

WHY ORNITHOLOGISTS SHOULD CARE ABOUT THE THEROPOD ORIGIN OF BIRDS

Author: Prum, Richard O.

Source: The Auk, 119(1) : 1-17

Published By: American Ornithological Society

URL: [https://doi.org/10.1642/0004-8038\(2002\)119\[0001:WOSCAT\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2002)119[0001:WOSCAT]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

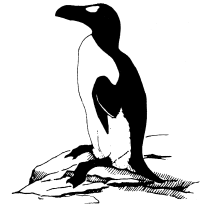
Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The Auk

A Quarterly
Journal of Ornithology

Vol. 119 No. 1 January 2002



The Auk 119(1):1–17, 2002

PERSPECTIVES IN ORNITHOLOGY

WHY ORNITHOLOGISTS SHOULD CARE ABOUT THE THEROPOD ORIGIN OF BIRDS

RICHARD O. PRUM¹

*Department of Ecology and Evolutionary Biology, and Natural History Museum, University of Kansas,
Lawrence, Kansas 66045, USA*

OVER THE LAST 25 years, few topics in systematics and paleontology have been as divisively debated as the origin of birds (Padian and Chiappe 1998; Feduccia 1999a, b; Dalton 2000). For most of the middle of the twentieth century, G. Heilmann's (1926) monumental analysis of the topic reigned unchallenged. Heilmann established definitively that birds are members of the Archosauria (the large reptilian clade that also includes crocodiles, pterosaurs, and dinosaurs). But Heilmann was unable to accept the voluminous evidence he gathered that placed birds within the carnivorous theropod dinosaurs because theropods apparently lacked a furcula, and Heilmann believed that lost features cannot re-evolve (Dollo's law). Instead, Heilmann (1926) concluded that birds had evolved from "thecodonts"—a polyphyletic garbage bag assemblage of early archosaurs. It is a tribute to the careful detail of Heilmann's treatise that his hypothesis was so influential given his own ambivalence about his conclusions. Heilmann described his thecodont hypothesis as "wholly without shortcomings" (i.e. character conflict) while essentially admitting that there was no evidence other than avian membership in the archosaurs to support it. Heilmann's hypothesis became unquestioned orthodoxy and was the basis of many scenarios

for the evolution of birds and feathers (e.g. Bock 1965).

In 1974, John Ostrom (1974) challenged the status quo by revitalizing the old hypothesis that birds were related to dinosaurs (Huxley 1868, 1870; Williston 1879) or, more specifically, to a group of the meat-eating theropod dinosaurs, represented by *Deinonychus* which he had recently described. Jacques Gauthier (1986) subsequently confirmed that birds were a lineage of theropod dinosaurs most closely related to dromaeosaurs (the lineage now commonly known as "raptors"), and that result has been generally confirmed by subsequent workers (Gauthier et al. 1988; Holtz 1994; Sereno 1997, 1999; Forster et al. 1998; Makovicky and Sues 1998; Zhou et al. 2000). The last 25 years have revealed many paleontological discoveries that have greatly expanded our knowledge and understanding of the diversity of theropod dinosaurs and Early Cretaceous birds. The result has been a steady increase in support for theropod origin of birds, despite arguments to the contrary (e.g. Martin 1983a, b, 1985; Feduccia 1985, 1999a, b; Ruben et al. 1997; Feduccia and Martin 1998; Dodson 2000; Martin and Czerkas 2000; Jones et al. 2001). However, with few exceptions (e.g. Whetstone and Martin 1981; Martin 1983a, b), critics have not proposed any explicit alternative hypothesis more detailed than Heilmann's (1926) original vague thecodont notion.

¹ E-mail: prum@ku.edu

The debate on bird origins has frequently been portrayed by critics of the theropod hypothesis as a battle between “paleontologists” and “ornithologists” (Feduccia 1999b). However, this analogy has been allowed to persist for decades because of the lack of ornithological participation in the debate rather than any general concordance of ornithological opinion. The lack of ornithological participation in this debate can be well documented: a computer search of the recent volumes of North American ornithological journals yields no research papers including the word dinosaur in the text. As far as I know, Zhou’s (1995) paper on *Mononychus* is the only article to appear in a major ornithological journal that deals even tangentially with the issue of avian origins since Martin et al. (1980).

Why is there so little ornithological interest and involvement in the question of bird origins? With covers and articles in *Science*, *Nature*, *Scientific American*, *Audubon*, and *National Geographic*, it cannot be because ornithologists are not aware of it. There are two primary reasons. First, most ornithologists have not become familiar enough with the primary literature describing the various characters to consider the evidence for themselves. Further, few ornithologists have formal paleontological training, and some may have relied on the criticism of a few to form the opinion that the evidence supporting the theropod hypothesis is flawed. The second reason is that many ornithologists are satisfied that the issue is irrelevant to their research and teaching. Like many natural historians over many centuries, ornithologists are generally convinced of the peculiar uniqueness of birds, because we gain our professional identities as “ornithologists” from it. Focusing on the apparent uniqueness of birds may reinforce our professional identities or self esteem, but it may not help us do the best possible ornithological research and teaching.

Why should ornithologists care about the theropod origin of birds? Because the theropod origin of birds is relevant to almost all aspects of avian biology and should influence the way we think about, study, and teach avian anatomy, behavior, physiology, ecology, and evolution. Here, I present my perspective on the evidence supporting the theropod origin of birds, the criticisms of the hypothesis, and the relevance of the theropod origin to ornithology in

hopes of generating a renewed interested and attention to this question within the ornithology community.

EVIDENCE FOR THE THEROPOD ORIGIN OF BIRDS

Evidence in support of the theropod origin of birds comes from all available sources of paleontological evidence—largely osteology, inferences about physiology and behavior, and more recently a variety of fossilized feathers. Since Gauthier (1986) produced the first phylogenetic analysis of the origin of birds, support of the theropod origin of birds has been repeatedly upheld in phylogenetic analyses (e.g. Benton and Clark 1988; Gauthier et al. 1988; Holtz 1994; Sereno 1997, 1999; Forster et al. 1998; Makovicky and Sues 1998). All analyses have supported the same position for birds, within a group of higher coelurosaurian theropods which are called maniraptorans—a group that includes dromaeosaurs, or raptors (e.g. *Deinonychus*, *Velociraptor*) and troodontids (e.g. *Troodon*) (Fig. 1). There have been and continue to be vigorous debates about the relative positions of various theropod groups that provide opportunities for disagreement among researchers (e.g. tyrannosaurs and troodontids; Holtz 1994; Sereno 1997, 1999; Makovicky and Sues 1998), but all analyses have supported an identical phylogenetic position for birds within the maniraptoran coelurosaur theropods.

Osteological evidence of the theropod ancestry of birds—that is, derived characters shared by birds and some portion of theropod dinosaurs—comes from essentially all parts of the body. The evidence has been well reviewed (e.g. Witmer 1991; Padian and Chiappe 1997, 1998; Sumida and Brochu 2000), but it is worthwhile to summarize here the extent and detail of the evidence explicitly for ornithologists.

Theropod dinosaurs were primitively bipedal, but there were several evolutionary trends in theropod morphology as they evolved more efficient bipedal locomotion (Gatesy 1990, 1991, 1995; Gatesy and Middleton 1997; Farlow et al. 2000; Hutchinson 2000a, b; Hutchinson and Gatesy 2000). Notably, the origins and insertions of muscles that move the hindlimbs changed radically, leaving observable traces on bones as they evolved. For example, in alligators and early theropods, the *M. caudofemoralis longus*

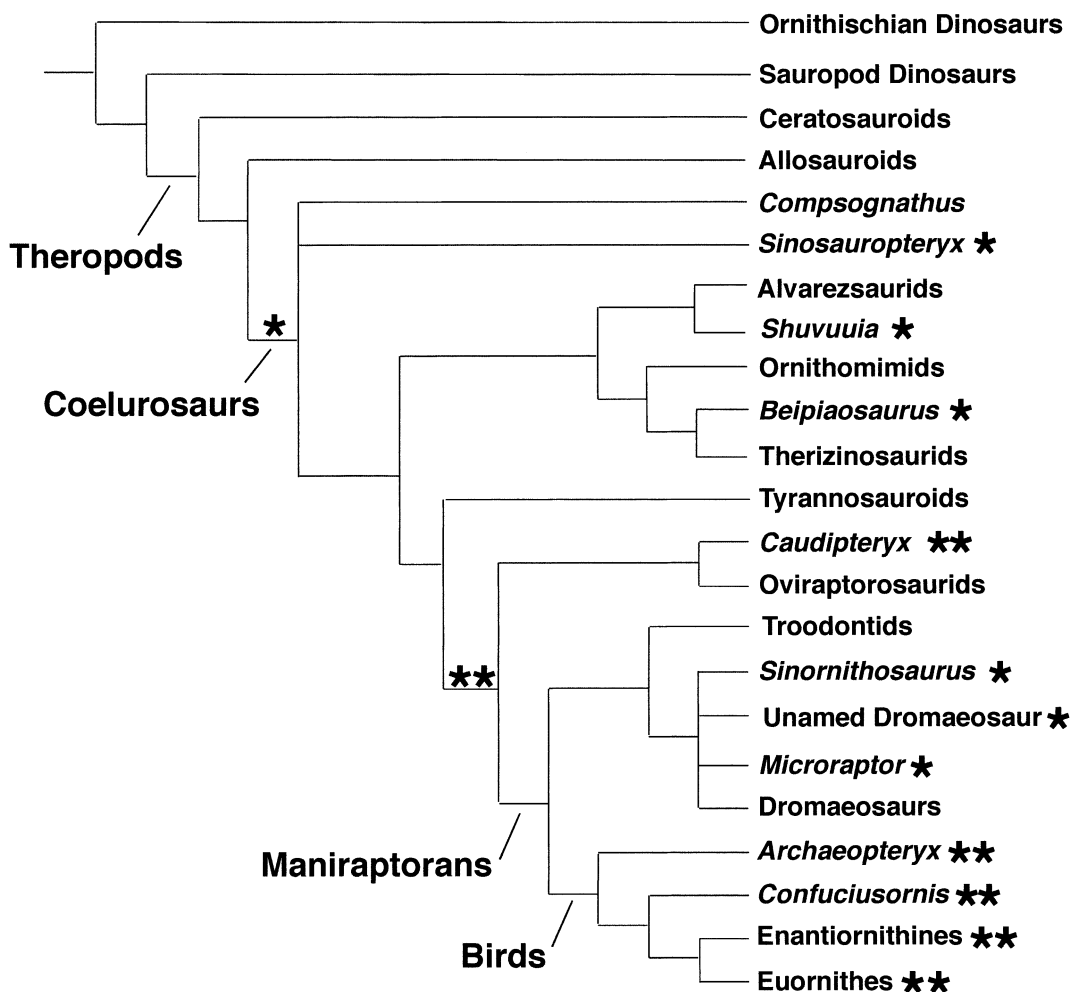


FIG. 1. A phylogeny of the theropod origin of birds based on Sereno (1999) with several new taxa added (Xu et al. 1999a, 1999b, 2000; Ji et al. 2001), and a phylogenetic hypothesis for the origin of feathers. The ornithischian and sauropod dinosaurs are the two immediate sister groups to the theropod dinosaurs. Taxa with feathers are labeled *, and taxa demonstrated to have fully modern, pennaceous feathers are labeled **. The lineages in which the first feathers and fully pennaceous feathers are most parsimoniously hypothesized to have evolved are labeled * and **, respectively.

originates far out on the tail and inserts on the fourth trochanter down the shaft of the femur; gradually, the origin of the muscle was displaced toward the base of the tail, and its insertion on the femur was reduced. In modern birds, that primitively important archosaurian locomotory muscle is reduced to a thin slip, one of those numerous curious, vestigial pieces of avian anatomy. Within theropods, the tail shortened, the basal portion of the tail shorted even further, and the distal elements of hindlimbs elongated. The fibula became a thin

splint in dromaeosaurs and birds. In the ankle, the ascending process of the astragalus became larger and evolved into the avian pretibial bone (Gauthier 1986; Rieppel 1993; Padian and Chiappe 1997, 1998). In the foot, the fifth toe was reduced to a single metatarsal, and the first toe was reduced and raised off the ground, leaving a functionally tridactyl foot. The first toe subsequently reevolved a lower position within birds with the evolution of the grasping hallux. The avian pelvis also shows a number of additional derived characters revealing the-

ropod ancestry (Farlow et al. 2000, Hutchinson 2000b). In the group of theropods called Tetanurans (coelurosaurs and carnosaurs), the pubis evolved a widened end, or pubic boot. In dromaeosaurs and birds, the pubic boot extends caudally and the pubis evolved a retroverted, or backward directed, position. Throughout theropods, the pubis evolved to become longer than the ischium. In the axial skeleton, theropods, like birds, have pneumatic cervical vertebrae that are likely indications of an early air sac system. Additional synapomorphies have been identified in the skull, including presence of an accessory antorbital fenestra and dorsal, caudal, and rostral tympanic recesses.

The pectoral girdle and forelimb also reveal suites of hierarchically nested morphological novelties supporting the theropod origin of birds. In the pectoral girdle, fused clavicles, or a furcula, are now known in many theropods (*contra* Heilmann 1926; Chure and Madsen 1996, Makovicky and Currie 1998, Norell et al. 1998). The furcula is remarkably birdlike in some dromaeosaurs (Xu et al. 1999a, Burnham et al. 2000). Also in dromaeosaurs and birds, we see the derived elongate coracoids, sternal plates (in some), and an increasingly laterally facing glenoid, or shoulder socket. Within the theropods lineage leading to birds, the forelimbs lengthened in proportion to the hindlimbs, and the hand elongated in relation to the rest of the forelimb. Also, some dromaeosaurs and birds even show a prominently bowed ulna (e.g. Burnham et al. 2000)—a feature that zooarcheologists still use to identify avian ulnae in human middens.

The wrist of higher coelurosaurs is characterized by the fused distal carpals 1 and 2 (Gauthier 1986; Padian and Chiappe 1997, 1998). In *Archaeopteryx*, dromaeosaurs, and even oviraptorans and troodontids, those fused distal carpals form a crescent-shaped bone generally called the semilunate carpal (Ostrom 1974; Gauthier 1986; Gauthier et al. 1988; Padian and Chiappe 1997, 1998). It is universally agreed that the function of that exceptional structure is to allow the wrists to swivel sideways. That feature was the character that first led Ostrom (1974) to question 50 years of orthodoxy and argue for the theropod origin of birds.

Theropods exhibit a simultaneous trend toward loss of digits and the evolution of a grasping hand. Primitively, dinosaurs have five fin-

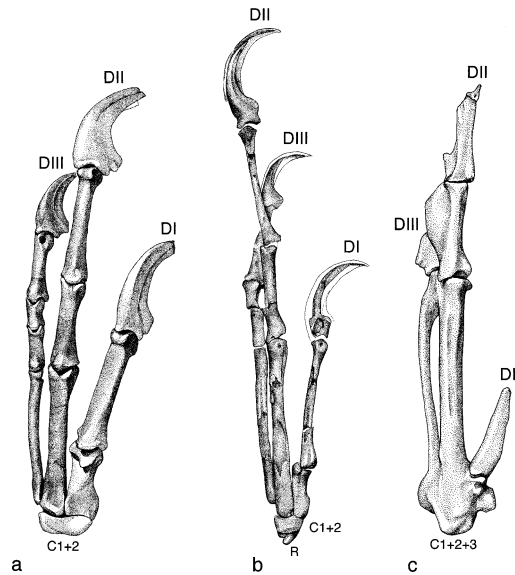


FIG. 2. Dorsal view of the left hands of (a) *Deinonychus antirrhopus*, (b) *Archaeopteryx lithographica*, and (c) *Nothura maculosa* (Tinamidae), from Wagner and Gauthier (1999). Notice the common phalangeal formulae and the similarities in proportions and shapes of the phalanges of digit 3 shared by *Deinonychus* and *Archaeopteryx*. DI–III, digits 1–3; C1–3, distal carpals comprising the semilunate carpal; R, radiale. (Reprinted with permission.)

gers. The outer two digits, number four and five, are reduced but present in *Herrerasaurus* (variously hypothesized to be a basal dinosaur, basal Saurischian dinosaur, or basal theropod). Subsequently, in theropods the outer digits of the hand are completely lost, leaving digits 1, 2, and 3, as in birds. The fingers of dromaeosaurs and *Archaeopteryx* also have the same phalangeal formula (number of phalanges in each digit); the first, second, and third digits have two, three, and four phalanges, respectively.

Theropods also share some remarkable, derived phalangeal proportion and shapes with *Archaeopteryx* (Wagner and Gauthier 1999, Hopson 2001). The second digit is longest in theropods and birds despite its fewer phalanges. In a few well-known dromaeosaurs (e.g. *Deinonychus*, *Bambiraptor*, and *Sinornithosaurus*) and in *Archaeopteryx*, the middle two phalanges in digit 3 are substantially shorter than either the first or fourth (Fig. 2). Further, those shorter, middle phalanges are twisted along their axes, so that the third digit does not flex parallel to the oth-

ers, but twists inward toward the center of the hand (Wagner and Gauthier 1999, Hopson 2001). That unique and bizarre morphology gives rise to the curious curled position of digit 3 in many *Archaeopteryx* specimens and related dromaeosaurs (e.g. *Sinornithosaurus*; Xu et al. 1999a). These new observations demonstrate that Heilmann's (1926) reconstruction of the hand of *Archaeopteryx* with digit 3 lying nicely parallel to digit 2 is incorrect. Digit 3 of *Archaeopteryx* moved independently of digit 2, maintaining a grasping function underneath the wing feathers as many specimens of *Archaeopteryx* show. A revised reconstruction of the hand of *Archaeopteryx* (Fig. 2) also explains the apparently anomalous insertion of the remiges on digit 2 (the middle digit) instead of digit 3, which would be the trailing edge of the wing.

In summary, osteological synapomorphies of birds and theropod dinosaurs come from the detailed similarities of many parts of the body—head to toe, tip to tail. As the recent debate over the phylogenetic position of *Mononychus* (Zhou 1995, Chiappe et al. 1996, Sereno 1999) and *Caudipteryx* (Ji et al. 1998, Feduccia 1999b, Jones et al. 2000a, Zhou 2000, Zhou and Wang 2000, Zhou et al. 2000) makes clear, it is increasingly difficult even to distinguish a bird from other theropods. This summary has almost excluded consideration of the newest, most exciting, and perhaps most compelling fossils finds from the Yixian formation of Liaoning, China. The explosion of critical specimens from those deposits in the last few years has revolutionized the quality and quantity of evidence bearing on the origin and early evolution of birds (Stokstad 2001). Those specimens include conclusive evidence of the strongest possible bird–theropod synapomorphy—completely modern feathers (see below)—and the oldest, most birdlike dromaeosaurs.

CRITICISMS OF THE THEROPOD ORIGIN OF BIRDS

Despite the wealth of and increasing strength of the evidence, the theropod hypothesis of the origin of birds has received unrelenting criticism for more than two decades. These criticisms can be grouped in several classes: general critiques of phylogenetic methods, criticisms of the validity and homology of specific characters, temporal disparity between the avian and theropod radiations, and *a priori* ar-

guments about functional and physiological plausibility. Although critiques have been effectively countered in the literature many times (e.g. Witmer 1991; Padian and Chiappe 1997, 1998; Sumida and Brochu 2000), criticisms have remained largely unchanged (e.g. Feduccia 1999a, b; Dodson 2000).

Criticisms of phylogenetic methods.—Since Gauthier (1986), the bird-origin debate has really been about methods of analysis. Two alternatives are represented: phylogenetic systematics, in which explicit historical hypotheses of relationships among monophyletic groups are proposed based on hypothesized shared derived characters; and traditional eclectic narrative methods, that have remained essentially unchanged since Heilmann (1926), in which no explicit analytical method is used, and no attempts are made to actually document the phylogenetic history of lineages related to birds. Now, phylogenetics is universally recognized in systematics and evolutionary biology, and even by U.S. courts (e.g. in cases of criminal HIV infection; Vogel 1997). But, critics of the theropod origin of birds have been a singular exception to that nearly universal intellectual trend. Steadfastly they have maintained that phylogenetics cannot be relied upon to solve the question of the origin of birds (e.g. Feduccia 1999b, Dodson 2000).

A few explicit alternative phylogenetic hypotheses to the theropod theory have been proposed in recent decades—that birds are related to crocodylians (Walker 1972; Whetstone and Martin 1981; Martin 1983a, b), or that birds are related to the early archosaur *Euparkeria* (Welman 1995). The crocodile hypothesis has been abandoned in recent years after scrutiny of the details, and several phylogenetic analyses have failed to support *Euparkeria* as a close avian relative (Sumida and Brochu 2000). Several early archosaurs or archosaurimorphs have also been proposed as candidate “thecondont relatives” of birds (e.g. *Longisquama*, *Scleromochlus*, and *Megalanicosaurus*), but not in the strict phylogenetic sense of exclusive, shared ancestry. Rather, it is usually stated that birds may have evolved through a similar morphological “stage” (e.g. Jones et al. 2001). Because those proposals are lacking in supporting details, they do not constitute credible alternative sister taxa. All detailed analyses of the array of alternative archosaurian sister-groups of birds have

demonstrated than none has any substantial support (Sumida and Brochu 2000). The most recent proposal of feathers in the Triassic *Longisquama* (Jones et al. 2000b) received immediate criticisms on numerous grounds (Reisz and Sues 2000, Prum 2001, Unwin and Benton 2001, Prum and Brush 2002). As Sumida and Brochu (2000) point out, no alternative has any more than a few superficially birdlike features; but phylogenetic analyses have already identified a group with numerous hierarchically distributed, derived morphological features shared with birds—theropod dinosaurs.

Criticisms of the characters.—A frequent criticism of the evidence in support of the theropod origin of birds has been “garbage in, garbage out.” The implication is that derived character states hypothesized to be shared by birds and theropods are too dissimilar, incorrectly homologized, or functionally important and therefore too convergent to be historically informative (e.g. see Martin et al. 1980, Martin and Stewart 1985, Feduccia 1999b).

Characters are often rejected on the basis of some preconceived notion about the evolutionary process (Padian 2001). For example, it is hypothesized that birds must have evolved flight from trees, so their ancestors must have been arboreal. Thus, bipedality of terrestrial theropods and birds must be convergent, and all hindlimb, pelvis, and tail characters can be discounted (Feduccia 1999b). However, in parallel with the universal adoption of phylogenetic methods in systematics, there has been an equivalent recognition that it is essential to establish a phylogenetic pattern before (e.g. Lauder 1990, Larson and Losos 1996, Lauder and Rose 1996), or independently of (e.g. Padian 2001), the analysis of functional and macroevolutionary process. The ability to merely conceive of two features as convergent is considered by critics to be sufficient criteria to reject a proposed synapomorphy completely: for example Feduccia and Martin’s (1998) critique of the *Velociraptor* wishbone. However, only a phylogenetic analysis that includes all proposed characters and taxa can resolve whether characters are phylogenetically informative. To reject a hypothesis of homology, it is necessary to show that the proposed similarities evolved convergently within a phylogenetic analysis including other phylogenetically informative characters (Patterson 1982, Pinna 1991).

Ironically, rejection of nearly any aspect of avian anatomy as phylogenetically informative will undermine any future attempts to support an alternative hypothesis. Thus, if the furcula shared by many higher theropods and birds can be ignored as uninformative, how can one argue that the presence of furcula in *Megalanosaurus* or *Longisquama* is somehow a valid character? Critics of the theropod hypothesis are predictably unconcerned about that problem because they do not actually intend to establish a sister group to birds.

In a few cases, valid criticisms of the character data have been made, but, tellingly, those criticisms have actually strengthened the support for the theropod hypothesis. For example, Ostrom (1974) originally homologized the semilunate carpal with the avian radiale, but Martin (1983a, b) pointed out that homology could not be correct because the semilunate carpal of *Archaeopteryx* becomes fused within the carpometacarpus in higher birds, and that the radiale is a proximal carpal(s). Following Martin’s observation that the semilunate carpal was composed of distal carpals, Padian and Chiappe (1997, 1998) recognized that the fusion of distal carpals 1 and 2 actually evolved much earlier in theropods than previously recognized by Ostrom (1974). Subsequently, the semilunate shape of that novel element was derived in the common ancestor of maniraptorans. A reanalysis based on Martin’s criticism provides an expanded historical context for the explanation of both the origin of the novel element and subsequent evolution of its unique semilunate shape.

If ornithologists want to evaluate the character analysis methods of some vocal critics of the theropod hypothesis, a good example can be found in the quasi-phylogenetic hypothesis of early bird phylogeny proposed by Larry Martin, Alan Feduccia, and colleagues (Hou et al. 1996). Those authors proposed that *Archaeopteryx* and *Confuciusornis* were the sister group to enantiornithine birds, and that *Liaoningornis* and *Chaoyangia* are the sister group to all other birds, including modern birds. However, because enantiornithines had many advanced flight features found in modern birds, that hypothesis requires the convergent evolution of the keeled sternum, the strut-like coracoid, the tarsometatarsus, the shortened tail, and the pygostyle. Curiously, the modern birds appear in their published phylogeny but not in

the unpublished data set or analysis on which it is based (Hou et al. 1996; supplemental materials can be found online, see Acknowledgements). The authors decided that the tarsometarsi in various birds were different enough to conclude that all of those characters are convergent within birds. Needless to say, most ornithologists would have difficulty in accepting that all those features had evolved convergently in birds. Numerous phylogenetic analyses (e.g. Chiappe 1995, Chiappe et al. 1999) have shown that enantiornithines are phylogenetically closer to extant birds than are *Archaeopteryx* or *Confuciusornis*, supporting a single origin of those advanced flight features and rejecting Hou et al.'s (1996) and Martin's (1983b) hypothesis of tarsometatarsus evolution. However, Hou et al. (1996) demonstrates the advantages of presenting an explicit hypothesis, and documents an ornithological example of the type of character analysis promoted by critics of the theropod hypothesis. It can be hoped that these and other critics of the theropod hypothesis will soon attempt a phylogenetic analysis of the nontheropod origin of birds that can be scrutinized as easily.

1–2–3 versus 2–3–4.—One criticism of the theropod hypothesis deserves detailed consideration because it has frequently been cited as the biggest obstacle to the theropod origin of birds. The avian hand has three digits. On the basis of phylogenetic analyses of digit reduction in dinosaurs, theropods are universally recognized as having digits 1–2–3 (Hinchliffe 1985; Wellnhofer 1985; Burke and Feduccia 1997; Padian and Chiappe 1997, 1998; Feduccia 1999a, b; Wagner and Gauthier 1999). In contrast, developmental biologists have traditionally referred to the digits of the hand in birds as 2–3–4 (Hinchliffe 1985; Burke and Feduccia 1997; Feduccia 1999a, b; Wagner and Gauthier 1999), because the first cartilage condensation to develop in the hand (and foot) of most amniotes becomes distal carpal 4 and metacarpal 4, and the most posterior digit in the avian hand ultimately develops above this first condensation (Hinchliffe 1985, Burke and Feduccia 1997). Thus, the traditional developmental hypothesis is that the digit that develops above metacarpal 4 is digit 4 because its identity is determined by its position. Therefore, fingers of birds must be digits 2–3–4, they cannot be homologous with those of theropods, and all similarities in pha-

langeal formula, proportions, shape, and function shared by fingers of birds and theropods must be convergent. That conclusion "is based upon classical homology and reliance on the principles of developmental position and connections" (Feduccia 1999b:385). Of course, such reasoning only further raises the question of how the digits of theropod hands could have developed in the absence of the essential fourth metacarpal developmental axis, but the extinction of nonavian theropods has conveniently prevented anyone from acquiring those data.

Wagner and Gauthier (1999) proposed the "frame-shift" hypothesis as a solution to this apparent conflict. Essentially, they hypothesized that the theropod hand evolved to develop digits 1–2–3 in positions 2–3–4. Comparing the frame-shift hypothesis to Lysenkoism, cold fusion, and a "cladistic jihad," Feduccia (1999a) suggested that Wagner and Gauthier (1999) were denying the developmental facts to maintain the credibility of the theropod hypothesis. Recently, however, Dahn and Fallon (2000) published a series of experiments on development of chick hindlimb digits that demonstrate that amniote digit identity is not an inherent property of the digit primordia or their positions. Rather, identity of the developing digit primordia is initially unspecified despite their positions. Instead, digit identity is determined by the interactions between the digit primordia and gradients of pattern formation genes (e.g. bone morphogenetic proteins, or "BMPs") in the interdigital mesoderm that surrounds the digit primordia early in development (Dahn and Fallon 2000). By transplanting digit primordia and the interdigital mesoderm within and among chick feet, they experimentally created homeotic transformations (i.e. changes to the identity of any digit) and grew any digit in any position (Fig. 3). Further, by experimentally manipulating BMP levels in the interdigital mesoderm, Dahn and Fallon (2000) could anteriorize or posteriorize all digits of the hand (as hypothesized by the frame-shift hypothesis; Fig. 3). They were even able to predictably grow digits with extreme phalangeal formulae that do not occur among known archosaurs. Interestingly, as developmental biologists, R. D. Dahn and J. F. Fallon (pers. comm.) were entirely uninvolved with the paleontological and systematic debate on the homology of digits of the avian hand.

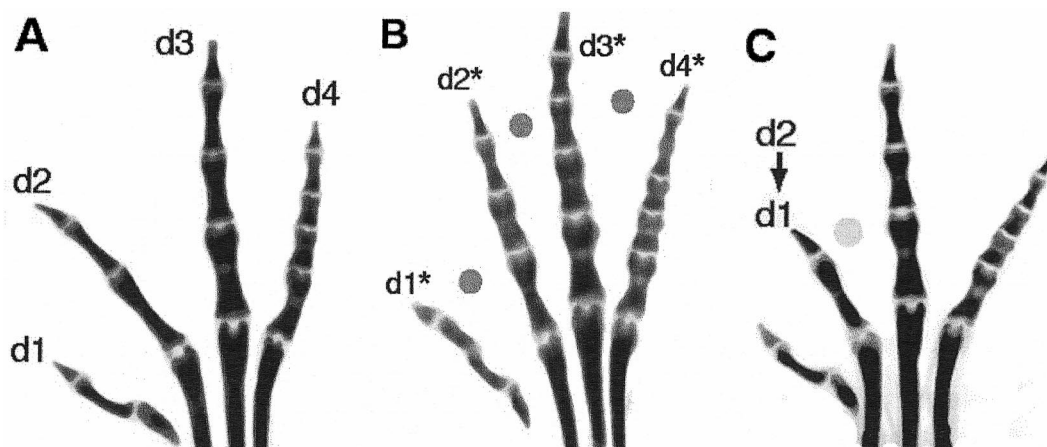


FIG. 3. Control and experimental homeotic transformations of digit identity in the foot of chicks (*Gallus gallus*) from Dahn and Fallon (2000). (A) The standard phalangeal formula with digits 1–4 having 2–5 phalanges, respectively. (B) Homeotic transformation of all digit identities produced by beads (dots) with Sonic Hedgehog protein between digits. Each digit has an additional phalanx, typical of posteriorization of digit identity. (C) Homeotic transformation of the identity of digit 2 to a digit 1 produced by a bead (dot) with Noggin protein between digits 2 and 3. The transformation of digit 2 to 1 is accomplished by the loss of a phalanx, or an anteriorization of digit identity. (Reprinted with permission.)

Dahn and Fallon's (2000) work provides molecular developmental evidence supporting the plausibility of the frame-shift hypothesis (Galis 2001). It is entirely plausible for theropods to have evolved changes in patterns of BMP expression in the developing hand that would lead to a frame-shift in digit identity. Furthermore, Dahn and Fallon's (2000) data falsify the primary assumption of 2–3–4 hypothesis: that the conserved patterns of metacarpal development within the hand dictate digit identity. Far from "accommodating the cladogram" (Feduccia 1999a), Wagner and Gauthier (1999) made a bold prediction that the developmental understanding of digit identity must be incomplete. Dahn and Fallon (2000) independently demonstrated that this prediction was correct. Although many details remain to be investigated, it is now clear that there is no conflict between the theropod hypothesis of bird origins and the facts of developmental biology.

"Temporal paradox".—Another criticism of the theropod hypothesis is the supposed "temporal paradox"—the notion that theropod diversity is too young to be phylogenetically closely related to birds. The objection has been that fossils presumed to be closest to birds are too late in time compared to the first bird, *Archaeopteryx*, approximately 148 my old (Sereni 1997). Many dromaeosaurs, ornithomimid, ovi-

raptoran, and other theropod fossils included in the hypothesis are best known from the Late Cretaceous, or about 80 Ma, but many are known from much earlier. The notion of a temporal paradox is based on several fundamental misconceptions about paleontology and evolutionary biology (Padian and Chiappe 1998), and by misrepresentation of the evidence (Padian and Chiappe 1998, Brochu and Norell 2000).

The first misconception is thinking purely in terms of prephylogenetic ancestor–descendant relationships. For example, A. Feduccia has often repeated that birds cannot be related to theropod dinosaurs because "you can't be your own grandmother." However, phylogenetic hypotheses are statements about the history of shared ancestry among lineages. The theropod hypothesis does not imply that *Deinonychus*, or any other Late Cretaceous dromaeosaur, is actually ancestral to birds. Rather, the theropod hypothesis proposes that those organisms shared an exclusive common ancestor. Further, Feduccia (1999b:90) has stated that "one could interpret the temporal evidence as indicating that birds and dinosaurs are indeed examples of convergent evolution." Such reasoning implies that distribution of stochastic samples in paleontological time can be used to reject a phylogenetic analysis based on many detailed

characters that are directly observable. Lastly, critics imply that such temporal disjunctions are rare or unexpected. But, as Padian and Chiappe (1998) point out, the fossil record of monotremes goes back less than 20 Ma, whereas the fossil record of therian mammals goes back 100 Ma. Yet, no one could credibly argue that this 80 my temporal disjunction could affect our confidence that monotremes are the sister group to all other extant mammals.

The magnitude of the supposed temporal paradox has also been greatly and repeatedly exaggerated. Recently, Feduccia and Martin (1998), Feduccia (1999b), and Dodson (2000) all characterized the temporal disjunction between *Archaeopteryx* and dromaeosaurs as between 60–80 my. Those authors have plainly ignored fragmentary fossils indicating existence of dromaeosaurs in the Late Jurassic (Jenson and Padian 1989). Furthermore, at least three taxa of basal dromaeosaurs are now known from the 124 Ma old Yixian formation of Liaoning, China (Xu et al. 1999b, 2000, 2001; Ji et al. 2001) which is only 24 my younger than *Archaeopteryx*. Not only are these new taxa the oldest, well-known dromaeosaurs, but they are the most birdlike theropods in many features, including their small size and obvious feathers. If a temporal paradox ever existed, it has been substantially reduced to between 0 and 24 my.

Stated phylogenetically, the temporal paradox assumes that sister taxa should have the same data of origin in the fossil record. That expectation is unrealistic given the inherent patchiness of the paleontological record. For example, the handful of specimens of *Archaeopteryx* are themselves amazing chronological outliers given the lack of any other known Jurassic birds. Until very recent discoveries from the Early Cretaceous in China (Stokstad 2001), even very few Early Cretaceous birds were known (Martin 1983a). Of course, the temporal disjunction between *Archaeopteryx* and other birds does not lead us to question the monophyly of birds. Furthermore, Brochu and Norell (2000) have demonstrated that the “temporal paradox” is equivalent or even greater for all proposed alternatives to the theropod hypothesis of avian origins.

Functional and physiological criticisms.—Another common method used to criticize the theropod hypothesis is to make *a priori* assumptions about which functional or physiological

transitions are evolutionarily likely or impossible, and then use that “knowledge” of how evolution works to reject phylogenetic analyses based on a wealth of character evidence. Examples include numerous analyses of the origin of avian flight (e.g. Feduccia 1985, Tarsitano 1985), lung ventilation (Ruben et al. 1997), and homeothermy and growth rates (Ruben and Jones 2000). These particular issues have been rebutted well elsewhere (Padian and Chiappe 1998, Padian et al. 2001, Perry 2001).

IMPLICATIONS OF THE THEROPOD ORIGIN OF BIRDS

Is the theropod origin of birds relevant to the biology of modern birds? Advances in applying phylogenetic methods to many questions in ecology and behavior have helped demonstrate the relevance of phylogenetic history of many aspects of avian biology, but many ornithologists may think that those ancient events are not important. Actually, I think that the implications of the theropod origin of birds to the biology of modern birds are many, broad, and varied, and that the theropod origin should be fundamental to how we think about and study avian biology. Here, I will review a series of examples.

Feathers.—Possession of feathers has been considered as synonymous with birds by human cultures essentially forever (with exceptions for angels; Pinna 1991). Recent paleontological discoveries have demonstrated that feathers originated and diversified in theropod dinosaurs before the origin of birds and of flight (Chen et al. 1998; Ji et al. 1998, 2001; Schweitzer et al. 1999; Sereno 1999; Xu et al. 1999a, b, 2000, 2001; Padian 2001; Sues 2001; Prum and Brush 2002). I discuss this topic here because I want to emphasize the implication of these data for how we think about and how we need to rethink avian biology (see Prum and Brush 2002 for thorough review).

In the last five years, the Early Cretaceous Yixian formation of China and the Late Cretaceous of Mongolia have produced fossils of eight nonavian theropod dinosaurs that have filamentous integumental appendages that have been hypothesized to be homologous with avian feathers: *Sinosauropteryx* (Chen et al. 1998), *Shuvuuia* (Schweitzer et al. 1999), *Beipiaosaurus* (Xu et al. 1999b), *Caudipteryx* (Ji et al.

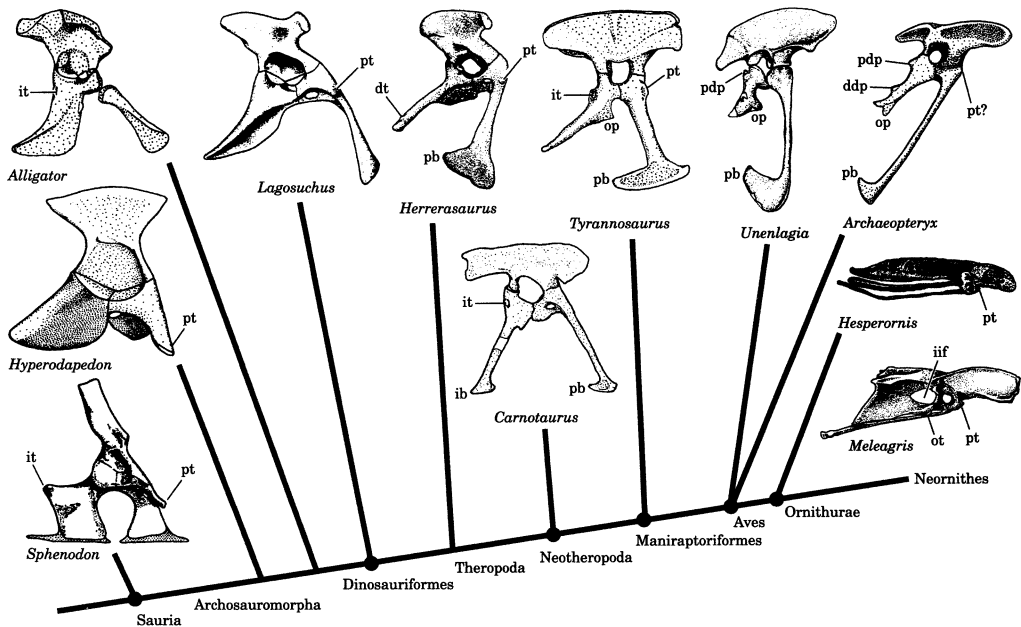


FIG. 4. Phylogenetic hypothesis of the evolution of pelvis shape and the origins of locomotor muscles in the reptile lineage leading to birds, from Hutchinson (2000b). (Reprinted with permission.)

1998), *Protarchaeopteryx* (Ji et al. 1998), *Sinornithosaurus* (Xu et al. 1999a, 2001), *Microraptor* (Xu et al. 2000), and an unnamed basal dromaeosaur (Ji et al. 2001). One of those taxa, *Caudipteryx*, has indisputable evidence of branched, pennaceous feathers (Ji et al. 1998), and repeated phylogenetic analyses based on numerous characters have demonstrated that *Caudipteryx* is a basal oviraptoran dinosaur (Serenio 1999, Zhou 2000, Zhou and Wang 2000, Zhou et al. 2000). Critics of the theropod hypothesis have called that taxon a secondarily flightless bird based only on its body proportions (Jones et al. 2000a), or brief discussion of a few characters in absence of any explicit analysis of the character data (e.g. Martin and Czerkas 2000). *Sinosauropteryx* is a basal coelurosaur with small (about 5–6 mm) integumentary appendages that are apparently cylindrical, and may also be branched in some fashion (Chen et al. 1998). *Beipiaosaurus* (a therizinosaur), and *Sinornithosaurus*, *Microraptor*, and another unnamed taxon (all basal dromaeosaurs) all have long filamentous integumentary appendages that are diverse in size and structure (Xu et al. 1999a, b, 2000, 2001; Ji et al. 2001). Detailed analyses of the structure of integumentary appendages of *Sinornithosaurus* have demonstrat-

ed that they share three unique features with avian feathers: multiple filament structure, basal branching, and serial branching (Fig. 4; Xu et al. 2001). Subsequently, the integumentary appendages of an unnamed but closely related dromaeosaur taxon further document a vane of parallel barbs running at an acute angle in exactly the conformation of a pennaceous feather (Ji et al. 2001). Those fossil structures are essentially indistinguishable from the contour feathers of confuciusornithine and enantiornithine birds preserved in the same strata.

New theropod integumental structures have been repeatedly dismissed as connective tissues, such as frayed collagen fibers or ossified tendons (Feduccia 1999a, b; Martin and Czerkas 2000; Ruben and Jones 2000). But none of those critics have explained why a therizinosaur would have 70 mm collagen filaments hanging of the trailing edge of its ulna in the exact position of avian remiges (Xu et al. 1999b); why a dromaeosaur (*Sinornithosaurus*) would have a 35 mm ossified tendon emerging from the tip of its snout (Xu et al. 2001); or why collagen fibers would be indistinguishable from feathers preserved in the same rock? Further, there is now paleobiochemical evidence that the filamentous integumentary append-

ages of *Shuvuuia*, an alvarezsaurid related to the ornithomimid theropods, are composed of β -keratin (Schweitzer et al. 1999) which occurs only in the epidermis.

The theropod origin of feathers (Padian 2001, Sues 2001, Prum and Brush 2002) has tremendous implications for avian biology. Possession of feathers is no longer synonymous with birds, nor did feathers evolve for flight. Feathers originated and diversified in terrestrial theropod dinosaurs, and were only subsequently co-opted to function in flight by birds (Prum and Brush 2002). Feathers can no longer be considered the reason why birds survived the Cretaceous-Tertiary boundary, because numerous lineages of feathered theropods went extinct at this time. Why did birds survive? That question can be addressed in future research without feathers as a consideration.

Flight.—The theropod origin of birds and feathers has important implications for the evolution of avian flight. The origin of birds, feathers, and avian flight are the central trinity of early avian evolution. Unfortunately, these three questions are frequently addressed as interdependent and correlated hypotheses. Critics of the theropod hypotheses usually advocate a thecodont origin of birds, an aerodynamic origin of feathers, and an arboreal origin of flight (Feduccia 1999b). In contrast, supporters of the theropod hypothesis have usually advocated a thermoregulatory origin of feathers and a terrestrial origin of flight (Ostrom 1974). Unfortunately, treating those hypotheses as necessarily interdependent is scientifically constraining, unproductive, and unnecessary. There is nothing about the theropod origin of birds that excludes the possibility that flight could have evolved from tress (e.g. Chatterjee 1997). However, the theropod origin of birds makes it clear that ancestors of birds were cursorial bipeds, and that many of the morphological features that were ultimately co-opted, or exapted (Gould and Vrba 1982), in the evolution of the wing and the flight stroke evolved in a terrestrial context for a purpose other than flight (Gauthier and Padian 1985; Padian and Chiappe 1997, 1998; Padian 2001). Those characters include numerous features of the forelimb, shoulder girdle, wrist, and manus that allowed birds to evolve a flight stroke from a prey grasping movement.

Rayner (1985) and others have pointed out that flying at faster speeds requires a simpler

wing “gait” (i.e. a continuous wing vortex), and fewer morphological specializations than does flying at slower speeds or taking off from the ground (which require a ring-vortex). This fact places a substantial functional challenge to how a terrestrial biped could have evolved flight purely from the ground. However, Burgers and Chiappe (1999) recently pointed out that previous models had ignored the fact that flapping feathered wings while running will considerably increase the ground speed before take off. Consequently, they hypothesize *Archaeopteryx* and the maniraptoran ancestors of all birds could have become airborne by flapping and running simultaneously. We may never have definitive evidence of the ecological context—arboreal or terrestrial—of the origin of flight in theropods, but it is clear from current evidence that the major components of the flight stroke had already evolved in bipedal theropods in a wholly terrestrial context (Gauthier and Padian 1985; Padian and Chiappe 1997, 1998).

Terrestrial locomotion.—The theropod origin of birds also has other important implications for the evolution of avian terrestrial locomotion. Gatesy and Dial (1996) observed that the evolution of avian flight required decoupling of the coordinated forelimb and hindlimb movements that are a primitive feature of reptilian locomotion, and the evolution of a novel neurological motor coupling of forelimb and tail movements. Because bipedal locomotion was primitive to theropods, forelimbs and hindlimb movements had already been evolutionarily decoupled within that lineage. Thus, as flight evolved in birds, new neuromuscular associations could evolve between wing and tail function required for controlled flight without compromising terrestrial locomotion. Gatesy and Dial's (1996) observations of avian locomotor modules underscores another challenge to the traditional arboreal theory of the origin of flight, which proposes that avian flight evolved directly from lizardlike quadrupedal arboreal ancestors.

Steve Gatesy and colleagues (Gatesy 1990, 1991, 1995; Gatesy and Dial 1996; Gatesy and Middleton 1997; Hutchinson and Gatesy 2000) have done a number of comparative analyses of the evolution of terrestrial locomotion in birds and other theropods. This body of work has underscored the functional continuity between

birds and other theropods, while also identifying derived features of avian locomotion and placing them in an historical context. For example, John Hutchinson (2000a, b) has done comparative phylogenetic analyses of the evolution of the shapes of the theropod and avian pelvis and femur; the origins, insertions, and sizes of various hindlimb muscles; and the locomotor consequences of those changes (Fig. 4). He concludes that many muscular features thought to be unique to birds can be understood historically as the extreme in a continuum of morphological character state evolution. Morphologically and functionally, extant birds are much less distinct, and therefore more easily understood, in the context of their theropod origin. This groundbreaking body of work by Gatesy, Hutchinson, and colleagues demonstrates vividly how the theropod hypothesis of avian origins provides an historical context for understanding extant avian diversity.

Nesting biology and clutch size.—Perhaps few features of avian biology have been as well studied as reproductive behavior and ecology. Yet it is little appreciated that fundamental aspects of avian reproductive biology evolved during early archosaurian and theropod ancestry. For example, birds are often considered unique among vertebrates for the extent and ubiquity of parental care. It is easy to see, however, that extensive parental care is primitive to archosaurs. Crocodylians have obligatory nest building, nest defense, and extensive post-hatching parental care. Young pterosaurs were incapable of flight during early growth, and must have received extensive parental care in early life (Ricqlès et al. 2000). The evidence of nesting and parental care in ornithischian, sauropod, and theropod dinosaurs is extensive (Currie and Padian 1997). Thus, this fundamental feature of avian biology is not exclusively avian, but essentially archosaurian.

The most dramatic evidence of similarity of paternal care in birds and other theropods comes from the nests of *Oviraptor* found in Mongolia (Clark et al. 1999). This striking fossil shows an *Oviraptor* (erroneously believed to be stealing eggs when first described!) lying on top of a terrestrial clutch of eggs in a perfectly fossilized brooding posture. Unlike the primitive archosaurian condition found in crocodiles, *Oviraptor* did not place vegetation over the top of the nest. The forelimbs of the brood-

ing individual are held at the sides but distinctly apart from the body as if covering the rest of the clutch with its wing feathers. Thus, another eminently avian feature—brooding—likely also had an origin somewhere in theropod dinosaurs prior to the evolution of birds.

David Varricchio and colleagues (Varricchio et al. 1999) have been conducting research on the nest of *Troodon formosus* that reveal some more remarkably birdlike details to theropod reproduction. *Troodon* and other theropods probably laid pairs of eggs, instead of single eggs as in most birds, because they still had two ovaries. The 24 eggs in each clutch were laid in pairs instead of all at once, which is the primitive condition of crocodylians and most other reptiles. Thus, the clutch appears to be composed over a series of days, and another distinct feature of avian reproduction appears to have originated in the theropod ancestors of birds. The typical avian traits of having one functional ovary and laying single eggs per day are apparently derived in birds. So, serial composition of the clutch was not a weight-reduction adaptation for flight because it apparently evolved in theropods before the origin of flight.

Another interesting feature of the *Troodon* nests is their clutch size. One of the fundamental limitations on the size of a clutch laid over a series of days is the time it takes for an unincubated egg to spoil. If a clutch takes too many days to complete, then the first eggs laid will begin to spoil before the entire clutch is incubated. Like birds, *Troodon* likely delayed brooding until the entire clutch was complete to synchronize hatching. Although the *Troodon* clutch size was 24, it was likely laid over ~12 days, corresponding to an avian clutch size of 12 eggs. So, it is possible that one of the primary determinants of clutch size in precocial birds has persisted since the origin of serial clutch assembly in the theropod ancestors of birds.

Growth and metabolic rates.—Avian growth and metabolic rates are of great interests to ecologists and physiologists. Recently, Padian et al. (2001) reviewed the evidence of dinosaur growth rates and metabolic rates inferred from paleohistology. A conservative conclusion is that dinosaurs evolved substantially higher growth rates than other archosaurs and reptiles, further substantiating the hypothesis that dinosaurs were not typical ectotherms. The

evolution of growth rates in early birds is also interestingly complex. Some lineages appear to show conspicuously slower growth rates than were typical of their theropod ancestors (e.g. confuciusornithine and enantiornithine birds). Padian et al. (2001) hypothesize that this may have been associated with the initial evolution of small size in early birds. Subsequently, growth rates increased again in modern birds. As with many other features of avian biology, investigation of the theropod context of avian origins establishes that many characteristics previously thought to be unique to birds can be understood to have evolved in their more ancient avian ancestors.

CONCLUSIONS

The theropod hypothesis of the origin of birds is the only phylogenetically explicit hypothesis available for the relationships of birds to other archosaurs. Shared derived anatomical characters in support of this hypothesis come from all parts of the skeleton, and recent fossil evidence also documents that fully modern, pennaceous feathers, and many birdlike reproductive behaviors evolved in theropod dinosaurs before the origin of birds. The theropod origin of birds has important implications for research and teaching in all fields of ornithology. The theropod hypothesis of the origin of birds has already generated startling new predictions about other fields of biology that have been confirmed by independent research—for example the development of digit identity in amniotes. The theropod hypothesis implies that numerous archetypical avian features evolved in theropod dinosaurs before the origin of birds or flight, including feathers, hollow bones, the wishbone, and likely air sacs, brooding, and serial composition of the clutch. Phylogenetic analyses of morphology further demonstrate that the evolution of avian anatomy can be coherently understood in terms of the theropod ancestry of birds (e.g. Hutchinson 2000a, b). These discoveries have not only expanded our knowledge of early bird evolution (Chiappe 1995, Padian and Chiappe 1998), but they challenge ornithologists to revise our diagnosis of what a bird is.

Our understanding the relevance of theropod origins to ornithology is just beginning. Numerous insights await future research. How

can ornithologists participate? First, the theropod origin of birds and general dinosaur biology should be taught in all introductory ornithology courses. *The Encyclopedia of Dinosaurs* (Currie and Padian 1997) is an excellent place to start for supplemental material. (Interested ornithologists can also contact the author for sample lecture notes.) Basic dinosaur biology and the theropod origin of birds should be incorporated in all future ornithology textbooks: there is not a single chapter of a standard ornithological text that could not include additional insights on avian biology based on their theropod origin. But textbooks are based on the scientific literature. It will be important for ornithologists to become broadly familiar with dinosaur diversity and apply their knowledge of birds to the larger field of dinosaur and archosaur biology. Ornithologists should develop research partnerships with dinosaur paleontologists, and paleontological papers on non-avian dinosaur biology with implications for ornithology should be published in ornithological journals. There are now many examples of research that bridges the narrowing gap between birds and other dinosaurs and genuinely contribute to ornithological knowledge (e.g. Gatesy and Middleton 1997; Wagner and Gauthier 1999; Hutchinson 2000a, b).

Until any credible alternative is proposed, it is time to abandon debate on the theropod origin of birds, and to proceed to investigate all aspects of the biology of birds in light of their theropod origin. This fertile frontier of knowledge promises to be among the most exciting developments in ornithology in the coming century, and ornithologists should be actively interested in and participating in this field. The time has come for our discipline to realize that ornithology is extant dinosaur biology. Ornithology can only profit as a result.

Note added in proof: Norell et al. (2002) describe a new specimen of a basal dromaeosaur (possibly a *Sinornithosaurus*) from the 124 Ma old Yixian formation of China that has preserved impressions of modern pennaceous feathers including a rachis, barbs, and a planar vane. Occasional separation of barbs in the feather vanes document presence of differentiated barbules as in *Archaeopteryx* and modern birds. Feathers on the tip of the tail are >19 cm long, and the beautifully preserved feathers on the upper hindlimbs are 13.5 cm long. This lat-

est discovery conclusively demonstrates the theropod origin of feathers and birds.

ACKNOWLEDGMENTS

I would like to thank K. Padian and T. Peterson for helpful comments on the manuscript. I would also like to thank C. Brochu, A. Brush, L. M. Chiappe, S. Gatesy, J. Gauthier, J. Hutchinson, K. Middleton, M. Norell, S. Sumida, G. Wagner, X. Xu, and Z. Zhou for additional inspiration in conversation and in print. Supplemental materials to Hou et al. 1996 can be found online at <http://www.sciencemag.org/feature/data/hou.shl>.

LITERATURE CITED

- BENTON, M. J., AND J. M. CLARK. 1988. Archosaur phylogeny and the relationships of the Crocodylia. Pages 295–338 in *The Phylogeny and Classification of Tetrapods*, vol. 1: Amphibians, Reptiles, and Birds (M. J. Benton, Ed.). Clarendon Press, Oxford.
- BOCK, W. J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Systematic Zoology* 14:272–300.
- BROCHU, C. A., AND M. A. NORELL. 2000. Temporal congruence and the origin of birds. *Journal of Vertebrate Paleontology* 20:197–200.
- 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 identification of homologies in the avian hand. *Science* 278:666–668.
- BURNHAM, D. A., K. L. DERSTLER, P. J. CURRIE, R. T. BAKKER, Z. ZHOU, AND J. H. OSTROM. 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. *University of Kansas Paleontological Contributions—New Series* 12–13:1–14.
- CAMPBELL, B., AND E. LACK. 1985. *A Dictionary of Birds*. T. A. and D. Poyser, London.
- CHATTERJEE, S. 1997. *The Rise of Birds: 225 Million Years of Evolution*. Johns Hopkins University Press, Baltimore, Maryland.
- CHEN, P.-J., Z. M. DONG, AND S. N. ZHEN. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian formation of China. *Nature* 391:147–152.
- CHIAPPE, L. M. 1995. The first 85 million years of avian evolution. *Nature* 378:349–355.
- CHIAPPE, L. M., Q. JI, S. JI, 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*, no. 242.
- CHIAPPE, L. M., M. A. NORELL, AND J. M. CLARK. 1996. Phylogenetic position of *Mononychus* from the Upper Cretaceous of the Gobi Desert. *Memoires of the Queensland Museum* 39:557–582.
- CHURE, D. J., AND J. H. MADSEN. 1996. On the presence of furculae in some non-maniraptoran theropods. *Journal of Vertebrate Paleontology* 16:573–577.
- CLARK, J. M., M. NORELL, AND L. M. CHIAPPE. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding posture over an oviraptorid nest. *American Museum Novitates* 3256:1–36.
- CURRIE, P. J., AND K. PADIAN, ED. 1997. *The Encyclopedia of Dinosaurs*. Academic Press, San Diego, California.
- DAHN, R. D., AND J. F. FALLON. 2000. Interdigital regulation of digit identity and homeotic transformation by modulated BMP signaling. *Science* 289:438–441.
- DALTON, R. 2000. Feathers fly in Beijing. *Nature* 405:992.
- DODSON, P. 2000. Origin of birds: The final solution? *American Zoologist* 40:505–512.
- FARLOW, J. O., S. M. GATESY, T. R. HOLTZ, JR., J. R. HUTCHINSON, AND J. M. ROBINSON. 2000. The theropod locomotion. *American Zoologist* 40:640–663.
- FEDUCCIA, A. 1985. On why the dinosaurs lacked feathers. Pages 75–79 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum Eichstätt, Germany.
- FEDUCCIA, A. 1999a. 1,2,3 = 2,3,4: Accommodating the cladogram. *Proceedings of the National Academy of Sciences USA* 96:4740–4742.
- FEDUCCIA, A. 1999b. *The Origin and Evolution of Birds*, 2nd ed. Yale University Press, New Haven, Connecticut.
- FEDUCCIA, A., AND L. D. MARTIN. 1998. Theropod-bird link reconsidered. *Nature* 391:754.
- 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.
- GALIS, F. 2001. Digit identity and digit number: Indirect support for the descent of birds from theropod dinosaurs. *Trends in Ecology and Evolution* 16:16.
- GARDINER, B. G. 1982. Tetrapod classification. *Zoological Journal of the Linnean Society* 74:207–232.
- GATESY, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology* 16:170–186.

- GATESY, S. M. 1991. Hind limb scaling in birds and other theropods: Implications for terrestrial locomotion. *Journal of Morphology* 209:83–96.
- GATESY, S. M. 1995. Functional evolution of the hind limb and tail from basal theropods to birds. Pages 219–234 in *Functional Morphology in Vertebrate Paleontology* (J. Thomason, Ed.). Cambridge University Press, Cambridge, United Kingdom.
- GATESY, S. M., AND K. P. DIAL. 1996. Locomotor modules and the evolution of avian flight. *Evolution* 50:331–340.
- GATESY, S. M., AND K. M. MIDDLETON. 1997. Bipedalism, flight, and the evolution of locomotor diversity. *Journal of Vertebrate Paleontology* 17: 308–329.
- GAUTHIER, J., A. G. KLUGE, AND T. ROWE. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105–209.
- GAUTHIER, J., AND K. PADIAN. 1985. Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. Pages 185–197 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- GAUTHIER, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoires of the California Academy of Sciences* 8:1–55.
- GOULD, S. J., AND E. S. VRBA. 1982. Exaptation—A missing term in the science of form. *Paleobiology* 8:4–15.
- HEILMAN, G. 1926. *The Origin of Birds*. H.F.G. Witherby, London.
- 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. Pages 141–147 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- HOLTZ, T. R. 1994. The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. *Journal of Paleontology* 68:1100–1117.
- HOPSON, J. A. 2001. Ecomorphology of avian and nonavian theropod phalangeal proportions: Implications for the arboreal versus terrestrial origin of bird flight. Pages 211–235 in *New Perspectives on the Origin and Early Evolution of Birds* (J. Gauthier and L. F. Gall, Eds.). Peabody Museum of Natural History, Yale University, New Haven, Connecticut.
- HOU, L., L. D. MARTIN, Z. ZHOU, AND A. FEDUCCIA. 1996. Early adaptive radiation of birds: Evidence from fossils from northeastern China. *Science* 274:666–668.
- HUELSENBECK, J. P., AND B. RANNALA. 1997. Phylogenetic methods come of age: Testing hypotheses in an evolutionary context. *Science* 276:227–232.
- HUTCHINSON, J. R. 2000a. The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131:169–197.
- HUTCHINSON, J. R. 2000b. The evolution of pelvic osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society* 131:123–168.
- HUTCHINSON, J. R., AND S. M. GATESY. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* 26:734–751.
- HUXLEY, T. H. 1868. Remarks upon *Archaeopteryx lithographica*. *Proceedings of the Royal Society of London* 16:243–248.
- HUXLEY, T. H. 1870. Further evidence of the affinity between dinosaurian reptiles and birds. *Quarterly Journal of the Geological Society of London* 26:12–31.
- JENSON, 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., P. J. CURRIE, M. A. NORELL, AND S.-A. Ji. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393:753–761.
- Ji, Q., M. A. NORELL, K.-Q. GAO, S.-A. Ji, AND D. REN. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* 410:1084–1088.
- JONES, T. D., J. O. FARLOW, J. A. RUBEN, D. M. HENDERSON, AND W. J. HILLENIUS. 2000a. Cursoriality in bipedal archosaurs. *Nature* 406:716–718.
- JONES, T. A., J. A. RUBEN, L. D. MARTIN, E. N. KUROCHKIN, A. FEDUCCIA, P. F. A. MADERSON, W. J. HILLENIUS, N. R. GEIST, AND V. ALIFANOV. 2000b. Non-avian feathers in a late Triassic archosaur. *Science* 288:2202–2205.
- JONES, T. D., J. A. RUBEN, P. F. A. MADERSON, AND L. D. MARTIN. 2001. *Longisquama* fossil and feather morphology. *Science* 291:1899–1902.
- LARSON, A., AND J. A. LOSOS. 1996. Phylogenetic systematics of adaptation. Pages 187–220 in *Adaptation* (G. V. Lauder and M. R. Rose, Eds.). Academic Press, San Diego, California.
- LAUDER, G. V. 1990. Functional morphology and systematics: Studying functional patterns in an historical context. *Annual Review of Ecology and Systematics* 21:317–340.
- LAUDER, G. V., AND M. R. ROSE, Eds. 1996. *Adaptation*. Academic Press, San Diego, California.
- MAKOVICKY, P. J., AND P. J. CURRIE. 1998. The presence of a furcula in tyrannosaurid theropods, and its phylogenetic and functional implications in an evolutionary context. *Science* 276:227–232.

- tions. *Journal of Vertebrate Paleontology* 18:143–149.
- MAKOVICKY, P. J., AND H.-D. SUES. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microventer celer* from the Lower Cretaceous of Montana. *American Museum Novitates* 3240:1–27.
- MARTIN, L. D. 1983a. The origin and early radiation of birds. Pages 291–338 in *Perspectives in Ornithology* (A. H. Brush and G. A. Clark, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- MARTIN, L. D. 1983b. The origin of birds and of avian flight. *Current Ornithology* 1:106–129.
- MARTIN, L. D. 1985. The relationship of *Archaeopteryx* to other birds. Pages 177–183 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- MARTIN, L. D., AND S. A. CZERKAS. 2000. The fossil record of feather evolution in the Mesozoic. *American Zoologist* 40:687–694.
- MARTIN, L. D., AND J. D. STEWART. 1985. Homologies in the avian tarsus. *Nature* 315:159.
- 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.
- NORELL, M., Q. JI, K. GAO, C. YUAN, Y. ZHAO, AND L. WANG. 2002. Dinosaur feathers. *Nature* 416: in press.
- NORELL, M., P. J. MAKOVICKY, AND J. M. CLARK. 1998. A *Velociraptor* wishbone. *Nature* 389:447.
- OSTROM, J. H. 1974. *Archaeopteryx* and the origin of flight. *Quarterly Review of Biology* 49:27–47.
- PADIAN, K. 2001. Cross-testing adaptive hypotheses: Phylogenetic analysis and the origin of bird flight. *American Zoologist* 41:598–607.
- PADIAN, K., AND L. M. CHIAPPE. 1997. Bird origins. Pages 71–79 in *Encyclopedia of Dinosaurs* (P. J. Currie and K. Padian, Eds.). Academic Press, San Diego, California.
- PADIAN, K., AND L. M. CHIAPPE. 1998. The origin and early evolution of birds. *Biological Reviews* 73: 1–42.
- PADIAN, K., A. J. D. RICQLÈS, AND J. R. HORNER. 2001. Dinosaurian growth rates and birds origins. *Nature* 412:405–408.
- PATTERSON, C. 1982. Morphological characters and homology. Pages 21–74 in *Problems in Phylogenetic Reconstruction* (K. A. Joysey and A. E. Friday, Eds.). Academic Press, London.
- PERRY, S. F. 2001. Functional morphology of the reptilian and avian respiratory systems and its implications for theropod dinosaurs. Pages 429–441 in *New Perspectives on the Origin and Early Evolution of Birds* (J. Gauthier and L. F. Gall, Eds.). Peabody Museum of Natural History, Yale University, New Haven, Connecticut.
- PINNA, M. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7:367–394.
- PRUM, R. O. 1999. Development and evolutionary origin of feathers. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 285:291–306.
- PRUM, R. O. 2001. *Longisquama* fossil and feather morphology. *Science* 291:1899–1900.
- PRUM, R. O., AND A. H. BRUSH. 2002. The evolutionary origin and diversification of feathers. *Quarterly Review of Biology* 77: in press.
- RAYNER, J. M. V. 1985. Cursorial gliding in proto-birds. Pages 289–302 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- REISZ, R. R., AND H.-D. SUES. 2000. The ‘feathers’ of *Longisquama*. *Nature* 408:428.
- RICQLÈS, A. J. D., K. PADIAN, J. R. HORNER, AND H. FRANCHILLON-VIEILLOT. 2000. Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): Anatomy, ontogeny, and biomechanical implications. *Zoological Journal of the Linnean Society* 129:349–385.
- RIEPPPEL, O. 1993. Studies on skeletal formation in reptiles. IV. The homology of the reptilian (amniote) astragalus revisited. *Journal of Vertebrate Paleontology* 13:31–47.
- RUBEN, J. A., AND T. A. JONES. 2000. Selective factors associated with the origin of fur and feathers. *American Zoologist* 40:585–596.
- RUBEN, J. A., T. A. JONES, N. R. GEIST, AND W. J. HILLENUS. 1997. Lung structure and ventilation in theropod dinosaurs and early birds. *Science* 278: 1267–1270.
- SCHWEITZER, M. H., J. A. WATT, R. AVCI, L. KNAPP, L. CHIAPPE, M. NORELL, AND M. MARSHALL. 1999. Beta-keratin specific immunological reactivity in feather-like structures of the Cretaceous alvarezsaurid, *Shuvuuia deserti*. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 285:146–157.
- SERENO, P. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Science* 25:435–489.
- SERENO, P. 1999. The evolution of dinosaurs. *Science* 284:2137–2147.
- STOKSTAD, E. 2001. Exquisite Chinese fossils add new pages to book of life. *Science* 291:232–236.
- SUES, H.-D. 2001. Ruffling feathers. *Nature* 410:1036–1037.
- SUMIDA, S. S., AND C. A. BROCHU. 2000. Phylogenetic context for the origin of feathers. *American Zoologist* 40:486–503.

- TARSITANO, S. F. 1985. The morphological and aerodynamic constraints on the origin of birds and avian flight. Pages 319–332 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- UNWIN, D. M., AND M. J. BENTON. 2001. *Longisquama* fossil and feather morphology. *Science* 291: 1900–1901.
- VARRICCHIO, D. J., F. JACKSON, AND C. N. TRUEMAN. 1999. A nesting trace with eggs for the Cretaceous theropod dinosaur *Troodon formosus*. *Journal of Vertebrate Paleontology* 19:91–100.
- VOGEL, G. 1997. Forensic science: Phylogenetic analysis: Getting its day in court. *Science* 275:1559–1560.
- 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 in the avian hand. *Proceedings of the National Academy of Sciences USA* 96:5111–5116.
- WALKER, A. D. 1972. New light on the origin of birds and crocodiles. *Nature* 237:257–263.
- WELLNHOFER, P. 1985. Remarks on the digit and pubis problem of *Archaeopteryx*. Pages 113–122 in *The Beginnings of Birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Freunde des Jura-Museum, Eichstätt, Germany.
- WELMAN, J. 1995. *Euparkeria* and the origin of birds. *South African Journal of Science* 91:533–537.
- WHETSTONE, K. N., AND L. D. MARTIN. 1981. New look at the origin of birds and crocodiles. *Nature* 279:234–236.
- WILLISTON, S. W. 1879. Are birds derived from dinosaurs? *Kansas City Review of Science* 3:457–460.
- WITMER, L. M. 1991. Perspectives on avian origins. Pages 427–465 in *Origins of the Higher Groups of Tetrapods* (H.-P. Schultze and L. Trueb, Eds.). Cornell University Press, Ithaca, New York.
- XU, X., Z.-L. TANG, AND X.-L. WANG. 1999b. A therizinosauroid dinosaur with integumentary structures from China. *Nature* 399:350–354.
- XU, X., X.-L. WANG, AND X.-C. WU. 1999a. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. *Nature* 401:262–266.
- XU, X., Z. ZHOU, AND R. O. PRUM. 2001. Branched integumental structures in *Sinornithosaurus* and the origin of feathers. *Nature* 410:200–204.
- XU, X., Z. ZHOU, AND X. WANG. 2000. The smallest known non-avian theropod dinosaur. *Nature* 408:705–708.
- ZHOU, Z. 1995. Is *Mononychus* a bird? *Auk* 112:958–963.
- ZHOU, Z. 2000. *Caudipteryx* and the origin of flight in birds. *Vertebrata Palasiatica* 38(Supplement):38.
- ZHOU, Z., AND X.-L. WANG. 2000. A new species of *Caudipteryx* from the Yixian formation of Liaoning, northeast China. *Vertebrata Palasiatica* 38: 113–127.
- ZHOU, Z., X.-L. WANG, AND X. XU. 2000. Important features of *Caudipteryx*—Evidence from two nearly complete new specimens. *Vertebrata Palasiatica* 38:241–254.