have tended to run all hypotheses through the filter of *Archaeopteryx*, almost as if we believed that it was truly the *first* bird, not just the *oldest known* or *most basal* bird.

The historical centrality of *Archaeopteryx* in the debate is quite understandable given that, until very recently, it was all we had—that is, it provided the only solid evidential basis for hypothesis testing. Although most analyses continue to support the basalmost avian position for *Archaeopteryx*, recent discoveries of Cretaceous birds and bird-like theropods have considerably lightened the load that *Archaeopteryx* must bear in teasing apart the details of early avian evolution (see discussion in Witmer, 1999). From *Unenlagia*, *Rahonavis*, and *Microraptor* to *Confuciusornis*, *Sinornis*, and *Concornis*, new finds are documenting the details of both the phylogenetic and functional transition to birds. *Archaeopteryx* will always merit a special place in the minds (and hearts) of scientists and the public in general. Only recently, however, could *Archaeopteryx* assume its proper role in the drama of the avian transition as one of a number of important players in an ensemble cast.

### The Significance of *Protoavis*

A particularly difficult question is whether this ensemble cast should rightly include the Texas fossils known as *P. texensis*. These fossils, whose discovery was announced only in 1986, have had a troubled and controversial history. In a long series of published works, Sankar Chatterjee (1987, 1988, 1991, 1995, 1997a, 1998b, 1999) argued that the *Protoavis* fossils are not only those of a bird but from a bird that lived 75 million years before *Archaeopteryx*! The fossils are generally attributed to two individuals excavated from the Early Norian Cooper Member of the Dockum Group of western Texas (Chatterjee, 1991), although other material from a different formation and county also was later referred to *P. texensis* (Chatterjee, 1995, 1997a, 1999; justification for this referral has not been presented, and I will not consider that material here). Although the report of any new Mesozoic bird is greeted with great interest, the reception of *Protoavis*

was unique, largely because of the implications that a Triassic bird holds. Perhaps surprisingly, despite the great age of the fossils, Chatterjee has never argued for any major changes in the general notion of avian ancestry from dromaeosaurlike coelurosaurian dinosaurs; in other words, *Archaeopteryx* remains the basal bird, and the Ostrom/Gauthier hypothesis of theropod relationships is not challenged. The irony that emerges is that *Protoavis* perhaps should have relatively little relevance for the origin of birds in that, according to Chatterjee's cladograms, *Protoavis* is nested well within Aves.

Skepticism about the avian status of *Protoavis* was immediate and did not necessarily follow along lines of allegiance to any particular theory of avian origins. For example, Feduccia (1996) and Martin (1998), on the one hand, and Ostrom (1987, 1991, 1996), Wellnhofer (1992, 1994), Chiappe (1995, 1998), and Sereno (1997b, 1999a), on the other hand, have all expressed doubt that the fossils of *Protoavis* are adequate to substantiate the claim of a Triassic bird. At the same time, Chatterjee has had some supporters, including Peters (1994), Kurochkin (1995), and Bock (1997, 1999). Why the controversy? A fuller critical appraisal of the status of *Protoavis* is presented elsewhere (Witmer, 2001), but a brief analysis is presented here.

Detractors of *Protoavis* have raised a variety of complaints, the most important of which relate to the taphonomy of the specimens and their preservation and preparation. With regard to the taphonomy, there is a widespread concern that *P. texensis* is a chimera, that is, a mixture of more than one species. Indeed, the quarry from which the specimens derive is a multispecific bonebed that has recorded many taxa (Chatterjee, 1985), and thus mixing is a possibility, as has already been suggested for other taxa from the same quarry (e.g., *Postosuchus kirpatricki*; Long and Murry, 1995). Chatterjee (1991, 1998b) has steadfastly maintained the association of the holotype and paratype skeletons of *Protoavis*, and Kurochkin (1995) offered his support based on his study of the original material. Nevertheless, the specimens were collected inadvertently while removing overburden with a jackhammer, and hence we can never be completely sure of the taphonomic setting. The possibility that *Protoavis* is a composite of several species is commonly voiced but, even if true, does not rule out the chance that some of the included bones are avian (Witmer, 1997c). However, as Chiappe (1998) correctly pointed out, the chimera problem presents itself most insidiously during phylogenetic analysis, the ultimate arbiter of avian origins, in that the mixture of taxa means a mixture of characters, all of which leads to phylogenetic nonsense. Thus, the taphonomic question—Is *Protoavis* a species or a fauna?—is a critical one, and one that is not likely to go away until new material is discovered.

And, according to many of those who have studied the specimens, new material is needed desperately. In other

words, a major concern has been that the *Protoavis* specimens are simply too poorly preserved, too scrappy, to be diagnostic. Unlike *Archaeopteryx* and the Cretaceous birds from Spain and China, *Protoavis* is not a “slab animal”; that is, it is not preserved in situ, but rather all the bones have been prepared free of the matrix. Thus, without the aid of the positional information that slab animals preserve, the identification of isolated elements is difficult and can lead to widely different interpretations. The other side of this coin is that all sides of the elements are available for study rather than being half entombed in stone, as is the case for slab birds such as *Archaeopteryx*. Nevertheless, it has been difficult to confirm not only many of the structures but even some of the bone identifications made by Chatterjee (Witmer, 2001b). Perhaps Padian and Chiappe (1998b:13) best characterized the situation by noting that the “material has become a paleontological Rorschach test of one's training, theoretical bias, and predisposition.” Coupled with this is the problem that the specimens are extensively reconstructed with plaster and epoxy, and it often seems that the published descriptions are of these reconstructed composites rather than of the fossils themselves.

But ultimately—even given the gravity of these and other concerns—it comes down to the fossils and their structures. Are there clearly interpretable anatomical clues revealing the phylogenetic relationships of the beast? Again, a more comprehensive skeletal analysis is presented elsewhere (Witmer, 2001b), but it is worthwhile to examine here a few of the more important anatomical systems. For Chatterjee (1991, 1995, 1997a, 1998b), the skull, particularly the temporal region, is the most critical, because he regarded *Protoavis* as possessing the ornithurine condition: that is, loss of the postorbital bone, leading to confluence of the orbit, dorso-temporal fenestra, and latero-temporal fenestra. Given that *Archaeopteryx*, *Confuciusornis sanctus* (Peters and Ji, 1998; Chiappe et al., 1999; Hou et al., 1999), and at least some enantiornithines (e.g., the Catalan hatchling, Sanz et al., 1997; *Protopteryx fengningensis*, Zhang and Zhou, 2000) retain both the postorbital bone and its contact with the squamosal, presence of the advanced ornithurine condition in *Protoavis* indeed would be highly significant and would, in fact, argue for a higher phylogenetic position within birds than that advocated by Chatterjee (1998b). Unfortunately, the temporal region of the holotype skull has been assembled from disarticulated pieces, and thus the identity and positions of elements are not certain. The most telling clues are found in the squamosal and quadrate; the absence of the postorbital is negative evidence and hence hard to evaluate. The squamosal identification is key, because the element would lack an articular surface for the postorbital, which implies absence of the postorbital bone itself. Similarly, the putative quadrates are important, because they would be drastically modified along the lines of

birds, presumably, according to Chatterjee, in association with avian craniofacial kinesis. The squamosal identification is defensible in that the element in question has a cotyla that could receive a quadrate, but other interpretations are possible. The quadrate identifications are less certain (see Witmer, 2001b). My general impression of the reconstructed temporal region is that Chatterjee's view is understandable and justifiable but is not sufficiently clear to merit drawing firm phylogenetic conclusions.

Without question, the braincase is the most easily interpreted part of the skull, at least with respect to bone identifications. It is doubtful that there are any indisputably avian apomorphies in the braincase. However, it is indeed the braincase of a coelurosaur in that it possesses cranial pneumatic recesses (including the caudal tympanic recess, which thus far is not known outside Coelurosauria), a large cerebellar auricular fossa, a metotic strut, and a vagal canal opening onto the occiput (Chatterjee, 1991, 1998b; Witmer, 1997d, 2001b), and thus the braincase may pertain to the oldest known coelurosaur.

Postcranially, little is unambiguously avian. Exceptions are the cervical vertebrae, which are truly heterocoelous, if only incipiently so; have prominent ventral processes (hypapophyses); and have large vertebral foramina. Of course, heterocoely has a fairly homoplastic distribution within birds (Martin, 1983; Chiappe, 1996), and *Protoavis* is not as heterocoelous as *Hesperornis* or most neornithines, but the vertebral structure nevertheless represents one of the few bona fide avian suites of *Protoavis*. There are many problems in the thoracic appendage (Witmer, 2001b), not least of which is the coracoid, which, although having a generally advanced avian shape, seems positively minuscule in comparison with the rest of the skeleton. I cannot confirm the remigial papillae on the ulna or manus. In fact, the identification of the four-digit manus itself has been called into question, with Sereno (1997b) regarding it as the foot of an archosaur. The pelvic appendage likewise is not particularly birdlike. Perhaps the most avian feature is a medial fossa within the os coxae regarded by Chatterjee (1995, 1998b) as a renal fossa; however, no other Mesozoic bird has a renal fossa, and the structure in *Protoavis* differs somewhat from that in neornithines (Witmer, 2001b).

It is probably fair to state that the case for the avian status of *P. texensis* is not as clear as generally portrayed by Chatterjee. The temporal configuration and vertebral morphology might argue for a position near Ornithurae, yet the long tail, the archaic ankle, the four-digit manus, and other features would argue for a basal position, probably well outside Aves. The braincase is more or less coelurosaurian. The taphonomic problems and the possibility that this is a chimera may make this an intractable problem. An option is simply to take Chatterjee's analyses at face value and proceed (as done by Dyke and Thorley, 1998), but this seems

naive at best. Critical study of the original material is absolutely necessary, but even here, in the absence of newly collected material of known association, firm conclusions will likely be elusive.

It would thus seem that *Protoavis* bears little significance for solving the riddle of the origin of birds. The specimens themselves are problematic, and so we rightly should be skeptical. But even assuming that Chatterjee has interpreted them 100% correctly, *Protoavis* would have little impact on the phylogenetic pattern of avian origins (Witmer, 1997c, 2001b; Dyke and Thorley, 1998). Then why the often vitriolic controversy? The reasons are complex, but probably a major component is that Chatterjee's acceptance of the Ostrom/Gauthier orthodoxy would require that virtually all theropod cladogenesis had taken place well back in the Triassic, at least in the Norian, if not earlier—that is, right at the very dawning of the dinosaurs. I have elsewhere (Witmer, 2001b) referred to this (somewhat whimsically) as the “Norian Explosion.” The problem is that we have no real evidence of such an explosion: no Norian tyrannosaurids, no Norian oviraptorosaurs, etc. Thus, many people simply have not accepted this proposition. This incongruity has not gone unnoticed and has been exploited by opponents of the idea of theropod relationships. For example, Martin (1988), Tarsitano (1991), and Bock (1997) were receptive to the avian status of *Protoavis* and pointed out that a Triassic bird would essentially disprove the prevailing notion of theropod relationships.

But a long view is appropriate. The origins of many theropod groups are constantly being pushed back further in time. Therizinosauroids have been reported from the Early Jurassic of China (Zhao and Xu, 1998; Xu et al., 2001a), and Chatterjee (1993) reported an ornithomimosaur from the Late Triassic of Texas, although such claims generally are controversial (Rauhut, 1997). As mentioned, *Protoavis* itself represents a temporal range extension for Coelurosauria. Whether the idea of a Triassic bird will ever be more palatable is hard to predict, but stranger things have happened in the history of science, and *Protoavis* may yet prove to be a key player. For the present, however, it is probably both prudent and justifiable to minimize the role that *Protoavis* plays in any discussions of avian ancestry.

## The Significance of the Feathered Chinese Dinosaurs

The 1990s will go down in history as a time when one of the most significant fossil deposits ever discovered was brought to light. The Lower Yixian Formation (Chaomidianzi Formation of some) and allied rock units in western Liaoning Province, People's Republic of China, have yielded a wealth of fossil vertebrates, preserving—in often astounding abundance—an entire fauna in all its diversity (Luo, 1999;

Swisher et al., 1999). The basal birds from these deposits are discussed in this volume by Zhou and Hou (Chapter 7). With regard to the origin of birds, several additional taxa are relevant, particularly because of the preservation of integumentary remains interpreted to be feathers or featherlike filaments. At this writing, six theropod taxa (other than the indisputable birds) have been reported to have “feathery” skin (with, no doubt, more taxa on the way): *Sinosauropteryx prima* (Ji and Ji, 1996; Chen et al., 1998), *Protarchaeopteryx robusta* (Ji and Ji, 1997; Ji et al., 1998), *Caudipteryx* spp. (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000), *Beipiaosaurus inexpectus* (Xu et al., 1999a), *Sinornithosaurus millenii* (Xu et al., 1999b; Ji et al., 2001, if the juvenile dromaeosaurid pertains to this species), and *Microraptor zhaoianus* (Xu et al., 2000). The obvious significance for the debate on avian origins is that if feathers are truly present in nonavian theropod dinosaurs, then this should effectively close the door to any opposition to the theropod hypothesis. The debate, for all intents and purposes, will be over.

Thus, it is necessary to assess these claims carefully. See also the chapters in this volume by Clark, Norell, and Makovicky (Chapter 2) and Zhou and Hou (Chapter 7) for their assessments. The controversy began when Ji and Ji (1996: translation courtesy of Chen P.-J. and P. J. Currie) identified feathers in *Sinosauropteryx* and argued that (1) they were similar to modern down in lacking rachis and barbs, and (2) they were restricted to a median frill running from the head to the tip of the tail dorsally and onto the ventromedian surface of the tail. For Ji and Ji (1996), the presence of feathers required the referral of *Sinosauropteryx* to Aves. In the subsequent furor, there was a retreat from their interpretation as true feathers, being instead “protofeathers” (e.g., Brush et al., 1997). Moreover, the status of *Sinosauropteryx* as a bird was questioned, as it clearly had the skeletal anatomy of a small theropod dinosaur. Indeed, Chen et al. (1998), based on additional specimens, formally referred *Sinosauropteryx* to Compsognathidae, a clade of relatively basal coelurosaurs. These authors also presented the first in-depth morphological analysis of the integumentary structures, describing them as coarse, probably hollow, filaments up to 40 mm in length; a chemical or elemental analysis has not been published. The ultimate question, of course, is, What makes these feathers or even “protofeathers” (Unwin, 1998)?

Indeed, Geist et al. (1997) and Feduccia (1999b) suggested that the structures in *Sinosauropteryx* were in fact *not* feathers at all and, moreover, that they were not external, epidermal appendages of any kind. Rather, they argued that, based on comparative anatomy, the fossil structures more closely resembled collagenous fibers supporting a midsagittal dermal frill, that is, *internal* structures that became frayed in the process of decomposition. Although the ap-

parent midline distribution of the filaments is indeed fully consistent with dermal frills, which are widely present in modern squamates and even well known in some dinosaur groups (e.g., sauropods: Czerkas, 1994; hadrosaurids: Lull and Wright, 1942), the filaments are not actually in the median plane in all regions but rather are in some places offset, such as the head region, which is not preserved in a straight lateral view (Padian et al., 2001). In fact, a routine finding with the Liaoning birds and dinosaurs is that the feathers or filaments are preserved as a halo around the skeletal remains. Thus, the “midline frill” is perhaps more safely interpreted as an artifact resulting from the animals being preserved lying more or less on their sides, such that the halo would roughly correspond to the median plane. Geist et al. (1997) suggested that another problem with the feather interpretation in *Sinosauropteryx* is that although some specimens may show a ruffle of fibers extending along the tail, another specimen shows a smooth outline along the tail.

It is valid to question whether these shortcomings falsify the feather hypothesis or may simply be ascribed to vagaries of preservation. Nevertheless, the inference of feathers in *Sinosauropteryx* has such profound implications—not only for the origin of birds but also for the origin of feathers and endothermy—that we should be compelled by the weight of evidence before accepting such momentous claims. In the acknowledged absence of calamus, rachis, and barbs, the identification of these structures as “true” feathers in *Sinosauropteryx* is clearly unjustified. Also problematic is the inference of “protofeathers.” Although true feathers certainly had epidermal precursors that lacked such definitive attributes as rachis and barbs, how would we recognize them? Chemical analysis showing unique feather proteins might provide valid evidence, but again such studies have not been performed. Significantly, according to Prum’s (1999, 2000) developmental model of feather evolution, the filaments of *Sinosauropteryx* are entirely consistent with an early stage of feather evolution. Moreover, Padian et al. (2001) argued that these filaments have enough morphological attributes in common with feathers that it is fair to accept that the filaments pass the similarity test of homology with avian feathers. Finally, the notion of feather precursors in *Sinosauropteryx* is significantly enhanced by the feathered theropods from the Yixian discussed later, leading Padian (1998:729) to state that “doubts [raised by Geist et al. (1997)] can now be put to rest.” Thus, in effect, the filaments of *Sinosauropteryx* might be regarded as passing the congruence test of homology, as well (Padian et al., 2001). Nevertheless, the evidence in *Sinosauropteryx* obviously should be judged on its own merits, and stemward inferences based on crownward observations require considerable justification (i.e., level II inference; Witmer 1995a).

Shortly after the announcement of *Sinosauropteryx*, Ji and Ji (1997) announced the discovery of another feathered creature, *Protarchaeopteryx robusta*. They regarded it as the sister group of *Archaeopteryx*, even placing it within Archaeopterygidae, but Ji et al. (1998) removed it from a position within Aves. Unlike the case of *Sinosauropteryx*, the feathers attributed to *Protarchaeopteryx* are absolutely indisputable, with clear rachis and barbs. Thus, if a phylogenetic placement outside birds is justified, then a feathered nonavian theropod would be at hand. Unfortunately, the unique specimen of *Protarchaeopteryx* (NGMC 2125) is quite poorly preserved, and many attributes either are open to interpretation or beyond reliable observation (e.g., about 50% missing data according to Ji et al., 1998). I was unable to confirm the two plesiomorphies identified by Ji et al. (1998) that would deny *Protarchaeopteryx* a higher position—a short frontal process of the premaxilla and serrated teeth. The premaxilla is badly damaged, and the teeth seemed to lack clear serrations; Ji et al. (1998) regarded the serrations as so small (7–10/mm) that they were not visible even with my hand lens, but one then wonders if something so small can be regarded as truly a “serration.” It may lack a reversed hallux, which would be an important plesiomorphy, but neither foot of the holotype is well preserved. Given the current state of our knowledge of *Protarchaeopteryx*, it is difficult to predict whether better specimens will show it to be outside or within Aves. It is even conceivable that a sister group relationship with *Archaeopteryx*, as originally suggested by Ji and Ji (1997), will be borne out (see Elzanowski, Chapter 6 in this volume). Certainly, *Protarchaeopteryx* is very close to the transition to birds, which makes its state of preservation all the more frustrating.

Much better preserved, however, is the material of *Caudipteryx* (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). *Caudipteryx* in many ways seems to be the perfect “feathered dinosaur.” It possesses clearly “avian” feathers (i.e., with calamus, rachis, and barbs), yet, unlike those of *Archaeopteryx*, these feathers are not part of a flight apparatus, and hence *Caudipteryx* obviously did not fly. Moreover, *Caudipteryx* lacks many of the derived bony features unique to “proper” birds and hence has justifiably been hailed as the first animal to be discovered that is both indisputably feathered and indisputably *not* a bird. Indeed, *Caudipteryx* truly begs the question of just what may be called a “bird” in the colloquial sense of the word.

As mentioned, feathers are known for the two widely studied specimens described by Ji et al. (1998); the several new specimens reported by Zhou and Wang (2000) and Zhou et al. (2000) confirm a consistent pattern. In their preserved state, well-developed feathers are largely restricted to the manus and distal portion of the tail. As far as can be discerned, the inner and outer vanes are symmetrical about the rachis. Ji et al. (1998) and Zhou and Wang (2000) reported

preservation of filamentous structures in the body regions, but the real question is whether the distribution of true feathers was more extensive in life or actually restricted to the tips of the hands and tail.

The association of true feathers with the skeletons of *Caudipteryx* is beyond any doubt, which is important because the skeleton is decidedly nonavian—that is, this is no chimeric association. The following discussion is not intended to be a description of the bony anatomy of *Caudipteryx* but rather a tabulation of its *primitive, nonavian* attributes (see also Zhou and Wang, 2000). Although it is more customary in this cladistic age to enumerate *derived* characters, documentation of the *primitive* characters of this feathered creature is necessary to counter claims that *Caudipteryx* is in fact “a secondarily flightless bird, a Mesozoic kiwi” (Feduccia, 1999a:4742; 1999b; see also Jones et al., 2000b). In addition to feathers, another significant avian apomorphy would be the shortened tail. In *Caudipteryx* there are only 22 caudal vertebrae, the same number as in *Archaeopteryx* and fewer than in any other known nonavian theropod (Ji et al., 1998). Moreover, the distal portion is clearly very stiff, although, as correctly noted by Ji et al. (1998; see also Zhou et al., 2000), definitely not fused into a pygostyle (or a “protopygostyle,” as Feduccia [1999a] called it). Other than its short length and distal stiffening, nothing about the tail is particularly birdlike. Its distal caudal vertebrae have very short centra (Ji et al., 1998), rather than the elongate distal centra observed in *Archaeopteryx* and *Rahonavis* (Forster et al., 1998). Moreover, the proximal caudal haemal arches (chevrons) are very long and spatulate, again unlike those of basal birds and unlike those of even most derived nonavian coelurosaurs. The closest match to the tail of *Caudipteryx* may well be among oviraptorosaurs. As particularly well demonstrated by *Nomingia* (Barsbold et al., 2000a,b), oviraptorosaurs display the following derived characters: a reduced number of caudal vertebrae (24 in *Nomingia*—only 2 more than in *Caudipteryx*), rigid distal tail with short centra, relatively long transverse processes on the proximal caudals (Sereno, 1999a), and elongate and spatulate haemal arches. Although Barsbold et al. (2000a,b) regarded the tail of *Nomingia* as bearing a “pygostyle,” it is certainly not homologous (or even that similar) to the avian structure, and I would tend to reserve that name for pygostylian birds (see Chiappe, Chapter 20 in this volume). In any event, the shortened tail of *Caudipteryx* is not particularly birdlike and is basically matched by the tails of oviraptorosaurs.

Zhou et al. (2000) advanced a few additional birdlike characters that, although they still regarded *Caudipteryx* as a nonavian dinosaur, “indicate that its phylogenetic position remains a debatable issue.” Not having examined their new specimens firsthand, I cannot comment in detail on the birdlike attributes, but a few points are pertinent. Of the

birdlike characters that they advance, some are clearly homoplasies (e.g., manual phalangeal formula of 2-3-2), some are more widely distributed in maniraptorans (e.g., tooth form, uncinat processes), and some are open to interpretation (e.g., the “partially reversed” hallux). They also pointed to the remarkably short trunk (only nine thoracic vertebrae) and elongate hindlimbs, birdlike features that had earlier attracted the attention of Jones et al. (2000b).

Jones et al. (2000b) argued that *Caudipteryx* possessed a strikingly birdlike attribute relating to the location of the center of mass and the proportions of the trunk and hindlimb; these parameters were entirely unlike those of any known nonavian theropods but indistinguishable from those of cursorial birds. They provided three alternatives to explain these data. First, perhaps simply *Caudipteryx* apomorphically and convergently developed a locomotor style similar to that of cursorial birds. Second, perhaps *Caudipteryx* was a nonavian theropod that had flight in its ancestry. And third, perhaps *Caudipteryx* was in fact “a secondarily, flightless, post-*Archaeopteryx*, cursorial bird” (Jones et al., 2000b). The authors clearly favor this third hypothesis. Testing all three hypotheses is firmly within the realm of phylogenetic analysis, and the paper of Jones et al. (2000b) was a functional analysis, not a comprehensive phylogenetic study.

Nevertheless, despite the presence of true feathers, birdlike hindlimb proportions, and perhaps other, less certain features, *Caudipteryx* displays a variety of plesiomorphic characters throughout the skeleton that, when taken together, clearly place it outside Aves. Ji et al. (1998) listed three such characters. Their first two characters are very similar and relate to the quadratojugal and its contact with the quadrate and squamosal. I concur that the quadratojugal of NGMC 97-9-A bears the primitive character of a relatively long dorsal (squamosal) process that probably is sutured to the quadrate, and the new specimens reported by Zhou et al. (2000) confirm this arrangement. *Caudipteryx* clearly lacks the small quadratojugal of birds, including such basal birds as *Archaeopteryx*, *Confuciusornis*, and enantiornithines.

The other plesiomorphic trait cited by Ji et al. (1998) involves the retention of a prominent, triangular obturator process of the ischium. Again, I fully agree, and I regard the shape of the ischium as one of the clearest manifestations of the position of *Caudipteryx* outside Aves. Basal birds have complex ischia (Forster et al., 1998) that generally are characterized by a small (or even absent) obturator process and instead a large, tablike (i.e., rectangular) proximodorsal process extending up toward the ilium. This is the condition in, for example, *Archaeopteryx*, *Confuciusornis*, and enantiornithines. The very birdlike theropod *Unenlagia comahuensis* (Novas and Puerta, 1997) presents the intermediate condition of possessing both a large obturator process and a proximodorsal process. The shape and orientation of the ischium

of *Caudipteryx* are clearly visible in the new material described by Zhou and Wang (2000; see also Zhou et al., 2000). Both ischia are well preserved and show only a single process that is large and triangular. This shape is exactly like that of the obturator process of, say, dromaeosaurids and oviraptorosaurs. Another primitive character thus would be the absence of the proximodorsal process.

A number of other primitive characters of *Caudipteryx* can be added to those discussed by Ji et al. (1998; see also Zhou and Wang, 2000, and Zhou et al., 2000). For example, the jugal is a typically nonavian theropodan jugal with a very large postorbital process. Birds, on the other hand, have lost the postorbital process of the jugal or, at most, have reduced it to a small process. Even taxa that retain a postorbital bone and a dorsotemporal arch (e.g., *Archaeopteryx*, the Catalan enantiornithine nestling, alvarezsaurids) lack a large postorbital process of the jugal and basically have a jugal bar. The postorbital bone of the enantiornithine *Protopteryx* has a long jugal process that might reach the jugal, but such a contact is not clear on the specimens (Zhang and Zhou, 2000). The only certain exception is *Confuciusornis*, which curiously possesses a complete postorbital bar formed by contact of the postorbital and jugal bones. But even in *Confuciusornis* most specimens have a relatively small postorbital process of the jugal (in some cases, little more than a bump), and the postorbital bone makes up almost all of the bar (Martin et al., 1998; Peters and Ji, 1998; Chiappe et al., 1999; Hou et al., 1999; Zhou and Hou, Chapter 7 in this volume). It may be noted here that the Eichstätt specimen of *Archaeopteryx* displays a somewhat bifid caudal extremity to the jugal. The dorsal prong of this bone could be interpreted as a postorbital process (e.g., Paul, 1988), but it seems to be situated too far caudally to reach the ventral ramus of the postorbital as preserved in the Berlin specimen (see also Chiappe et al., 1999); hence, I tend to agree more with the restoration of *Archaeopteryx* produced by Chatterjee (1991).

Another primitive character of *Caudipteryx* is the relatively very deep mandibular fenestra, as evidenced by the deep caudal embayment of the dentary of the paratype skull. Absence of a mandibular fenestra had been thought to characterize Aves because such an opening is absent in *Archaeopteryx*, hesperornithids, *Ichthyornis*, and neornithines, but the discovery of mandibular fenestrae in *Confuciusornis* (Martin et al., 1998; Chiappe et al., 1999; Zhou and Hou, Chapter 7 in this volume) makes this assessment a bit problematic. Nevertheless, the fenestra in *Confuciusornis* is not nearly as deep as in *Caudipteryx* and has an unusual form and thus may well be a reversal. The mandibular fenestra of *Caudipteryx*, on the other hand, is very comparable to that of dromaeosaurids, oviraptorosaurs, and other nonavian coelurosaurs and thus represents the primitive condition.

The thoracic girdle of *Caudipteryx* is also quite primitive and has none of the avian apomorphies seen in members of Aves. For example, the scapula has a relatively broad blade with a pronounced distal expansion, indicating the retention of a broad suprascapular cartilage. The blade clearly is not the slender and elongate structure seen in all basal birds. The shape of the coracoid is more or less that of a conventional nonavian coelurosaur coracoid, with a quadrilateral shape, proximal supracoracoidal nerve foramen, and moderate biceps tubercle. The coracoid certainly is not the elongate “straplike” bone seen in ornithothoracine birds. Another primitive trait here relates to the orientation of the girdle in that it is located on the lateral aspect of the thorax with the scapula at an angle to the axial column rather than on the dorsal aspect of the thorax with the scapula parallel to the column. The former condition is the primitive condition, whereas the latter condition is observed in all birds (Jenkins, 1993), including *Archaeopteryx*, *Confuciusornis*, and other basal birds. One hesitates to make too much of the orientation of elements in two-dimensional specimens, but, taken at face value (and all specimens agree on this point), *Caudipteryx* again displays the primitive condition.

The pelvic girdle of *Caudipteryx* presents primitive, nonavian characters beyond the ischiadic shape noted earlier. For example, the ilium is relatively very tall directly above the acetabulum, and its preacetabular portion is not expanded cranially; this is the typical condition for most nonavian coelurosaurs. In birds, on the other hand, the ilium is relatively low, with a greatly elongate preacetabular portion (see Elzanowski, Chapter 6 in this volume; Zhou and Hou, Chapter 7 in this volume). The pubic apron is extensive in *Caudipteryx*, measuring about 56% of total pubic length in the holotype. This is considerably more than the 45% measured in the London *Archaeopteryx*, the bird with the longest known pubic apron, and may even exceed that of some dromaeosaurids (Norell and Makovicky, 1997, 1999). Finally, Zhou and Wang (2000) and Zhou et al. (2000) noted that the pubis is not retroverted (as argued by Feduccia, 1999b) but rather is directed cranially, as in most nonavian theropods.

The picture that emerges from this brief survey of *Caudipteryx* is of a feathered theropod dinosaur that is probably well outside the avian lineage. I have not performed a more extensive formal analysis, but it seems readily apparent that it would be much less parsimonious to include *Caudipteryx* within Aves. And this point leads to the question of the phylogenetic position of *Caudipteryx*. The analysis of Ji et al. (1998) was not very inclusive, using only *Velociraptor* as an outgroup to the Chinese taxa and birds. My initial study of the specimens suggested a number of derived features pointing to oviraptorosaur relationships for *Caudipteryx*, including the following. The jaws are almost completely edentulous in *Caudipteryx*, which is indeed a re-

semblance to oviraptorosaurs, but even more striking is the conformation of the jaws. In both groups, the dentary is very deep between the mandibular fenestra and the symphyseal portion, which is deflected ventrally; moreover, the symphyseal portion is medially inflected, and the caudal processes of the dentary diverge widely around the mandibular fenestra, both of which are attributes of oviraptorosaurs (Makovicky and Sues, 1998). The premaxilla has an extensive prenasal portion (which is also an avian apomorphy), and the naris itself is retracted (extensively in oviraptorosaurs). Finally, the maxilla is very characteristic, being a relatively small, rostrally displaced triangular element. Many of the postcranial elements compare well with oviraptorosaurs but also with other clades of coelurosaurs. However, the tail of *Caudipteryx*, as detailed previously, is quite similar to that of oviraptorosaurs in that both are short and proximally very thick. Given that my observations were not part of a comprehensive phylogenetic analysis, it was gratifying to see these impressions of an oviraptorosaurian *Caudipteryx* borne out by numerous cladistic analyses presented at the Ostrom Symposium at Yale University in 1999 (e.g., by P. C. Sereno, T. R. Holtz, M. A. Norell, and P. J. Currie), suggesting broad independent discovery of these relationships (and a heartening affirmation of phylogenetic systematics). Barsbold et al. (2000a,b) also regarded *Caudipteryx* as a basal oviraptorosaur. More significant, *Caudipteryx* was included in the very extensive phylogenetic analysis of Sereno (1999a). Sereno scored *Caudipteryx* for 204 characters (only 16% missing data) and found not only that *Caudipteryx* is well outside Aves but also that it is indeed a basal oviraptorosaur, sharing a dozen characters with oviraptoroids.

Thus, feathers of essentially modern structure do indeed predate the group conventionally known as “birds.” This finding may seem shocking, but it is to be expected. This surprise again may relate to the pervasive sense of *Archaeopteryx* as truly the Urvogel, or “first bird.” Common sense, of course, dictates that the elaborate feathers of *Archaeopteryx*, arranged as they are in their “modern” array of primaries and secondaries, must have had predecessors. However, *Caudipteryx* will likely remain difficult for some to accept, perhaps because it is such a dramatic repudiation of opposition to the theropod origin of birds.

In fact, more “feathered dinosaurs” are likely to come to light. For example, Xu et al. (1999a) described *Beipiaosaurus*, a new therizinosauroid theropod from the Lower Yixian Formation that bears filamentous dermal structures that are perhaps similar to those of *Sinosauropteryx*. These structures lack the unambiguous feather structure seen in *Caudipteryx* (i.e., they lack calamus, rachis, and barbs), but they are clearly present on areas of the body that cannot be explained away as remnants of a median frill. In *Beipiaosaurus*, filamentous structures are associated with ele-

ments of both fore- and hindlimbs. The best-preserved filaments are attached to the ulna, where some approach 70 mm in length. Xu et al. (1999a) describe some filaments as distally branched and with hollow cores. These filaments have the same “protofeather” problems as did those of *Sinosauropteryx* (i.e., Are filaments truly the evolutionary precursors of feathers?), but their association with the limbs and their considerable length clearly indicate that they are some kind of epidermal appendage rather than an artifact of desiccating dermal collagen (see also Prum, 1999).

Another nonavian theropod with preserved integumentary filaments is the Yixian dromaeosaurid *Sinornithosaurus millenii* (Xu et al., 1999b). Unfortunately, the filaments are not in their natural positions, and thus, for example, the cluster of filaments adjacent to the skull cannot be reliably attributed to the head region. A very significant finding of *Sinornithosaurus* is a negative one, and that is the absence of hand and tail feathers. No true feathers (i.e., with rachis and barbs) of the sort seen in birds and *Caudipteryx* have been recovered with *Sinornithosaurus*. This is a bit troubling because the phylogenetic hypothesis of Sereno (1999a) predicts that, minimally, hand and tail feathers should be found in dromaeosaurids. However, given that the integumentary structures are not in life position and that the *Sinornithosaurus* specimen is generally jumbled somewhat on the slab, it is probably best not to make too much of this absence and assume that it is preservational. Close examination reveals some details suggesting that the filaments of *Sinornithosaurus* are more structured than those of *Sinosauropteryx* and *Beipiaosaurus* and hence more similar to avian feathers. Xu et al. (2001b) documented branching of some filaments, the compound construction of filamentous bundles, and even the occurrence of basal tufts of filaments, all features indicative of a more structurally complex integumentary covering. This report was followed shortly by the announcement by Ji et al. (2001; see also Norell, 2001) of a new specimen of a juvenile dromaeosaurid that is very similar to *Sinornithosaurus* and may even be the same species. The specimen preserves the integument in place and affirms the complex nature of the integument in dromaeosaurids. Not only does the juvenile specimen show branching and tufted filaments, but it also shows fibers branching off of a central axial filament—that is, it shows structure that could be interpreted as being the rachis and barbs of a “true” feather. Moreover, Ji et al. (2001) argued that the structures were so well ordered that birdlike barbules almost certainly had to have been present. As in *Caudipteryx*, the tail and forelimbs have the best-organized integumentary structures.

*Microraptor*, the tiny dromaeosaurid reported by Xu et al. (2000), lacks hand and tail feathers but has the now typical filamentous coat. As in the juvenile dromaeosaurid, some integumentary impressions bear a rachislike structure, suggesting that true feathers might have been present

in this animal, although this finding awaits confirmation with better-preserved material.

It is also relevant at this point to mention the findings of Schweitzer et al. (1999) on the biochemistry and morphology of fibrous integumentary structures recovered from the head region of the alvarezsaurid *Shuvuuia* from Mongolia (see also Chiappe, Norell, and Clark, Chapter 4 in this volume). Schweitzer et al. (1999) reported two important observations about these structures. First, biochemical studies are consistent with their being composed of beta keratin, a protein found in the feathers and scales of sauropsids. Second, the structures were apparently hollow. At present, the only structures known to be both hollow and composed of beta keratin are avian feathers. These findings are more provocative than conclusive, and, given the controversial phylogenetic position of alvarezsaurids (see Novas and Pol, Chapter 5 in this volume), one should be hesitant to make too much of these findings. Nevertheless, they may be legitimate evidence for feather or featherlike structures outside Aves.

In sum, the significance of these Chinese (and Mongolian) fossils for the debate on avian origins, in one sense, should be minimal. That is, we should not be surprised at the identification of feathers in a group of animals that a broad consensus had always thought was close to avian ancestry. The discovery of feathers in, say, *Caudipteryx* simply adds one more apomorphy to the long list of derived characters linking birds with theropod dinosaurs. The disproof of feathers in any of these Chinese forms would simply remove one character; all the others would remain. Likewise, forcing *Caudipteryx* to be within Aves because of its possession of true feathers (Cai and Zhao, 1999) would not automatically strip it of its clear theropod heritage. Thus, in this context, feathered dinosaurs are not that important. But, of course, in this high-profile, high-energy debate, rhetoric, regrettably, sometimes seems paramount to evidence. Feathers—that quintessentially avian trait—have always been the great definer of birds. The presence of unambiguous feathers in an unambiguously nonavian theropod has the rhetorical impact of an atomic bomb, rendering any doubt about the theropod relationships of birds ludicrous.

## The Relationship of the Origin of Flight to the Origin Of Birds

The origin of birds is, at its core, a matter of genealogy. That is, regardless of your systematic philosophy—whether it be cladistic, phenetic, or eclectic—avian ancestry is a question of phylogeny, or, more precisely, phylogenetic reconstruction. For most biologists, phylogenetic reconstruction has become more or less synonymous with phylogenetic systematics or cladistics, whereby the distribution of attributes among taxa forms the primary raw data used to develop hy-

potheses of relationship. The debate on the origin of birds, however, has been unusual in that a different approach has been applied by a minority of workers for many years (Witmer, 1991, 1997b, 1999). This approach is (1) to create the most likely scenario for the origin of avian flight, (2) to deduce from this scenario the morphological features likely to be present in the hypothetical “proavis,” and then (3), as I have said before (Witmer, 1997b:1209), “to search the animal kingdom for a match.” Thus, *functional* hypotheses on the origin of *flight* are being used to test *phylogenetic* hypotheses on the origin of *birds*. This distinction between the functional and phylogenetic approaches to avian origins has not been widely appreciated.

For decades, of course, discussions on the origin of flight in birds have been dominated and dichotomized by the arboreal hypothesis (a.k.a. the “trees down” theory) and the cursorial hypothesis (a.k.a. the “ground up” theory). The cursorial hypothesis has been closely associated with the notion of relationships to theropod dinosaurs, whereas the arboreal hypothesis has been tied to the “alternative ancestry” hypothesis (that is, the origin of birds from a usually poorly defined group other than theropods, most often basal archosaurs). It is my intention in this section neither to evaluate these ideas nor to provide a historical account; these are beyond the scope of this chapter (see Hecht et al., 1985; Feduccia, 1996; Shipman, 1997a). Rather, my goal is to examine how these two functional hypotheses relate to the phylogenetic question of avian origins. Moreover, it is worthwhile to question the strict coupling of the cursorial hypothesis with theropods, on the one hand, and the arboreal hypothesis with alternative ancestors, on the other hand (Witmer, 1999). For example, is the arboreal hypothesis truly inconsistent with theropod relationships?

Opponents of theropod relationships have argued strongly for a tight linkage between these functional and phylogenetic issues. For example, Feduccia (1996:viii) stated that “a dinosaurian origin of birds is inextricably linked with the cursorial, or ground-up origin, of avian flight, which is a biophysical impossibility.” Martin (1998:40) characterized the debate on avian origins exclusively in functional terms, claiming that “in the great bird-dinosaur debate, the participants huddle in two camps, which paleontologists have nicknamed ‘ground up’ and ‘trees down.’” Bock so intertwined the functional and phylogenetic questions that he entitled a paper “The Arboreal Theory for the Origin of Birds” and used “origin of birds” and “origin of flight” almost interchangeably (Bock, 1985). Tarsitano (1985, 1991) also strongly advocated this approach. The basic premise here is that flight began in animals that lived in high places (trees, in most formulations) and made use of gravity and expanded body surface area to slow descent during falls and leaps; hence, these animals should have been small, quadrupedal, and with arboreal adaptations—

attributes not typical of theropod dinosaurs (Martin, 1983, 1991, 1998; Tarsitano, 1985, 1991; Feduccia and Wild, 1993; Feduccia, 1996, 1999a).

Again, my intent is not to explore this model or its theoretical premises but rather to evaluate the validity of the approach. We are faced with two interesting and obviously related issues: the genealogical ancestry of birds, and the evolution of flight in birds. The question then becomes, Is resolution of one issue logically prior to resolution of the other? The answer is yes, and most theorists would argue that workers such as Martin, Feduccia, and Tarsitano have the logical order reversed. In other words, the phylogenetic question of avian ancestry must precede the functional question of how flight arose. There is a fairly extensive literature on the relationship of functional inference to phylogenetic inference, most prominently discussed by Lauder (1981, 1990, 1995; Lauder and Liem, 1989), although others have commented on the issue (e.g., Padian, 1982, 1985, 1995; Liem, 1989; Bryant and Russell, 1992; Weishampel, 1995; Witmer, 1995a). These authors all agree that functional hypotheses and scenarios are best tested within the context of a strict hypothesis of phylogenetic relationships, primarily for the simple reason that evolutionary history constrains functional systems and their evolution. The evolutionary “starting point” for any functional transition is absolutely critical. The evolutionary trajectory from a *Megalancosaurus*-like form to a flying bird will be much different from the trajectory from a *Deinonychus*-like form to a flying bird, regardless of whether these “starting points” are arboreal, terrestrial, aquatic, or whatever. Determining this evolutionary “starting point” is a matter of genealogy, that is, of phylogenetic inference, not functional inference. Thus, the details of any functional transition, such as the origin and refinement of flight, can be best dissected with the tool of a well-resolved phylogenetic hypothesis (see Cracraft, 1990; Chiappe, 1995; Sereno, 1997b, 1999a).

Bock (1965, 1985, 1986), on the other hand, has argued vigorously and persuasively for the validity of what amounts to a “function-first,” scenario-based kind of approach, couched in the philosophical terms of historical-narrative explanations. Nevertheless, most current opinion has found such scenario building in the absence of a strict phylogenetic hypothesis to fall short on the grounds of testability. More to the point, it seems unjustified to believe that such scenarios—no matter how intuitively appealing, such as is the case with the arboreal theory—can overturn as well substantiated a phylogenetic hypothesis as is the theropod hypothesis. The hypothesized steps in the functional transition from an arboreal proavis to a flying bird are generally tested by only plausibility or modeling rather than hard data. On the other hand, phylogenetic hypotheses are much better grounded in tangible evidence—in this case, actual objects (bones) that can be observed, measured, and

compared—and hence cladograms are subject to more rigorous tests.

But, in many respects, it is the role that cladistic analysis has played in the theropod hypothesis that has elicited the opposition. Opponents of theropod relationships have simultaneously waged a war against phylogenetic systematics, because, for authors like Feduccia (1996), Martin (1998), and Bock (1999), “cladistic analysis . . . lies at the core of the debate concerning bird origins” (Feduccia, 1996:59). Such statements are a little difficult to reconcile with the fact that, say, John Ostrom (1973, 1976), who is not a cladist, formulated the theropod hypothesis using precisely the systematic methodology these authors advocate. Nevertheless, more recent authors have indeed employed phylogenetic systematics, and some reviewers of Feduccia’s 1996 book agreed that differing systematic philosophies are part of the source of the conflict (Norell and Chiappe, 1996; Sereno, 1997a; Witmer, 1997b; see, in particular, Padian, 1997, for an analysis of this issue). What is pertinent here for the “function versus phylogeny” debate is that, given the role of cladistic analysis in (1) modern functional inference in general and (2) the theropod hypothesis for avian ancestry in particular, it seems unlikely that those in the Feduccia/Martin school will adopt the “phylogeny-first, function-second” approach to understanding the origin of flight advocated here.

Perhaps the greatest irony for this whole issue is that there probably is no adequate justification for tightly coupling the cursorial theory with theropod relationships and the arboreal theory with alternative ancestry. It is conceivable that the Feduccia/Martin school is correct that the arboreal model for the origin of flight is the superior model—but the evolutionary starting point may in fact be a small theropod dinosaur. Why must these functional and phylogenetic models be coupled (Witmer, 1999)? The coupling of these models has more to do with the tactics of the debate than the debate itself. Advocates of the alternative-ancestry/arboreal pairing have pointed to the large size of such obviously terrestrial theropods as *Tyrannosaurus* or even *Deinonychus* in the hope of illustrating how ludicrous the notion of an arboreal/theropod origin of birds is (e.g., Tarsitano, 1985; Martin, 1991, 1997; Feduccia, 1996, 1999b). Advocates of the theropod/cursorial pair called attention to the same terrestrial attributes of theropods in arguing for their position (e.g., Ostrom, 1986). In general, each camp has chosen a single point on which to be immovable and hence forces the functional or phylogenetic issue to fall in line with that point. For the Feduccia/Martin school, the arboreal theory is unshakable, and hence all phylogenetic possibilities must be concordant—and theropods, they argue, are the height of discord. On the other hand, the theropod school has remained intransigent on the phylogenetic issue, and hence the functional transition to flight has been constrained.

As outlined previously, the theropod school is on much firmer theoretical ground in placing phylogeny logically prior to function. In fact, it was this kind of reasoning that helped bolster the cursorial origin of avian flight. That is, since the theropod outgroups of *Archaeopteryx* and other birds were more or less large animals, the origin of flight clearly is best understood in this terrestrial or cursorial context (Padian, 1982; Gauthier and Padian, 1985; Padian and Chiappe, 1998a,b). However, as noted by Sereno and Rao (1992), arboreality was apparently an early adaptation for birds. Hence, the debates about the arboreality versus terrestriality of *Archaeopteryx* have always been seen as critical. Arguments on both sides have been presented for decades (see Hecht et al., 1985; Paul, 1988; Feduccia, 1996; Padian and Chiappe, 1998a,b), and, once partisanship is eliminated, no clear consensus emerges. Interestingly, independent studies on pedal proportions in *Archaeopteryx* and other taxa (Hopson and Chiappe, 1998; Zhou, 1998) have agreed in showing that the feet of *Archaeopteryx* are basically intermediate between those of a terrestrial cursor and those of an arboreal bird. Thus, *Archaeopteryx* itself is inconclusive in establishing the phylogenetic level at which arboreality occurred (assuming for the sake of argument that it occurred only once).

The question ultimately comes down to the actual theropod ancestor of birds: what it looked like and how it lived its life. Although virtually all recent analyses put Dromaeosauridae or Troodontidae (or the two together as Deinonychosauria) as the sister group of Aves, neither is truly the ancestor, and hence known forms like *Deinonychus* or *Troodon* can only go so far as models for the true avian ancestor (see Gates, Chapter 19 in this volume, for an insightful discussion). Virtually all early birds are small animals, so, at some point in the transition to birds, miniaturization took place. Small size has many virtues. That is, in the absence of the constraints imposed by large mass, small animals can exploit a broad behavioral repertoire without necessarily having to develop novel morphological adaptations. This line of reasoning is obviously leading toward the possibility that the miniaturization took place within a lineage that we would probably recognize as “nonavian,” that is, a lineage of little dinosaurs. If such a tiny theropod habitually used trees or other high places (and one can easily envision many sound reasons for doing so), then perhaps the arboreal model propounded by opponents of theropod relationships would apply equally well to theropods. This notion is not new, and a number of workers have argued for an arboreal origin of avian flight from tiny, dromaeosaur-like ancestors (Abel, 1911; Paul, 1988, 1996, 2002; Witmer, 1995c; Chatterjee, 1997a,b; Xu et al., 2000; Zhou and Wang, 2000). In particular, Chatterjee and Paul have developed fairly elaborate models and have identified a number of features of dromaeosaurlike theropods that may indicate ar-

boreal capabilities. Significantly, a variety of tiny theropods, such as *Bambiraptor* (Burnham et al., 2000) and *Micro-raptor* (Xu et al., 2000), have begun to turn up in the fossil record.

It is not my aim here to evaluate models for an arboreal origin of avian flight from theropod dinosaurs. Although the idea has a lot of merit, virtually all models on the origin of avian flight are so speculative and so data-poor that any satisfactory resolution is unlikely any time soon. In fact, there are serious testability problems for all these models. For example, mathematical models for the origin of avian flight abound (e.g., Caple et al., 1983; Balda et al., 1985; Norberg, 1985; Rayner, 1985; Pennycuick, 1986; Herzog, 1993; Ebel, 1996; Burgers and Chiappe, 1999), but they all suffer to varying extents from testability problems—and this problem pertains to all models, regardless of the phylogenetic starting point. The fact is that we simply have paltry data on the functional capabilities of any of the principal taxa (e.g., dromaeosaurids, troodontids, Triassic archosauromorphs like *Megalanacosaurus* or *Longisquama*). Despite numerous studies, even the basic lifestyle of *Archaeopteryx* is disputed. It is conceivable that the origin of flight—as a matter of scientific discourse—is out of reach. We may simply never have the appropriate data to adequately test any models. In fact, this is probably the reason that the debate on the origin of flight has raged uncontrolled for a century with no sign of resolution in sight. All ideas remain active because almost none can be falsified.

It is fair to regard the foregoing as overly pessimistic, but one thing that must be true is that modeling the origin of avian flight is a very poor research strategy for discovering the origin of birds. The origin of flight is logically and methodologically secondary to the phylogenetic origin of birds. There is currently no good reason to rigidly couple models of the origin of flight with particular phylogenetic clades. And, perhaps most troubling, the details (or even the broader pattern) of the functional transition to powered flight may be lost in time and virtually unrecoverable in any rigorous scientific sense.

### The Status of Alternatives to the Theropod Hypothesis

There is no question that the theropod origin of birds is by far the most popular hypothesis on avian ancestry. The question then arises, Are there credible alternatives? In most previous reviews (e.g., Ostrom, 1976; Gauthier, 1986; Witmer, 1991; Feduccia, 1996; Padian and Chiappe, 1998b), the debate on avian origins was divided into three competing hypotheses: (1) the theropod hypothesis, (2) the crocodylomorph hypothesis, and (3) the basal archosauriform or “thecodont” hypothesis. However, in recent years it has become apparent that there really are just two major hy-

potheses: (1) the theropod hypothesis and (2) the “not-theropod” or, as I have termed it previously, “the alternative ancestry hypothesis.” Relationship to crocodylomorphs, originally proposed by Walker (1972), seems to have simply faded away in that earlier advocates, such as Martin (1983, 1991), Walker (1990), and Tarsitano (1991), have not renewed their support. The basal archosauriform hypothesis received a significant boost from Welman (1995), who suggested that *Euparkeria* shares with *Archaeopteryx* to the exclusion of theropods and crocodylomorphs a large suite of derived characters in the cranial base. This new “thecodont” hypothesis has received to date no additional adherents and was severely challenged by the detailed analysis of Gower and Weber (1998). Thus, for the present, the crocodylomorph and basal archosauriform hypotheses no longer appear to merit serious consideration.

Indeed, opposition to the theropod origin of birds has become almost exclusively just that, an argument of opposition rather than an argument of advocacy. Criticism is a necessary and appropriate part of the scientific process, and opponents have published a number of papers taking issue with certain of the characters (Martin et al., 1980; Martin, 1983, 1997; Tarsitano, 1991; Feduccia, 1996). It is not my goal here to analyze these criticisms or to provide responses, although a few will be touched on in the next section. My main point here is that opponents have sought to destroy but not build in that they have lost sight of the goal of phylogenetically linking birds to actual taxa. The cladistic approach is more constructive in that a particular phylogenetic hypothesis is refuted not simply by criticizing the characters but rather by offering an alternative that better accounts for the available data, that is, an hypothesis that is more parsimonious, a shorter tree. In 1991, I stated: “At present, supporters of relationships of birds with crocodylomorphs, ‘thecodonts,’ or mammals have failed to produce a competing cladogram, and in this respect the coelurosaurian hypothesis is uncontested” (Witmer, 1991:457).

That statement still stands today, largely because there are no serious alternative phylogenetic hypotheses. For some time, opponents have offered a variety of small, generally poorly preserved Triassic forms as being relevant to the debate (Martin, 1983, 1991, 1997, 1998; Tarsitano, 1985, 1991; Feduccia and Wild, 1993; Feduccia, 1996). These Triassic taxa include *Megalanacosaurus*, *Cosesaurus*, *Scleromochlus*, and *Longisquama*. These forms do not constitute a clade but are a hodgepodge of basal archosaurs or basal archosauromorphs. *Megalanacosaurus* and *Cosesaurus* both pertain to the archosauromorph clade Prolacertiformes (Sanz and Lopez-Martinez, 1984; Renesto, 1994). *Scleromochlus* has been thought to be related to a variety of taxa, most commonly pterosaurs and dinosaurs (Padian, 1984; Gauthier, 1986; Benton, 1999). *Longisquama* has never been

subjected to adequate phylogenetic scrutiny; Sharov (1970) placed it in “Pseudosuchia,” and Haubold and Buffetaut (1987) agreed, although Charig (1976:9) argued that “the justification for this assignment is obscure.” Tarsitano (1991:549) and Feduccia (1996:86) referred to these taxa as “avimorph thecodonts” in that they regarded them as basically birdlike. The resemblances, however, have never been particularly strong or numerous. Authors such as Feduccia, Martin, and Tarsitano generally have not considered these taxa to be truly ancestral to birds but rather as merely representative of what their hypothesized arboreal proavis was like. In other words, these taxa show that there were small, arboreal, quadrupedal animals running around before *Archaeopteryx* (although it should be pointed out that the preferred habitat and mode of life of these animals are perhaps not as obvious as commonly portrayed).

But even given that such animals existed and are consistent with the arboreal theory for the origin of avian flight, this does not constitute actual evidence relevant to the ancestry of birds. For example, unless *Megalancosaurus* is being considered as close to the ancestry of birds, whether or not it has a “straplike scapula” or a “birdlike orbit” (Feduccia and Wild, 1993) is of questionable significance. It is conceivable that viable candidates for avian ancestry could emerge from such a nexus of “avimorph” forms, but such hypotheses will continue to be relegated to the fringe unless they are framed in explicit phylogenetic terms and take head-on the theropod hypothesis on its own terms.

Nevertheless, one of these “avimorph” forms captured broad attention when Jones et al. (2000a:2205) pointed to a number of features of the integumentary appendages of *Longisquama* that led them to conclude that these structures represent “nonavian feathers, probably homologous to those in birds.” The most compelling resemblances center on the presence of a calamuslike base wrapped in a presumably epidermal sheath, indicating that the appendages probably developed in a follicle, as is characteristic of feathers and unlike scales. However, their interpretation of the structures coming off the central axis as separate “barbs” seems overly generous at best. These structures unite distally, forming a continuous ribbon around the periphery of the appendage. This distal union is completely unlike the situation in avian feathers, and even if a few tolerably similar examples—all of which are specialized feathers—can be found among birds, it is clearly not the primitive avian condition (Kellner, Chapter 16 in this volume). It seems more likely that the “barbs” identified by Jones et al. (2000a) are in fact plications or corrugations in a continuous structure, which would be more consistent with a modified scale than a feather. Reisz and Sues (2000) also were critical of the hypothesis of Jones et al. (2000a), advancing many of the same arguments just articulated.

Still, Jones et al. (2000a) regarded the structures as feathers probably homologous to those of birds. The implications of such a hypothesis were not explored in the paper. For example, if feathers are a very basal innovation among archosaurs, then this would constitute strong support for the interpretation of the filaments of, say, *Sinosauropteryx* as feathers (which would be ironic given that Jones and colleagues were such vocal opponents of feathered dinosaurs). But if feathers are a basal character evolving in the Triassic, then where are all the Triassic and Jurassic fossil feathers? There are abundant unequivocal fossil feathers in the Cretaceous, but none prior to those of *Archaeopteryx* in the Late Jurassic (see Kellner, Chapter 16 in this volume).

The Jones et al. (2000a) paper carefully avoided any statement on the origin of birds, but the authors were very vocal in the associated media furor (e.g., see Stokstad, 2000), arguing that the finding of feathers in *Longisquama* refuted the theropod hypothesis and that *Longisquama* itself is “an ideal bird ancestor” (J. A. Ruben quoted in Stokstad, 2000:2124). This example of disparity between scientific and public statements is just the latest in the long history of the debate on avian origins, and it is best to focus on the scientific evidence. In this case, the paper of Jones et al. (2000a) offered no scientific statement on the ancestry of birds. In fact, their claims of homology of the integumentary appendages of *Longisquama* with avian feathers was an incidental point of the paper, based basically on their opinions and not on a careful phylogenetic treatment, which is the ultimate arbiter of homology. It is fair to say that Jones et al. (2000a) demonstrated that the integumentary appendages of *Longisquama* are more interesting and unusual than previously thought. Beyond that—and in the absence of a phylogenetic analysis—*Longisquama* and its appendages are as irrelevant to the debate on the origin of birds as are the other “avimorph” forms.

In sum, at present there remains no credible alternative to maniraptoran theropod dinosaurs for the origin of birds. Previous tangible alternatives (crocodylomorphs, basal archosauriforms such as *Euparkeria*) have been refuted or summarily dropped because of lack of interest. What has replaced these are intangible “models” that conform to preconceived notions on how bird flight evolved, that is, taxa that, although not truly related to birds, are “much like what we would expect” the true ancestors to be. In some ways, it seems as if the search for real avian relatives has been supplanted by the mission to discredit both the theropod hypothesis and the cladistic methodology that continues to corroborate the hypothesis. Fossils such as *Longisquama* may someday emerge as more relevant players in the debate, but if the media hype surrounding the Jones et al. (2000a) paper was any indication, even *Longisquama* will be just another attempt to develop a rhetorical weapon to attack the theropod hypothesis and cladistics.

## The Status of the Theropod Hypothesis

The only explicit hypothesis for the phylogenetic relationships of birds states that avian ancestry is fully embedded somewhere within the nexus of maniraptoran theropod dinosaurs, probably nearest to Dromaeosauridae and/or Troodontidae among known groups. As such, it is “the only game in town.” As mentioned previously, opponents of theropod relationships have regarded the hypothesis as basically an unfortunate outcome of sloppy application of phylogenetic systematics. However, the idea was formulated by Ostrom (1973) and initially supported (e.g., Bakker and Galton, 1974; Thulborn, 1975; Thulborn and Hamley, 1982) without cladistics. In large measure, the many cladistic studies that have followed have served mostly to support, clarify, and update Ostrom’s original work. More important, they have repeatedly tested the hypothesis (although, to be fair, it must be pointed out that they rarely include nondinosaurian taxa in the analysis). Among the more important cladistic studies are those of Padian (1982), Thulborn (1984), Gauthier (1986), Holtz (1994), Novas (1996), Forster et al. (1998), Sereno (1999a), and Clark, Norell, and Makovicky (Chapter 2 in this volume).

Until the reemergence of Alan Feduccia in the debate in the mid-1990s, opposition to the theropod hypothesis had become basically mute, and, in my opinion, theropod advocates had become complacent (Witmer, 1997b). But Feduccia reenergized the opposition, enlisting new recruits (e.g., J. A. Ruben) and strengthening former alliances (e.g., with L. D. Martin). The warfare metaphor is intended to be lighthearted, but there is clearly a sense that this group feels as if it is fighting a holy war against a great oppressor; Feduccia (quoted in Shipman, 1997b:29) went so far as to regard Ruben as a “comrade in the war against hot-blooded dinos.” This group has offered criticisms on a number of fronts. Much of the criticism has taken the form of comments to the media, book reviews (Martin, 1988, 1998), popular articles or books (Feduccia, 1994, 1996, 1999b), and other outlets outside normal peer review (e.g., Martin 1997). Chief among these criticisms is that relating to the functional problems of evolving flight in an arboreal context when theropods seem to have been such obligate terrestrial animals; having discussed the multiple fallacies in this general approach earlier, I will turn to other issues. More specific challenges can be grouped into three categories: (1) the time problem, (2) problems of morphological interpretation or homology, and (3) single problems of such significance that they alone would falsify the theropod hypothesis. Martin (1997:337) regarded these criticisms as causing a “collapse of various anatomical arguments for a bird-dinosaur connection followed by determined efforts [by advocates of theropod relationships] to bolster failing characters.” However, I do not regard such efforts at “damage

control” (as he later put it [Martin, 1998:42]) as inappropriate but rather as a normal part of the scientific process in which new data or claims are evaluated. In this light, let us briefly examine these three categories.

The “time problem”—or “temporal paradox,” as it is often known—relates to the fact that the closest nonavian theropod sister groups of birds are all Cretaceous in age and hence younger than *Archaeopteryx*. The issue has been raised many times over the years, but Feduccia has wielded it as a bludgeon. For example, he stated that “to such workers [paleontologists] it is inconsequential that birdlike dinosaurs occur some 75 million or more years after the origin of birds” (Feduccia, 1996:vii). Elsewhere, Feduccia (1994:32, italics in original) painted an even worse picture, claiming that “most of the supposed similarities between the *urvögel* [meaning specifically *Archaeopteryx*] and dinosaurs are seen in birdlike dinosaurs that lived 80 to 100 million years later.” The latter date in the second quote would actually put these “birdlike dinosaurs” in the Eocene (!)—perhaps a simple mistake on Feduccia’s part, but it reflects a consistent hyperbolic exaggeration of the time discordance (Witmer, 1997b).

It is true that, say, *Velociraptor* is 70 My younger than *Archaeopteryx*, but other dromaeosaurids and troodontids are much closer in age to *Archaeopteryx*: *Deinonychus* is 35 My younger, *Utahraptor* is only 25 My younger, *Sinornithosaurus* is only about 20 My younger, and *Sinovenator* is less than 17 My younger (Swisher et al., 1999; Xu et al., 2002). There are much greater time discordances in the dinosaur fossil record (Sereno, 1997b, 1999a) than this one. But, moreover, there are a variety of fragmentary specimens (mostly teeth) of animals that closely resemble those of dromaeosaurids and troodontids recovered from Middle Jurassic deposits that predate *Archaeopteryx* by 20 My (Evans and Milner, 1994; Metcalf and Walker, 1994). Similarly, Zinke (1998) reported on an extensive collection of theropod teeth from deposits perhaps just slightly older than *Archaeopteryx*; Zinke made firm assignments of these teeth to Dromaeosauridae (29 teeth), Troodontidae (14 teeth), and Tyrannosauridae (3 teeth). Finally, Jensen and Padian (1989) described fragmentary but provocative skeletal material of maniraptoran theropods from the Late Jurassic Morrison Formation. Even if some of these precise taxonomic assignments do not stand scrutiny, they clearly indicate that there were nonavian maniraptorans that existed prior to *Archaeopteryx*. Moreover, Brochu and Norell (2000) pursued the temporal paradox issue by comparing stratigraphic consistency indices and other phylogenetic metrics among various hypotheses for avian origins, and they found that the theropod hypothesis actually compares favorably to the alternatives when considered globally across the cladogram. Thus, not only is the time problem not particularly severe, it does

not even exist, and its perpetuation in the face of such data is untenable.

Opponents of theropod relationships have questioned either the interpretation or the homology of a number of characters (see Martin, 1983, 1991, 1997, 1998; Tarsitano, 1991; Feduccia, 1996, 1999a). Only one of the higher-profile characters will be discussed here as an example, and that is the semilunate carpal, one of the classic Ostrom characters. Ostrom (1973) originally—and erroneously—regarded the element in *Deinonychus* as a radiale (i.e., a proximal carpal element), even though it clearly was much more tightly articulated to the metacarpus than to the antebrachium. Gauthier (1986), without fanfare, corrected this error and regarded it as a distal carpal, which is the identity of the semilunate element in birds. Nevertheless, the homology has been vigorously questioned (see Martin, 1991, 1997; Feduccia, 1996, and references therein). Until relatively recently, the complete carpal structure was understood for relatively few theropods. However, the wrist is now known in many theropods, and the presence of a semilunate carpal characterizes a broad taxon (Neotetanurae), where it can be seen to be a distal carpal element (Serenó, 1999a). For example, within coelurosaurians there are specimens (e.g., *Scipionyx samniticus* [Dal Sasso and Signore, 1998] and *Sinornithoides youngi* [Russell and Dong, 1993; personal observation of IVPP V9612]) that clearly show the semilunate carpal to be *distal* to another carpal element (the radiale), clinching its identity as a distal carpal. Neither Feduccia (1996) nor Martin (1997) cited the new evidence from *Sinornithoides*, despite the fact that Russell and Dong (1993:2169) clearly identified both a radiale and a semilunate carpal. There seems to be little reason to doubt the homology of the carpal elements of nonavian maniraptorans, *Archaeopteryx*, and other birds. Some of the challenges to other characters have been addressed by other workers, for example, the furcula and sternum (Norell and Makovicky, 1997; Norell et al., 1997; Makovicky and Currie, 1998; Clark et al., 1999; Sereno, 1999a) and the pelvis (Norell and Makovicky, 1997, 1999).

Two issues have been proposed as being so important that they alone would have the power to overthrow the entire theropod hypothesis. These issues are the homology of the manual digits and the evolution of the lung ventilatory mechanism. The question of digital homologies has a fairly long and extensive history (see Hinchliffe and Hecht, 1984) but basically involves a conflict between paleontology and embryology. There is almost unanimous agreement that the pattern of digit reduction observed throughout theropod phylogeny indicates that the digits of maniraptorans are I-II-III (Ostrom, 1976; Gauthier, 1986; Tarsitano, 1991; Feduccia, 1996; Sereno, 1997b; Chatterjee, 1998a; Padian and Chiappe, 1998b). Thus, those who regard birds as dinosaurs accept that birds also retain digits I–III. The con-

flikt arises because embryologists have repeatedly come up with the result that the avian hand skeleton has digits II–IV (Hinchliffe and Hecht, 1984; Hinchliffe, 1985; Shubin and Alberch, 1986). Opponents of theropod relationships (Tarsitano and Hecht, 1980; Martin, 1991; Tarsitano, 1991; Feduccia, 1996) seized on this as a potentially fatal flaw: if birds truly evolved from dinosaurs, then birds would have had to have lost one finger (I) and gained another (IV)—an unlikely proposition.

For more than a decade this debate was basically a stalemate, until a paper published by Burke and Feduccia (1997) reopened the issue. The paper offered few new data or insights; instead, it largely restated the conflict, updated the embryological component by integrating the primary-axis paradigm of Shubin and Alberch (1986), and asserted that these data refute the theropod relationships of birds. There are valid complaints that can be leveled at the Burke and Feduccia study (e.g., see Chatterjee, 1998a; Garner and Thomas, 1998; Padian and Chiappe, 1998a,b; Zweers and Vanden Berge, 1998), and I could add some additional ones. But rather than expand this discussion with elaborate counterpoints, a broader issue needs to be raised, and that is the relationship between different kinds of data, in this case paleontological and embryological. There is a sense among some that the embryological signal must be correct because it involves seemingly high-tech bench science and makes reference to hox genes, as opposed to the dust and dirt of paleontology. The fact is that both disciplines require a lot of interpretation of the data. The observed embryonic condensations and their pattern of connectivity do not come with unequivocal labels but rather require much interpretation before elements can be identified. For instance, the structure that Burke and Feduccia (1997) identified as a transient metacarpal V in chicken hand development could indeed be just that, but it is never part of the metacarpal arcade and could just as easily be regarded as a bifurcation of the adjacent carpal condensation. Given that these embryological data are no “cleaner” than paleontological data, I am reluctant to accept their implications, particularly when studies by Hinchliffe (e.g., 1985) clearly document that avian hand development is a complicated and unusual system (with the ulnare progressively disappearing and replaced by a mysterious “X element” of uncertain origin). Thus, I do not find compelling the paper of Wagner and Gauthier (1999) that argued that, in effect, both embryologists and paleontologists are correct. They suggested that there has been a “frame shift” in “developmental identities” over the course of theropod phylogeny such that embryonic condensations II–IV differentiate into definitive digits I–III somewhere near the origin of Tetanurae. It is a tidy and intriguing hypothesis, but it seems largely untestable (since the embryology of fossil taxa is unknowable) and probably is circular (they must “postulate a frame shift” and hence

cannot then use these data to *deduce* a frame shift). In sum, unless some new line of evidence arises, I continue to find the I-II-III assessment to be the most conservative and the best supported.

Whereas the discussion on digital homologies often seems to be a tired topic, a fresh new challenge came from a paper by J. A. Ruben and colleagues (1997). In this paper, they argued that theropod dinosaurs lacked an avian-style flow-through lung (i.e., with abdominal air sacs, etc.) but rather had a crocodylianlike “hepatic piston” whereby the lungs were ventilated with the assistance of a hepatic-diaphragmatic complex that was retracted (like a piston) by diaphragmatic muscles attaching to the pubis. Despite obvious significance for dinosaur physiology, what has engendered more controversy is a statement in the Ruben et al. (1997) paper suggesting that the presence of such a lung ventilatory system in theropods would effectively deny them the possibility of being the progenitors of birds. Their point is that the hepatic piston is an evolutionarily canalized system that could never evolve into an avian system. Thus, despite all the evidence from cladistics, birds could not have had their origins among theropod dinosaurs.

Evaluating this proposition involves two separate issues. First, did theropods actually have a crocodylianlike hepatic piston? And second, even if they did, how do we know that such a system could not evolve into the avian system? The first issue is really beyond the scope of this chapter. Nevertheless, Ruben et al. (1997:1270) stated that “the hepatic-piston diaphragm systems in crocodylians and theropods are convergently derived.” Thus, the theropod system would constitute, according to the inferential hierarchy of Witmer (1995a), a level III inference, that is, a relatively weak soft-tissue inference requiring exceptionally compelling morphological evidence. The second issue is more pertinent here in that it speaks directly to the origin of birds. The problem with the claim of canalization by Ruben et al. (1997) is that it is based not so much on evidence as on authority. That is, canalization is asserted rather than demonstrated. These authors have argued that, basically, “you can’t get there from here.” How could we test this hypothesis that the avian system could not evolve from the presumed hepatic piston of theropod? An obvious test is a phylogenetic one: integrate it with other data and let it play out on the cladogram. Given the considerable evidence that birds are embedded within Theropoda, it would seem that indeed “you *can* get there from here,” even if the physiological or anatomical mechanism is at present obscure.

In sum, regardless of whether the inference of the hepatic-pump ventilatory system in theropods is sufficiently robust to be sustained, there seems to be little in the Ruben et al. (1997) paper that requires an overhaul of our views on avian origins. Significantly perhaps, in a more recent paper that sought to bolster the theropod hepatic-

pump hypothesis, Ruben et al. (1999) made no mention of any relevance of this research to the origin of birds, although Feduccia (1999a) continued to tout such evidence as damning to the theropod hypothesis.

Despite such external challenges to the theropod origin of birds, this hypothesis has survived and continually gains news adherents. This final section will examine briefly the theropod hypothesis from within, particularly with regard to the diversity of opinion. In my 1991 review, I was able to report a fair amount of diversity within the general notion that birds were somehow closely related to theropods. At that time, there were active hypotheses that suggested that birds were closest to coelophysoids, troodontids, oviraptorosaurs, dromaeosaurids, and *Avimimus* (see Witmer, 1991, and references therein). At the dawn of the twenty-first century, there is remarkably little diversity. Instead, the phylogenetic analyses from all the sources cited earlier seem to be converging on close relationships to Dromaeosauridae, Troodontidae, or a Deinonychosauria clade (Dromaeosauridae + Troodontidae).

Still there is diversity. A recent development that has not received wide attention derives from the collaboration of G. A. Zweers and J. C. Vanden Berge (Zweers et al., 1997; Zweers and Vanden Berge, 1998). These authors have devised an elaborate and intriguing scheme for the evolution of the feeding or trophic apparatus in birds. Despite Feduccia’s consistent portrayal (e.g., Feduccia, 1994, 1996) of the origin debate as basically a dichotomy between ornithologists and paleontologists, Zweers and Vanden Berge, two of the leading anatomical ornithologists in Europe and North America, respectively, firmly embedded birds within Theropoda. In fact, they not only “embedded” birds within Theropoda but actually “scattered” avian clades throughout Theropoda in that they, somewhat reminiscent of Lowe (1935, 1944), argued for the polyphyly of birds (Zweers and Vanden Berge, 1998). In their scheme, *Archaeopteryx*, Alvarezsauridae, and Enantiornithes form a clade with dromaeosaurids as the basal taxon; hoatzins, cranes, and palaeognaths form a clade with *Hesperornis*, *Ichthyornis*, and ornithomimids; and all other birds and *Confuciusornis* form a clade with troodontids as its basal taxon. It is impossible to do justice here to the complexity of the functional arguments presented in these papers, although they are very enlightening and engaging whether or not one accepts the authors’ phylogenetic scheme. In fact, throughout both papers, particularly Zweers et al. (1997), it is not that clear whether the scheme is intended to reflect a hypothetical functional framework or a true depiction of phylogeny. But in Zweers and Vanden Berge (1998:183) it eventually becomes clear that they indeed regard birds as polyphyletic, describing “successive waves of avian radiation.” Nevertheless, they recognized that “at several points this scenario does not coincide with the most recent avian phylogeny,

which remains to be explained” (Zweers and Vanden Berge, 1998:183).

Indeed, it is likely that their scheme would be found to be less parsimonious than a cladogram produced by, say, Chiappe or Sereno. But their notion of “successive waves of avian radiation” is not entirely new and represents just the most recent version of the idea that birds and “conventional” theropods are more intertwined than commonly thought. For example, G. S. Paul (1984, 1988, 2002) suggested that perhaps the traditional ancestor-descendant relationships have been interpreted backward: perhaps some “conventional” theropods (such as dromaeosaurids, troodontids, oviraptorosaurs) are in fact secondarily flightless descendants of a persistent lineage of “protobirds.” This protobird lineage would have had its origins in the Jurassic period with *Archaeopteryx*, becoming progressively more birdlike in the Cretaceous. Paul (2002) cited a variety of lines of evidence by which “neoflightless” taxa could be identified, pointing in particular to the shoulder girdle and thoracic appendage. In some ways, this hypothesis arises from the realization that, unlike in other groups of flying vertebrates (i.e., bats and pterosaurs), flightlessness has been a recurrent evolutionary theme of birds. Thus, what would a flightless form look like at about the *Archaeopteryx* stage? It might look very much like a small dromaeosaur. Paul (2002) acknowledged that the cladistic representation and discovery of such a pattern are problematic. Paul is not alone in deriving some “nonavian” theropods from birds. For example, Elzanowski (1995, 1999) and Lü (2000) regarded oviraptorosaurs as being not just very closely related to birds but potentially a clade of early flightless birds. If this is proven true, Feduccia (1999a), perhaps ironically, would then be correct that the basal oviraptorosaur *Caudipteryx* is just a Mesozoic kiwi after all! Finally, Olshevsky (1994) proposed the “Birds Came First” (BCF) theory, which maintains that the evolution of archosaurs is characterized by an arboreal “central line” of “dino-birds” that sprouted terrestrial branches, giving rise to the various clades of archosaurs. Throughout the Mesozoic, this central line would have gotten more and more birdlike, and thus their terrestrial offshoots also became progressively birdlike. As in Paul’s hypothesis, the Cretaceous coelurosaurs would be secondarily flightless.

All these latter ideas are truly out of the mainstream of current thought and present some problems for testing by phylogenetic analysis. In a sense, they are similar to the scenario-based, “function-first” methodology criticized in an earlier section. Nevertheless, they merit the scrutiny that they have never adequately received. As a class, they are all very similar in that they propose an iterative process to the evolution of birds and theropods. For what it is worth, these proposals have the distinct advantage that all the supposed time discordances basically disappear yet all the anatomical

similarities remain homologous. The “successive waves of avian radiation” scheme described by Zweers and Vanden Berge is not far removed from the successive waves of theropod descent from an avian stem envisioned by Paul and Olshevsky. In all these formulations, the evolution of birds and theropods is hopelessly intertwined. The current orthodoxy (Ostrom, 1976; Gauthier, 1986; Sereno, 1999a) has produced a fairly tidy phylogenetic pattern. These nonstandard views are decidedly untidy, yet they still should receive serious consideration, and this will happen only when they are framed in explicit, phylogenetic terms.

## Conclusions

The issues surrounding the origin of birds are wide ranging, and this chapter has attempted to capture this diversity. As a result, it is a bit of a hodgepodge and has sought to touch on those issues that, in particular, have controlled the debate. Throughout the chapter, I have focused on the debate itself, because *how* things are discussed affects *what* is discussed. That is, rhetoric and science are, lamentably, inextricably linked. As I am neither a sociologist nor a psychologist, I have tried not to delve into matters of motivation, politics, and ego. Nevertheless, in this modern media age, it would be naive to think that these factors have not helped shape the debate, and the sociology of the debate would be a very interesting study indeed. Science and the scientific method, however, will ultimately prevail and produce a broad consensus on at least the major issues.

For paleontologists faced with controversy, the traditional appeal is for more and better fossils. In this case, however, methodology—not fossils—will have to be the key to achieving agreement and converting dissenters. We already have abundant well-preserved fossils documenting the transition to birds among theropod dinosaurs. Yet those opposed to theropod relationships remain unwilling to accept and apply the cladistic methodology that has elucidated this transition. If the theropod ancestry of birds is the nonsense that some would have us believe, why is it that so many highly trained specialists seem to keep confusing birds for dinosaurs or vice versa? The list of taxa that have bounced back and forth between birds and theropods is quite long: Alvarezsauridae, *Archaeopteryx* (Eichstätt specimen), *Archaeornithoides*, *Avimimus*, *Avisaurus*, *Bradycneme*, *Caenagnathus*, *Caudipteryx*, *Limnornis*, Oviraptoridae, *Palaeocursornis*, *Protarchaeopteryx*, *Protoavis*, *Wyleyia*. It would seem to be simple common sense to think that birds and dinosaurs must have *some* close relationship if we have such trouble telling them apart. Of course, evolutionary convergence is the usual explanation invoked by opponents of theropod relationships to explain the resemblances. But this, too, seems to fly in the face of logic: on

the one hand, we are told that the similarities have arisen because of convergence—the independent acquisition of similar attributes due to similar function and mode of life—but then, on the other hand, we are told that theropods and the ancestors of birds had totally different body plans, body sizes, preferred habitats, and modes of life (i.e., large, bipedal, terrestrial theropods versus small, quadrupedal, and arboreal alternative ancestors). How can they have it both ways? Cladistic methodology argues that convergence and homology are not asserted or assumed but rather are hypothesized and subsequently tested within a comprehensive phylogenetic analysis. I fully expect that, if we had the *true* and complete phylogenetic tree, we would indeed find that some of the characters shared by birds and maniraptoran theropods were convergently acquired—but certainly not *all* of them, considering that there is hardly a bone of the body that fails to show synapomorphies at some level.

The debate on avian ancestry has had a long and contentious history, and this is likely to continue for some time. It all started with *Archaeopteryx*, and *Archaeopteryx* remains the central figure, although, if the situation is as complicated as Paul (2002) or Zweers and Vanden Berge (1998) suggest, this may prove to have been folly. A remarkable development witnessed in recent years is that, as support for the theropod origin of birds mounts and becomes more refined, the opposition has taken on a shrill tone and has seemingly abandoned the search for cogent and articulate alternative hypotheses, instead choosing to attack the dinosaur hypothesis, its methodology, and even its purveyors. Ironically, virtually all recent thought on the relationship of functional to phylogenetic inference has challenged the “function-first” approach advocated by those arguing for an arboreal origin of avian flight from nontheropodan ancestors. But ultimately the debate will be resolved by both fossils and philosophy. For example, the recent discovery of nonavian theropods with true feathers, such as *Caudipteryx*, has already satisfied many people that the debate is over. History, however, would suggest that such a view is unwarranted. The irony of paleontological discovery has always been that the picture seems simpler and more understandable with fewer fossil taxa; as new taxa are discovered, the water often becomes muddier. Hypotheses fall, to be replaced by new ones. The theropod ancestry of birds has weathered many challenges, and I predict that it will continue to do so. But if new fossils are discovered (as we know they will) and if minds remain open (as we hope they will), the true nature of this relationship may be much more complicated than we can even envision today.

#### Acknowledgments

For comments on this chapter, I thank L. M. Chiappe, K. Padian, and J. C. Sedlmayr. For sharing unpublished information, I thank

S. Chatterjee, L. M. Chiappe, P. J. Currie, T. D. Jones, G. S. Paul, J. A. Ruben, Xu X., and Zhou Z. Funding was provided by the National Science Foundation (IBN-9601174) and the Ohio University College of Osteopathic Medicine.

#### Literature Cited

- Abel, O. 1911. Die Vorfahren der Vögel und ihre Lebensweise. *Verhandlungen der Zoologischen-botanischen Gesellschaft, Vienna* 61:144–191.
- Ackerman, J. 1998. Dinosaurs take wing. *National Geographic* 194(1):74–99.
- Bakker, R. T., and P. M. Galton. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature* 248:168–172.
- Balda, R. P., G. Caple, and W. R. Willis. 1985. Comparison of the gliding to flapping sequence with the flapping to gliding sequence; pp. 267–277 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- Barsbold R. 1979. Opisthopubic pelvis in the carnivorous dinosaurs. *Nature* 279:792–793.
- . 1983. Carnivorous dinosaurs from the Cretaceous of Mongolia. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition* 19:5–119. [Russian, English summary]
- Barsbold R. and Perle A. 1979. Modification of saurischian pelvis and parallel evolution of carnivorous dinosaurs. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition* 8:39–44. [Russian, English summary]
- . 1980. Segnosauria, a new infraorder of carnivorous dinosaurs. *Acta Palaeontologica Polonica* 25:187–195.
- Barsbold R., P. J. Currie, N. P. Myhrvold, H. Osmólska, Tsogtbaatar K., and M. Watabe. 2000a. A pygostyle from a nonavian theropod. *Nature* 403:155–156.
- Barsbold R., H. Osmólska, M. Watabe, P. J. Currie, and Tsogtbaatar K. 2000b. A new oviraptorosaur (Dinosauria, Theropoda) from Mongolia: the first dinosaur with a pygostyle. *Acta Palaeontologica Polonica* 45:97–106.
- Benton, M. J. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London B* 354:1423–1446.
- Bock, W. J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Systematic Zoology* 14:272–287.
- . 1985. The arboreal theory for the origin of birds; pp. 199–207 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- . 1986. The arboreal origin of avian flight; pp. 57–72 in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. California Academy of Sciences, San Francisco.
- . 1997. Review of: *The Origin and Evolution of Birds*, by A. Feduccia. *Auk* 114:531–534.
- . 1999. Review of: *The Mistaken Extinction: Dinosaur Evolution and the Origin of Birds*. *Auk* 16:566–568.
- Bock, W. J., and P. Bühler. 1995. Introduction to the symposium. *Archaeopteryx* 13:3–4.
- Brinkman, D. L., R. L. Cifelli, and N. J. Czaplewski. 1998. First occurrence of *Deinonychus antirrhopus* (Dinosauria: Theropoda) from the Antlers Formation (Lower Cretaceous:

- Aptian-Albian) of Oklahoma. Oklahoma Geological Survey Bulletin 146:1–27.
- Brochu, C. A., and M. A. Norell. 2000. Temporal congruence and the origin of birds. *Journal of Vertebrate Paleontology* 20:197–200.
- Brush, A. H., L. D. Martin, J. H. Ostrom, and P. Wellnhofer. 1997. Bird or dinosaur?—statement of a team of specialists. *Episodes* 20(1):47.
- Bryant, H. N., and A. P. Russell. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London B* 337:405–418.
- . 1993. The occurrence of clavicles within Dinosauria: implications for the homology of the avian furcula and the utility of negative evidence. *Journal of Vertebrate Paleontology* 13(2):171–184.
- Burgers, P., and L. M. Chiappe. 1999. The wing of *Archaeopteryx* as a primary thrust generator. *Nature* 399:60–62.
- Burke, A. C., and A. Feduccia. 1997. Developmental patterns and the identification of homologies in the avian hand. *Science* 278:666–668.
- Burnham, D. A., K. L. Derstler, P. J. Currie, R. T. Bakker, Zhou Z., and J. H. Ostrom. 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. University of Kansas Paleontological Contributions, New Series 13:1–14.
- Cai Z. and Zhao L. 1999. A long tailed bird from the Late Cretaceous of Zhejiang. *Science in China (Series D)* 42(4):434–441.
- Caple, G., R. P. Balda, and W. R. Willis. 1983. The physics of leaping animals and the evolution of preflight. *American Naturalist* 121:455–467.
- Charig, A. J. 1976. Order Thecodontia Owen 1859; pp. 7–10 in O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, Teil 13. Gustav Fischer Verlag, New York.
- Chatterjee, S. 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. *Philosophical Transactions of the Royal Society of London B* 309:395–460.
- . 1987. Skull of *Protoavis* and early evolution of birds. *Journal of Vertebrate Paleontology* 7(Supplement to 3):14A.
- . 1988. Functional significance of the semilunate carpal in archosaurs and birds. *Journal of Vertebrate Paleontology* 8(Supplement to 3):11A.
- . 1991. Cranial anatomy and relationships of a new Triassic bird from Texas. *Philosophical Transactions of the Royal Society of London B* 332:277–342.
- . 1993. *Shuvosaurus*, a new theropod. *National Geographic Research and Exploration* 9:274–285.
- . 1995. The Triassic bird *Protoavis*. *Archaeopteryx* 13:15–31.
- . 1997a. *The Rise of Birds: 225 Million Years of Evolution*. Johns Hopkins University Press, Baltimore, 312 pp.
- . 1997b. The beginnings of avian flight; pp. 311–335 in D. L. Wolberg, E. Stump, and G. Rosenberg (eds.), *Dinofest International: Proceedings of a Symposium Held at Arizona State University*. Academy of Natural Sciences, Philadelphia.
- . 1998a. Counting the fingers of birds and dinosaurs. *Science* 280:355a.
- . 1998b. The avian status of *Protoavis*. *Archaeopteryx* 16:99–122.
- . 1999. *Protoavis* and the early evolution of birds. *Palaeontographica*, Abteilung A 254:1–100.
- Chen P.-J., Dong Z.-M., and Zhen S.-N. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* 391:147–152.
- Chiappe, L. M. 1992. Enantiornithine (Aves) tarsometatarsi and the avian affinities of the Late Cretaceous Avisauridae. *Journal of Vertebrate Paleontology* 12:344–350.
- . 1995. The first 85 million years of avian evolution. *Nature* 378:349–355.
- . 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantiornithes and *Patagopteryx deferrariisi*; pp. 203–244 in G. Arratia (ed.), *Contributions of Southern South America to Vertebrate Paleontology*. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie 30. Verlag Dr. Friedrich Pfeil, Munich.
- . 1997. Aves; pp. 32–38 in P. J. Currie and K. Padian (eds.), *The Encyclopedia of Dinosaurs*. Academic Press, New York.
- . 1998. Review of: *The Rise of Birds: 225 Million Years of Evolution*, by S. Chatterjee. *American Zoologist* 38(4):797–798.
- Chiappe, L. M., M. A. Norell, and J. M. Clark. 1996. Phylogenetic position of *Mononykus* (Aves: Alvarezsauridae) from the Late Cretaceous of the Gobi Desert. *Memoirs of the Queensland Museum* 39(3):557–582.
- Chiappe, L. M., Ji S., Ji Q., and M. A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *Bulletin of the American Museum of Natural History* 242:1–89.
- Chure, D. J., and J. H. Madsen Jr. 1996. On the presence of furculae in some non-maniraptoran theropods. *Journal of Vertebrate Paleontology* 16(3):573–577.
- Clark, J. M., M. A. Norell, and L. M. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an oviraptorid nest. *American Museum Novitates* 3265:1–36.
- Cousins, F. W. 1973. The alleged evolution of birds (*Archaeopteryx*); pp. 89–99 in D. W. Patten (ed.), *Symposium in Creation III*. Baker Book House, Grand Rapids, Mich.
- Cracraft, J. 1990. The origin of evolutionary novelties: pattern and process at different hierarchical levels; pp. 21–44 in M. H. Nitecki (ed.), *Evolutionary Innovations*. University of Chicago Press, Chicago.
- Currie, P. J. 1997. “Feathered” dinosaurs; p. 241 in P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, New York.
- . 1998. *Caudipteryx* revealed. *National Geographic* 194(1):86–89.
- Currie, P. J., and Zhao X. J. 1993. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. *Canadian Journal of Earth Sciences* 30:2231–2247.
- Czerkas, S. 1994. The history and interpretation of sauropod skin impressions. *Gaia* 10:173–182.
- Dal Sasso, C., and M. Signore. 1998. Exceptional soft-tissue preservation in a theropod dinosaur from Italy. *Nature* 392:383–387.
- de Beer, G. R. 1954. *Archaeopteryx lithographica: A Study Based upon the British Museum Specimen*. Natural History Museum, London, 68 pp.

- . 1956. The evolution of ratites. *Bulletin of the British Museum (Natural History), Zoology* 4(2):59–70.
- de Queiroz, K., and J. A. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definition of taxon names. *Systematic Zoology* 39:307–322.
- . 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23:449–480.
- Dingus, L., and T. Rowe. 1997. *The Mistaken Extinction: Dinosaur Evolution and the Origin of Birds*. W. H. Freeman and Company, New York, 332 pp.
- DiSilvestro, R. L. 1997. In quest of the origin of birds. *BioScience* 47(8): 481–485.
- Dyck, J. 1985. The evolution of feathers. *Zoologica Scripta* 14(2):137–154.
- Dyke, G. J., and J. Thorley. 1998. Reduced cladistic consensus methods and the inter-relationships of *Protoavis*, *Avimimus* and Mesozoic birds. *Archaeopteryx* 16:123–129.
- Ebel, K. 1996. On the origin of flight in *Archaeopteryx* and in pterosaurs. *Neues Jahrbuch für Geologie und Paläontologie* 202:269–285.
- Elzanowski, A. 1995. Cranial evidence for the avian relationships of Oviraptorosauria. *Journal of Vertebrate Paleontology* 15(Supplement to 3):27A.
- . 1999. A comparison of the jaw skeleton in theropods and birds, with a description of the palate in Oviraptoridae; pp. 311–323 in S. L. Olson (ed.), *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution*, Washington, D.C., 4–7 June 1996. *Smithsonian Contributions to Paleobiology* 89, Washington.
- Evans, S. E., and A. R. Milner. 1994. Middle Jurassic microvertebrate assemblages from the British Isles; pp. 303–321 in N. C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, New York.
- Feduccia, A. 1993. Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science* 259:790–793.
- . 1994. The great dinosaur debate. *Living Bird* 13:29–33.
- . 1995. Explosive evolution in Tertiary birds and mammals. *Science* 267:637–638.
- . 1996. *The Origin and Evolution of Birds*. Yale University Press, New Haven, 420 pp.
- . 1999a. 1, 2, 3, = 2, 3, 4: accommodating the cladogram. *Proceedings of the National Academy of Sciences* 96:4740–4742.
- . 1999b. *The Origin and Evolution of Birds*, 2nd edition. Yale University Press, New Haven, 466 pp.
- Feduccia, A., and L. D. Martin. 1998. Theropod-bird link reconsidered. *Nature* 391:754.
- Feduccia, A., and R. Wild. 1993. Birdlike characters in the Triassic archosaur *Megalancosaurus*. *Naturwissenschaften* 80:564–566.
- Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279:1915–1919.
- Garner, J. P., and A. L. R. Thomas. 1998. Counting the fingers of birds and dinosaurs. *Science* 280:355a.
- Gatesy, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* 16(2):170–186.
- Gatesy, S. M., and K. P. Dial. 1996a. Locomotor modules and the evolution of avian flight. *Evolution* 50(1):331–340.
- . 1996b. From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. *Evolution* 50(5):2037–2048.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds; pp. 1–55 in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. California Academy of Sciences, San Francisco.
- Gauthier, J., and L. F. Gall (eds.). 2001. *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of an International Symposium in Honor of John H. Ostrom*. Yale University Press, New Haven.
- . 2001. The role of *Protoavis* in the debate on avian origins; pp. 537–548 in J. Gauthier and L. F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of an International Symposium in Honor of John H. Ostrom*. Yale University Press, New Haven.
- Gauthier, J., and K. Padian. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight; pp. 185–197 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- Geist, N. R., T. D. Jones, and J. A. Ruben. 1997. Implications of soft tissue preservation in the compsognathid dinosaur, *Sino-sauropteryx*. *Journal of Vertebrate Paleontology* 17(Supplement to 3):48A.
- Gibbons, A. 1996. New feathered fossil brings dinosaurs and birds closer. *Science* 274:720–721.
- . 1997a. Feathered dino wins a few friends. *Science* 275: 1731.
- . 1997b. Plucking the feathered dinosaur. *Science* 278: 1229.
- Gower, D. J., and E. Weber. 1998. The braincase of *Euparkeria*, and the evolutionary relationships of birds and crocodylians. *Biological Reviews* 73:367–411.
- Griffiths, P. J. 1996. The isolated *Archaeopteryx* feather. *Archaeopteryx* 14:1–26.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen*. Zweiter Band: Allgemeine Entwicklungsgeschichte der Organismen. G. Reimer, Berlin.
- . 1876. *The History of Creation*, Volume II (Lankester Translation). Appleton, New York, 544 pp.
- Haubold, H., and E. Buffetaut. 1987. A new interpretation of *Longisquama insignis*, an enigmatic reptile from the Upper Triassic of Central Asia. *Comptes Rendus de l'Académie des Sciences du Paris* 305:65–70.
- Hecht, M. K., J. H. Ostrom, G. Viohl, and P. Wellnhofer. 1985. Preface; p. 7 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- Heilmann, G. 1926. *The Origin of Birds*. Witherby, London, 208 pp.
- Herzog, K. 1993. Stammesgeschichtliche Entwicklung des Flugvermögens der Vögel. *Archaeopteryx* 11:49–61.
- Hinchliffe, J. R. 1985. “One, two, three” or “two, three, four”: an embryologist’s view of the homologies of the digits and carpus of modern birds; pp. 141–147 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- Hinchliffe, J. R., and M. K. Hecht. 1984. Homology of the bird wing skeleton: embryological versus paleontological evidence. *Evolutionary Biology* 18:21–39.

- Holtz, T. R., Jr. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68:1100–1117.
- Hopson, J. A., and L. M. Chiappe. 1998. Pedal proportions of living and fossil birds indicate arboreal or terrestrial specialization. *Journal of Vertebrate Paleontology* 18(Supplement to 3):52A.
- Hou L.-H., L. D. Martin, Zhou Z.-H., A. Feduccia, and Zhang F. 1999. A diapsid skull in a new species of the primitive bird *Confuciusornis*. *Nature* 399:679–682.
- Hutchinson, J. R. 2001a. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131:123–168.
- . 2001b. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131:169–197.
- Huxley, T. H. 1867. On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. *Proceedings of the Zoological Society of London* 1867:415–472.
- . 1868. On the animals which are most nearly intermediate between birds and reptiles. *Annals and Magazine of Natural History* 4(2):66–75.
- Jenkins, F. A., Jr. 1993. The evolution of the avian shoulder joint. *American Journal of Science* 293-A:253–267.
- Jensen, J. A., and K. Padian. 1989. Small pterosaurs and dinosaurs from the Uncompahgre fauna (Brushy Basin Member, Morrison Formation: ?Tithonian), Late Jurassic, western Colorado). *Journal of Paleontology* 63:364–373.
- Ji Q. and Ji S.-A. 1996. On discovery of the earliest bird fossil in China and the origin of birds. *Chinese Geology* 23:30–33. [Chinese]
- . 1997. *Protoarchaeopteryx*, a new genus of Archaeopterygidae in China. *Chinese Geology* 23:38–41. [Chinese]
- Ji Q., P. J. Currie, M. A. Norell, and Ji S.-A. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761.
- Ji Q., M. A. Norell, Gao K.-Q., Ji S.-A., and Ren D. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* 410:1084–1088.
- Jones, T. D., J. A. Ruben, L. D. Martin, E. N. Kurochkin, A. Feduccia, P. F. A. Maderson, W. J. Hillenius, N. R. Geist, and V. Alifanov. 2000a. Nonavian feathers in a Late Triassic archosaur. *Science* 288:2202–2205.
- Jones, T. D., J. O. Farlow, J. A. Ruben, D. M. Henderson, and W. J. Hillenius. 2000b. Cursoriality in bipedal archosaurs. *Nature* 406:716–718.
- Kurochkin, E. N. 1995. Synopsis of Mesozoic birds and early evolution of Class Aves. *Archaeopteryx* 13:47–66.
- Kurzanov, S. M. 1985. The skull structure of the dinosaur *Avimimus*. *Paleontological Journal* 1985(4):92–99.
- . 1987. Avimimidae and the problem of the origin of birds. *Transactions of the Joint Soviet-Mongolian Paleontological Expedition* 31:31–94. [Russian, English summary]
- Lauder, G. V. 1981. Form and function: structural analysis in evolutionary morphology. *Paleobiology* 7:430–442.
- . 1990. Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecology and Systematics* 21:317–340.
- . 1995. On the inference of function from structure; pp. 1–18 in J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.
- Lauder, G. V., and K. F. Liem. 1989. The role of historical factors in the evolution of complex organismal functions; pp. 63–78 in D. B. Wake and G. Roth (eds.), *Complex Organismal Functions: Integration and Evolution in Vertebrates*. John Wiley and Sons, New York.
- Liem, K. F. 1989. Functional morphology and phylogenetic testing within the framework of symecomorphosis. *Acta Morphologica Neerlandoscandinavica* 27:119–131.
- Long, R. A., and P. A. Murry. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History and Science, Bulletin* 4:1–254.
- Lowe, P. R. 1935. On the relationship of Struthionines to the dinosaurs and to the rest of the avian class, with special reference to the position of *Archaeopteryx*. *Ibis* 5(2):398–432.
- . 1944. An analysis of the characters of *Archaeopteryx* and *Archaeornis*. Were they birds or reptiles? *Ibis* 86:517–543.
- Lü J. 2000. Oviraptorosaurs compared to birds. *Vertebrata Palasiatica* 38(Supplement):18.
- Lull, R. S., and N. E. Wright. 1942. Hadrosaurian dinosaurs of North America. *Geological Society of America, Special Papers* 40:1–242.
- Luo Z. 1999. A refugium for relicts. *Nature* 400:23–25.
- Makovicky, P. J., and P. J. Currie. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications. *Journal of Vertebrate Paleontology* 18(1):143–149.
- Makovicky, P. J., and M. A. Norell. 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). *American Museum Novitates* 3247:1–16.
- Makovicky, P. J., and H.-D. Sues. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. *American Museum Novitates* 3240:1–27.
- Martin, L. D. 1983. The origin and early radiation of birds; pp. 291–338 in A. H. Brush and G. A. Clark (eds.), *Perspectives in Ornithology*. Cambridge University Press, Cambridge.
- . 1988. Review of: *The Origin of Birds and the Evolution of Flight*, edited by K. Padian. *Auk* 105(3):596–597.
- . 1991. Mesozoic birds and the origin of birds; pp. 485–540 in H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, N.Y.
- . 1995. A new skeletal model of *Archaeopteryx*. *Archaeopteryx* 13:33–40.
- . 1997. The difference between dinosaurs and birds as applied to *Mononykus*; pp. 337–343 in D. L. Wolberg, E. Stump, and G. Rosenberg (eds.), *Dinofest International: Proceedings of a Symposium Held at Arizona State University*. Academy of Natural Sciences, Philadelphia.
- . 1998. The big flap. *Sciences* 38(2):39–44.
- Martin, L. D., J. D. Stewart, and K. N. Whetstone. 1980. The origin of birds: structure of the tarsus and teeth. *Auk* 97:86–93.
- Martin, L. D., Zhou Z., Hou L., and A. Feduccia. 1998. *Confuciusornis sanctus* compared to *Archaeopteryx lithographica*. *Naturwissenschaften* 85:286–289.
- Mayr, E. 1997. Review of: *The Origin and Evolution of Birds*, by A. Feduccia. *American Zoologist* 37(2):210–211.

- McDonald, K. 1996. A dispute over the evolution of birds. *Chronicle of Higher Education* 25 Oct. 1996:A14–A15.
- Metcalf, S. J., and R. J. Walker. 1994. A new Bathonian microvertebrate locality in the English Midlands; pp. 322–331 in N. C. Fraser and H.-D. Sues (eds.), *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*. Cambridge University Press, New York.
- Morell, V. 1997. The origin of birds: the dinosaur debate. *Audubon* 99(2):36–45.
- Norberg, U. M. 1985. Evolution of flight in birds: aerodynamic, mechanical, and ecological aspects; pp. 293–302 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- Norell, M. A. 2001. The proof is in the plumage. *Natural History* 110(6):58–63.
- Norell, M. A., and L. M. Chiappe. 1996. Flight from reason [Review of: *The Origin and Evolution of Birds*, by A. Feduccia]. *Nature* 384:230.
- Norell, M. A., and P. J. Makovicky. 1997. Important features of the dromaeosaur skeleton: information from a new specimen. *American Museum Novitates* 3215:1–28.
- . 1999. Important features of the dromaeosaurid skeleton II: information from newly collected specimens of *Velociraptor mongoliensis*. *American Museum Novitates* 3282:1–45.
- Norell, M. A., P. J. Makovicky, and J. M. Clark. 1997. A *Velociraptor* wishbone. *Nature* 389:447.
- Norell, M. A., P. J. Makovicky, and P. J. Currie. 2001. The beaks of ostrich dinosaurs. *Nature* 412:873–874.
- Novas, F. E. 1996. Alvarezsauridae, Cretaceous basal birds from Patagonia and Mongolia. *Memoirs of the Queensland Museum* 39:675–702.
- Novas, F. E., and P. F. Puerta. 1997. New evidence concerning avian origins from the late Cretaceous of Patagonia. *Nature* 376:390–392.
- Olshevsky, G. 1994. The birds first? A theory to fit the facts. *Omni* 16:34–38, 40–43, 80–84.
- Olson, S. L. 1999. Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996. *Smithsonian Contributions to Paleobiology* 89, Washington.
- Ostrom, J. H. 1973. The ancestry of birds. *Nature* 242:136.
- . 1976. *Archaeopteryx* and the origin of birds. *Biological Journal of the Linnean Society* 8:91–182.
- . 1986. The cursorial origin of avian flight; pp. 73–81 in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. California Academy of Sciences, San Francisco.
- . 1987. *Protoavis*, a Triassic bird? *Archaeopteryx* 5:113–114.
- . 1991. The bird in the bush. *Nature* 353:212.
- . 1996. The questionable validity of *Protoavis*. *Archaeopteryx* 14:39–42.
- Owen, R. 1863. On the *Archeopteryx* of von Meyer, with a description of the fossil remains of a long-tailed species, from the lithographic stone of Solenhofen. *Philosophical Transactions of the Royal Society of London* 153:33–47.
- Padian, K. 1982. Macroevolution and the origin of major adaptations: vertebrate flight as a paradigm for the analysis of patterns. *Proceedings of the Third North American Paleontological Convention* 2:387–392.
- . 1984. The origin of pterosaurs; pp. 163–168 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto Verlag, Tübingen.
- . 1985. The origins and aerodynamics of flight in extinct vertebrates. *Palaeontology* 28:413–433.
- . 1995. Form versus function: the evolution of a dialectic; pp. 264–277 in J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.
- . 1997. The continuing debate over avian origins [Review of: *The Origin and Evolution of Birds*, by A. Feduccia]. *American Scientist* 85:178–180.
- . 1998. When is a bird not a bird? *Nature* 393:729–730.
- Padian, K., and L. M. Chiappe. 1998a. The origin of birds and their flight. *Scientific American* 278(2):28–37.
- . 1998b. The origin and early evolution of birds. *Biological Reviews* 73:1–42.
- Padian, K., J. R. Hutchinson, and T. R. Holtz Jr. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Journal of Vertebrate Paleontology* 19:69–80.
- Padian, K., Ji Q., and Ji. S. 2001. Feathered dinosaurs and the origin of avian flight; pp. 117–135 in D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Indianapolis.
- Parkes, K. C. 1966. Speculations on the origin of feathers. *Living Bird* 5:77–86.
- Paul, G. S. 1984. The archosaurs: a phylogenetic study; pp. 175–180 in W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto Verlag, Tübingen.
- . 1988. *Predatory Dinosaurs of the World*. Simon and Schuster, New York, 464 pp.
- . 1991. The many myths, some old, some new, of dinosaurology. *Modern Geology* 16:69–99.
- . 1996. Complexities in the evolution of birds from predatory dinosaurs: *Archaeopteryx* was a flying dromaeosaur, and some Cretaceous dinosaurs may have been secondarily flightless; p. 15 in H. F. James and S. L. Olson (eds.), *Program and Abstracts of the Fourth International Meeting of the Society of Avian Paleontology and Evolution*. Smithsonian Institution, Washington.
- . 2002. *Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds*. Johns Hopkins University Press, Baltimore.
- Pennycuik, C. J. 1986. Mechanical constraints on the evolution of flight; pp. 83–98 in K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. California Academy of Sciences, San Francisco.
- Pérez-Moreno, B. P., J. L. Sanz, A. D. Buscalioni, J. L. Moratella, F. Ortega, and D. Rasskin-Gutman. 1994. A unique multi-toothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature* 370:363–367.
- Peters, D. S. 1994. Die Entstehung der Vögel. Verändern die jüngsten Fossilfunde das Modell? *Senckenberg-Buch* 70:403–424.
- . 1995. *Acta Palaeornithologica*. 3. Symposium SAPE. Courier Forschungsinstitut Senckenberg 18, Frankfurt, 361 pp.
- Peters, D. S., and E. Görgner. 1992. A comparative study on the claws of *Archaeopteryx*; pp. 29–37 in K. E. Campbell Jr. (ed.),

- Papers in Avian Paleontology Honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Los Angeles.
- Peters, D. S., and Ji Q. 1998. The diapsid temporal construction of the Chinese fossil bird *Confuciusornis*. *Senckenbergiana lethaea* 78:153–155.
- Prum, R. O. 1999. Development and evolutionary origin of feathers. *Journal of Experimental Zoology* 285:291–306.
- . 2000. Feather development and the homology of avian feathers and dinosaur integumental filaments. *Vertebrata Palasiatica* 38(Supplement):25–26.
- Rasskin-Gutman, D. 1997. Pelvis, comparative anatomy; pp. 536–540 in P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, New York.
- Rauhut, O. W. M. 1997. Zur Schädelanatomie von *Shuvosaurus inexpectatus* (Dinosauria; Theropoda); pp. 17–21 in S. Sachs, O. W. M. Rauhut, and A. Weigert (eds.), 1. Treffen der deutschsprachigen Palaeoherpetologen, Düsseldorf, Extended Abstracts—Terra Nostra 7/97.
- Rayner, J. M. V. 1985. Cursorial gliding in proto-birds: an expanded version of a discussion contribution; pp. 289–292 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- . 1991. Avian flight evolution and the problem of *Archaeopteryx*; pp. 183–212 in J. M. V. Rayner and R. J. Wootton (eds.), *Biomechanics in Evolution*. Cambridge University Press, New York.
- Reisz, R. R., and H.-D. Sues. 2000. The “feathers” of *Longisquama*. *Nature* 408:428.
- Renesto, S. 1994. *Megalancosaurus*, a possibly arboreal archosauromorph (Reptilia) from the Upper Triassic of northern Italy. *Journal of Vertebrate Paleontology* 14:38–52.
- Rowe, M. P. 2000. Inferring the retinal anatomy and visual capacities of extinct vertebrates. *Palaeontologia Electronica* 3:1–43.
- Ruben, J. A. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Annual Review of Physiology* 57:69–95.
- . 1996. Evolution of endothermy in mammals, birds and their ancestors; pp. 347–376 in I. A. Johnston and A. F. Bennett (eds.), *Animals and Temperature: Phenotypic and Evolutionary Adaptation*. Cambridge University Press, New York.
- . 1997. Review of: *The Origin and Evolution of Birds*, by A. Feduccia. *BioScience* 47:392–394.
- Ruben, J. A., T. D. Jones, N. R. Geist, and W. J. Hillenius. 1997. Lung structure and ventilation in theropod dinosaurs and early birds. *Science* 278:1267–1270.
- Ruben, J. A., C. Dal Sasso, N. R. Geist, W. J. Hillenius, T. D. Jones, and M. Signore. 1999. Pulmonary function and metabolic physiology of theropod dinosaurs. *Science* 283:514–516.
- Russell, D. A., and Dong Z.-M. 1993. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People’s Republic of China. *Canadian Journal of Earth Science* 30:2107–2127.
- Sanz, J. L., and N. Lopez-Martinez. 1984. The prolacertid lepidosaurian *Cosesaurus aviceps* Ellenberger & Villalta, a claimed “protoavian” from the middle Triassic of Spain. *Geobios* 17:741–753.
- Sanz, J. L., L. M. Chiappe, B. P. Pérez-Moreno, J. J. Moratalla, F. Hernández-Carrasquilla A. D. Buscalioni, F. Ortega, F. J. Poyato-Ariza, D. Rasskin-Gutman, and X. Martínez-Delclòs. 1997. A nestling bird from the Lower Cretaceous of Spain: implications for avian skull and neck evolution. *Science* 276:1543–1546.
- Sanz, J. L., B. P. Pérez-Moreno, and F. J. Poyato-Ariza. 1998. Living with dinosaurs. *Nature* 393:32–33.
- Schweitzer, M. H., J. A. Watt, R. Avci, L. Knapp, L. M. Chiappe, M. A. Norell, and M. Marshall. 1999. Beta-keratin specific immunological reactivity in feather-like structures of the Cretaceous Alvarezsaurid, *Shuvuuia deserti*. *Journal of Experimental Zoology* 285:146–157.
- Sereno, P. C. 1997a. Ancient aviary, featherweight phylogeny [Review of: *The Origin and Evolution of Birds*, by A. Feduccia]. *Evolution* 51(5):1689–1690.
- . 1997b. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences* 25:435–489.
- . 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie* 210:41–83.
- . 1999a. The evolution of dinosaurs. *Science* 284:2137–2147.
- . 1999b. Definitions in phylogenetic taxonomy: critique and rationale. *Systematic Biology* 48:329–351.
- Sereno, P. C., and Rao C. 1992. Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. *Science* 255:845–848.
- Sharov, A. G. 1970. An unusual reptile from the Lower Triassic of Fergana. *Paleontological Journal* 1970:112–116.
- Shi L. and Zhang F. 2000. 5th International Meeting of the Society of Avian Paleontology and Evolution and the Symposium of Jehol Biota (Abstracts). *Vertebrata Palasiatica* 38(Supplement):1–63.
- Shipman, P. 1997a. *Taking Wing: Archaeopteryx and the Evolution of Bird Flight*. Simon and Schuster, New York, 336 pp.
- . 1997b. Birds do it . . . did dinosaurs? *New Scientist* 153(2067):26–31.
- Shubin, N. H., and P. Alberch. 1986. A morphogenetic approach to the origin and basic organization of the tetrapod limb. *Evolutionary Biology* 20:319–387.
- Simpson, G. G. 1946. Fossil penguins. *Bulletin of the American Museum of Natural History* 87:1–95.
- Steadman, D. W. 1998. Review of: *The Origin and Evolution of Birds*, by A. Feduccia. *Wilson Bulletin* 110(1):140–141.
- Stokstad, E. 2000. Feathers, or flight of fancy. *Science* 288:2124–2125.
- Swisher, C. C., III, Wang Y. Q., Wang Z.-L., Xu X., and Wang Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400:58–61.
- Tarsitano, S. 1985. The morphological and aerodynamic constraints on the origin of avian flight; pp. 319–332 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), *The Beginnings of Birds*. Freunde des Jura-Museums, Eichstätt.
- . 1991. *Archaeopteryx: Quo vadis?*; pp. 541–576 in H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, N.Y.
- Tarsitano, S., and M. K. Hecht. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zoological Journal of the Linnean Society* 69:149–182.

- Thomas, A. L. R., and J. P. Garner. 1998. Are birds dinosaurs? *Trends in Ecology and Evolution* 13(4):129–130.
- Thulborn, R. A. 1975. Dinosaur polyphyly and the classification of archosaurs and birds. *Australian Journal of Zoology* 23:249–270.
- . 1984. The avian relationships of *Archaeopteryx*, and the origin of birds. *Zoological Journal of the Linnean Society* 82:119–158.
- Thulborn, R. A., and T. L. Hamley. 1982. The reptilian relationships of *Archaeopteryx*. *Australian Journal of Zoology* 30:611–634.
- Unwin, D. M. 1998. Feathers, filaments and theropod dinosaurs. *Nature* 392:119–120.
- Varricchio, D. J., F. Jackson, J. J. Borkowski, and J. R. Horner. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* 385:247–250.
- Wagner, G. P., and J. A. Gauthier. 1999. 1, 2, 3 = 2, 3, 4: a solution to the problem of the homology of the digits of the avian hand. *Proceedings of the National Academy of Sciences* 96:5111–5116.
- Walker, A. D. 1972. New light on the origin of birds and crocodiles. *Nature* 237:257–263.
- . 1990. A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa. *Philosophical Transactions of the Royal Society of London B* 330:1–120.
- Weishampel, D. B. 1995. Fossils, function, and phylogeny; pp. 34–54 in J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.
- Weishampel, D. B., and C.-M. Jianu. 1996. New theropod dinosaur material from the Hateg Basin (Late Cretaceous, western Romania). *Neues Jahrbuch für Geologie und Paläontologie* 200(3):387–404.
- Wellnhofer, P. 1992. *Protoavis*: der älteste Vogel? *Naturwissenschaftliche Rundschau* 45(3):107–108.
- . 1994. New data on the origin and early evolution of birds. *Comptes Rendus de l'Académie des Sciences, Paris, Series II* 319:299–308.
- Welman, J. 1995. *Euparkeria* and the origin of birds. *South African Journal of Science* 91:533–537.
- Witmer, L. M. 1990. The craniofacial air sac system of Mesozoic birds (*Aves*). *Zoological Journal of the Linnean Society* 100:327–378.
- . 1991. Perspectives on avian origins; pp. 427–466 in H.-P. Schultze and L. Trueb (eds.), *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Cornell University Press, Ithaca, N.Y.
- . 1995a. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils; pp. 19–33 in J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, New York.
- . 1995b. Homology of facial structures in extant archosaurs (birds and crocodylians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology* 225:269–327.
- . 1995c. *The Search for the Origin of Birds*. Franklin Watts, New York, 64 pp.
- . 1997a. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Memoirs of the Society of Vertebrate Paleontology, Journal of Vertebrate Paleontology* 17(Supplement to 1):1–73.
- . 1997b. Flying feathers [Review of: *The Origin and Evolution of Birds*, by A. Feduccia]. *Science* 276:1209–1210.
- . 1997c. Foreword; pp. vii–xii in S. Chatterjee, *The Rise of Birds: 225 Million Years of Evolution*. Johns Hopkins University Press, Baltimore.
- . 1997d. Craniofacial air sinus systems; pp. 151–159 in P. J. Currie and K. Padian (eds.), *The Encyclopedia of Dinosaurs*. Academic Press, New York.
- . 1999. New aspects of avian origins: roundtable report; pp. 327–334 in S. L. Olson (ed.), *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution*, Washington, D.C., 4–7 June 1996. *Smithsonian Contributions to Paleobiology* 89, Washington.
- . 2001a. Nostril position in dinosaurs and other vertebrates and its significance for nasal function. *Science* 293:850–853.
- . 2001b. The role of *Protoavis* in the debate on avian origins; pp. 537–548 in J. A. Gauthier and L. F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of an International Symposium in Honor of John H. Ostrom*. Yale University Press, New Haven.
- Witmer, L. M., and W. D. Maxwell. 1996. The skull of *Deinonychus* (Dinosauria: Theropoda): new insights and implications. *Journal of Vertebrate Paleontology* 16(Supplement to 3):73A.
- Witmer, L. M., and D. B. Weishampel. 1993. Remains of theropod dinosaurs from the Upper Cretaceous St. Mary River Formation of northwestern Montana, with special reference to a new maniraptoran braincase. *Journal of Vertebrate Paleontology* 13(Supplement to 3):63A.
- Xu X., Tang Z.-L., and Wang X.-L. 1999a. A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399:350–354.
- Xu X., Wang X.-L., and Wu X.-C. 1999b. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401:262–266.
- Xu X., Zhou Z., and Wang X.-L. 2000. The smallest known non-avian theropod dinosaur. *Nature* 408:705–708.
- Xu X., Zhao X., and J. M. Clark. 2001a. A new therizinosaur from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. *Journal of Vertebrate Paleontology* 21:477–483.
- Xu X., Zhou Z., and R. O. Prum. 2001b. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* 410:200–204.
- Xu X., M. A. Norell, Wang X.-L., P. J. Makovicky, and Wu X.-C. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415:780–784.
- Zalewski, D. 1996. Bones of contention. *Lingua Franca* 6(6):22–24.
- Zhang F. and Zhou Z. 2000. A primitive enantiornithine bird and the origin of feathers. *Science* 290:1955–1959.
- Zhao X. and Xu X. 1998. The oldest coelurosaurian. *Nature* 394:234–235.

- Zhou Z. 1998. Origins of avian flight: evidence from fossil and modern birds. *Journal of Vertebrate Paleontology* 18(Supplement to 3):88A.
- Zhou Z., and Wang X.-L. 2000. A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. *Vertebrata Palasiatica* 38:113–130.
- Zhou Z., Wang X.-L., Zhang F., and Xu X. 2000. Important features of *Caudipteryx*—evidence from two nearly complete specimens. *Vertebrata Palasiatica* 38:241–254.
- Zinke, J. 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrift* 72:179–189.
- Zweers, G. A., and J. C. Vanden Berge. 1998. Birds at geological boundaries. *Zoology: Analysis of Complex Systems (ZACS)* 100:183–202.
- Zweers, G. A., J. C. Vanden Berge, and H. Berkhoudt. 1997. Evolutionary patterns of avian trophic diversification. *Zoology: Analysis of Complex Systems (ZACS)* 100:25–57.