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Author: Feduccia, Alan

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Commentary

Birds are Dinosaurs: Simple Answer to a Complex Problem

ALAN FEDUCCIA[1]
Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA

Richard Prum's (2002) rancorous, unreviewed essay on the theropod origin of birds is a one-sided view of a difficult problem, full of anatomical misconceptions that are highly misleading, and advocates that (p. 13), ''it is time to abandon debate on the theropod origin of birds.'' His article is essentially a restatement and defense of a current dogma of paleontology—that birds are living dinosaurs, directly descended from, or having shared common ancestry with, one of the most highly derived and specialized groups of Cretaceous theropods, the dromaeosaurs (and Cretaceous troodontids), that are presumed to have had ghost lineages going back into the Jurassic Period. Advocates on both sides of the debate agree that birds are related to dinosaurs, but opponents of the birds-are-dinosaurs movement, including myself, advocate a common shared ancestry of birds and dinosaurs from basal archosaurs, with less specialized anatomical baggage, at a much earlier time.

The ''birds are living dinosaurs'' hypothesis dates back almost three decades to when John Ostrom (see Ostrom 1976), combining studies of his earlier discovery of the late, early Cretaceous dromaeosaur *Deinonychus* with his speculations on hot-blooded (endothermic) dinosaurs, presented his new dinosarurian origin of birds theory. At its inception, all theropods were highly energized, endothermic reptiles (endothermic homeotherms), and the smaller theropods had acquired feathers for insulation. *Archaeopteryx* was an earthbound feathered theropod that could not fly (Bakker 1975) but later learned to fly from the ground up (Ostrom 1979). At that time, the dinosaurian origin of birds had, of course, nothing to do with cladistic theory, but was based on the overall similarity of *Deinonychus* to *Archaeopteryx*. By 1978, *Archaeopteryx* was said to support ''two theories: warm-bloodedness in dinosaurs and dinosaurian ancestry of birds'' (Ostrom 1978:168). I wrote the first rebuttal to hot-blooded dinosaurs (Feduccia 1973), and a mountain of evidence has been marshaled against endothermy in dinosaurs during the last three decades (Morell 1996).

Nevertheless, Ostrom (1976) reconstructed the *Archaeopteryx* skeleton to closely resemble that of the known theropods; it was a terrestrial predator, and

sported a vertical pubis, with fully developed pubic foot and a predatory hand. Often a hypertrophied second foot sickle claw, like that of *Deinonychus*, was on display. Now, with the discovery of early Cretaceous dromaeosaurs with somewhat retroverted pubes, *Archaeopteryx* has gradually had its pubis pushed back to the opisthopubic position to conform to the most current view of dromaeosaurs and is often depicted as a terrestrial predator, with a sickle claw (Paul 2002), despite evidence that *Archaeopteryx* was arboreal (Feduccia 1993), and clearly did not possess such a claw. Because all the known theropods were terrestrial predators, Ostrom (1979) suggested that the flight feathers must have elongated in the context of insect traps and were later preadapted for flight. The dinosaurian origin of birds thus originated as a strange amalgam of overall similarity and evolutionary scenarios involving endothermy and ground-up flight. Prum's (2002) assertion that I have linked the dinosaurian origin of birds to ground-up flight is a misstatement; my exposition was a reaction to the then current paleontological dogma. It was Ostrom who argued that the discovery of *Deinonychus* provided evidence for a ground-up origin of flight (Dingus and Rowe 1998). Later, Padian (beginning 1983) spent decades trying unsuccessfully to make a convincing argument for ground-up flight origin in birds and pterosaurs, which he considered a corollary of a theropod–pterosaur sister-group hypothesis.

Paleontologists Dingus and Rowe (1998) linked the dinosaur ancestry of birds with the origin of flight from the ground up, and the thecodont (basal archosaur) hypothesis with the origin of flight from the trees down. ''Our map [of avian relationships] suggests that flight evolved from the ground up, but exactly how this happened is another question altogether.'' As Bock (1999) noted, ''If the origin of birds and the origin of flight are tightly linked in this fashion, then the available discussion of all specialists in vertebrate flight is that the origin of avian flight from the ground up is exceedingly improbable, which would fatally weaken the dinosaur ancestry of birds.''

Prum (2002) has now established an even more elaborate evolutionary scenario for the evolution of flight and feathers in birds, involving the origin of

[1] E-mail: feduccia@bio.unc.edu

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feathers from ''dino-fuzz'' filaments (Feduccia 1999) as an insulatory mechanism (but with no evidence for endothermy in dromaeosaurs), the origin of a flight morphology in a terrestrial setting, and then the final achievement of ''flight'' from the trees down. That complex scenario, involving endothermy and preadaptations, has no name as yet. The last attempt to explain flight in dinosaurs was the ''ground down'' theory, a version of trees down, but involving jumping from rocks or leaping from cliffs, which was, in essence, a version of the trees down theory, biophysically. An arboreal flight origin from theropods was previously suggested by Chatterjee (1997) and Xu et al. (2000).

In 1986, Gauthier codified the theropod origin of birds in a cladistic context and it has been the dogma of vertebrate paleontology and the popular press since that time. Although most fields of science are struggling with methodology, systematics (and particularly vertebrate paleontology) has adopted a single, inviolate approach to establishing phylogeny. Statements by Prum (2002:4) such as, ''it is universally agreed,'' and ''conclusive evidence of the strongest possible,'' and ''wealth of and increasing strength of the evidence'' (p. 5) characterize the zeal of the new school of cladism.

The problem, of course, is that if the generated phylogeny is wrong (e.g. clades of hesperornithiforms, loons and grebes; clades of hawks and owls, Cracraft 1982, 1986; lungfish and tetrapods, Rosen et al. 1981), then the cladistic inference can lead to disastrous effects. Classic examples include the ground-up origin of flight (now on display in many general biology texts), and its corollary, the ground-up origin of pterosaurs (Padian 1983), now completely rejected (Unwin and Henderson 2002). Philosopher David Hume urged that one should hold it more likely that one had been deceived than the laws of nature should stand suspended (Close 1993). In the final analysis we must test hypotheses of homology by examining individual characters independently of cladistic hypotheses to avoid the circular reasoning engendered by that approach.

The new version of cladistics can be termed a clado-phenetic approach; it involves coding vast numbers of primitive and derived characters, often to conform to the preconceived phylogeny advocated by the investigator. As James Clark (1992:533) noted, ''similarity lies in the eye of the beholder, and the particular hypothesis being advocated strongly colors perceptions of morphological resemblance.'' Whatever the case, cladistics is incapable of recognizing massive convergence (Dodson 2000), and there are numerous examples, notable within the clades of loons and grebes, hawks and owls, and dromornithids and ratites, where the methodology has produced a false phylogeny.

An astounding recent example of the pitfalls of the new approach was the announcement of the discovery of feathered dinosaurs in *Nature* featuring a painting of two feathered dinosaurs from China (Ji et al. 1998), named *Caudipteryx* and *Protarchaeopteryx*. The paper was followed quickly by the pronouncement by *Nature* editor Gee (1998) that ''the debate is over'', presaging the comment by Prum (2002: 13) that, ''it is time to abandon debate. . . . '' But, not so fast. That particular cladistic analysis was based on a sloppy analysis of some 90 characters, of which nearly half were primitive and nearly half were not present in the fossil taxa. The remaining characters included sutured, rather than ligamentous, quadratojugal-quadrate contact, quadratojugal contact with the squamosal, and presence of obturator process of the ischium, and in *Caudipteryx* all of these features are ambiguous. They claimed serrated teeth were present in *Protarchaeopteryx*, but none of those examining the actual specimen, including myself, could see any serrations, and the photograph in *Nature* shows no serrations. And, in the original description (Ji and Ji 1997), a special point is made that *Protarchaeopteryx* teeth are characterized by the lack of serrations. Jones et al. (2000a) have subsequently shown conclusively that these taxa are secondarily flightless birds, ''Mesozoic kiwis,'' and have nothing to do with dinosaurs.

Although Prum (2002) makes it sound as though the debate largely centered on the origin of flight coupled to bird origins, that is not the case, and I certainly agree that the discovery of small theropods capable of tree-climbing renders certain aspects of that argument moot. Yet, one must realize that some 30 years were spent by a large number of paleontologists writing scores of papers trying to make a convincing argument for a ground-up origin of flight (Padian and Chiappe 1998a, b). Most recently Padian and Chiappe (1998a) erroneously portray the arboreal and highly skilled flier *Confuciusornis* as a terrestrial, feathered predator in a preposterous posture which adorned the cover of *Scientific American.* Olson (2000:839) set the record straight in a review of a monograph on the famous Chinese bird by Chiappe et al. (1999):

> The authors, steeped in cladistic fundamentalism, have been among the more insistent proponents of the origin of birds from theropod dinosaurs, with its attendant corollaries, such as the origin of flight from the ground up. . . . This paper will stand as an exemplar of manipulation of information to conform to preconceived ideas, but it is otherwise insufficiently credible or comprehensible to constitute a lasting addition to knowledge.

Carpus and hand.—It is surprising that Prum (2002), with his strict cladistic approach, would expend so much space trying to make the argument that the avian digits are I, II, III, and homologous to those of the highly derived and unique theropod hand, because the identity of the avian digits is irrelevant to cladistic anal-

ysis. Gauthier's basic tree topology is recovered whether or not hand characters are used or deleted (Wagner and Gauthier 1999). The reason, however, is clear: scientists still recognize the importance of key characters, and it was noted early in the debate that if one key synapomorphy (referring to the digital mismatch) were falsified, it would reduce all the other synapomorphies to the status of parallelism or homoplasy (Howgate 1985). Thus, the true identity of the avian digits is of critical importance.

First, the representation of the carpus of *Archaeopteryx* appears to be anatomically incorrect (Prum 2002; Fig. 2, reprinted from Wagner and Gauthier [1999]). The carpus of *Archaeopteryx* is represented as having three carpal elements, but it has four. Two are the ulnare and radiale, which connect manus to forearm, and the third and largest is the semilunate bone. The fourth is a relatively small bone that fuses to metacarpal III (IV?) in late birds (Zhou and Martin 1999). No theropod has been described with those four carpals in an avian anatomical arrangement. The carpal elements in the theropods are all over the map, ranging from seven in primitive forms to advanced ornithomimids, which lack a semilunate bone. However, there is superficial resemblance of the semilunate bone in a number of dromaeosaurs to that of *Archaeopteryx*, but is probably a compounded proximal element in dromaeosaurs and represents a single distal carpal in birds. Ostrom (1990:270–271) in a diagnosis of the Dromaeosauridae noted that, ''carpals consist solely of proximal elements: a semilunate radiale . . . plus an oval wedge-shaped ulnare.'' A complete description of the wrist and manus is provided by Zhou and Martin (1999) and Gishlick (2001), and will not be repeated here. However, the fact that dromaeosaurs have two carpal elements, *Archaeopteryx* have four, and the fact that in the early Cretaceous *Confuciusornis* the semilunate fuses to the middle metacarpal as in *Archaeopteryx* does not lend much confidence to the idea that the semilunate of birds is homologous to that of described dromaeosaurs, where it is likely a compounded element composed of two carpal elements.

Substantial embryological evidence from a variety of amniotes indicates the identity of avian digits to be II–III–IV (Burke and Feduccia 1997), but that was challenged by Wagner and Gauthier (1999), who accept a cladistically based hypothesis of direct descent of birds from theropod dinosaurs. They accepted the identification of the embryonic avian digit condensations as II–III–IV, but argued that changes in digit identity are the result of homeotic changes, that is, changes of the identity of one structure into that of another, so that the digits of theropod dinosaurs—I–II–III, are the same as the avian digits—II–III–IV. According to their frame-shift hypothesis, developmental properties controlling digits I–III are shifted onto embryonic condensations CII–CIV. In other words, the remaining avian digits are I–III, which develop from condensations CII–CIV.

Their argument gained indirect support from Drossopoulou et al. (2000) who presented evidence for the developmental independence of the determination of digit number and digit identity. They manipulated sonic hedgehog (*Shh*) gene to produce phenotypes with the same number of supernumerary digits, but with differences in digit identity. Their evidence showed that homeotic changes in digit identity are possible without a change in digit number. Later, Dahn and Fallon (2000) experimentally created homeotic transformations of manal digits, and were able to grow any digit in any position. Those manipulations show that digit identity is determined by digit primoidea interactions with gradients of pattern formation genes, in the form of bone morphogenetic proteins in interdigital mesoderm. However, those experiments show only what morphological changes are possible to manipulate experimentally, not what actually happened in evolution, and one question is why homeosis would occur at all, much less in manus, but not pes? One can generate all sorts of ''hopeful monsters'' in the genetics laboratory, but they have little, if any, evolutionary viability. It is conceivable that such genetic mechanisms might be decoupled even if avian fore- and hindlimbs exhibit the same, highly conserved developmental pattern, but it is not necessarily parsimonious to postulate that such a change might occur in one, but not the other of serially homologous elements. Abdominal B-related genes in the Hox A and D clusters show a consistent pattern of expression in fore- and hindlimbs in chick and mouse (Nelson et al. 1996), suggesting that the ontogenetic pattern is primitive and homologous in amniotes. Furthermore, there is no demonstrable evidence for a single homeotic frame shift in any known amniote, in manus or pes, nor is there any evidence for a shift in theropod hands throughout their evolution. The suggestion by Wagner and Gauthier (1999) that the kiwi hand shows a homeotic change stretches credulity. One could ask why should an animal undergo a homeotic change in the hand when there is simply no selective advantage to modifying a functionless hand? Why would there be an additional frame shift, if there were an initial frame shift in the lineage of theropods leading to birds? Another difficulty is that evolutionary changes in early limb development are extremely constrained because of negative pleiotropic effects of deleterious mutations (Galis et al. 2001). During the critical early developmental stages in alligator, turtle, and bird, the basic program is morphologically identical, the condensations develop similarly, and they retain fidelity to the developing digits.

Much has been made of the fact that *Archaeopteryx* and primitive archosaurs have the same 2–3–4 phalangeal formula (2–3–4–5–3 in pentadactyl archosa-

rus); tridactyl dinosaurs have digits I, II, III, with a phalangeal formula of 2–3–4–x–x. But phalangeal formulae are developmentally plastic and in basal theropods reduction of phalanges in digits IV and V occurs, going from the ancestral formula (2–3–4–5–3) reduced to 2–3–4–3–2, to 2–3–4–1–x, and later to 2–3–4–x–x. Reduction of phalanges is a simple matter, and for *Archaeopteryx* to attain a formula of 2–3–4 for digits II, III, IV, a simple symmetrical reduction of one phalanx per digit is required. Such a reduction of only the most distal phalanges can be accomplished by experimental blockage of bone morphogenetic protein 4 (*BMP4*) signaling which mediates apotosis in the avian limb bud (Zhou and Niswander 1996). Furthermore, individual specimens of *Archaeopteryx* have varying phalangeal pes formulae, and in the trend towards modern birds the manal formula has changed to 2–2–1 (*Gallus*; sometimes reduced to 1–2–1), and 2–3–1 in *Struthio*. The secondarily flightless Mesozoic *Caudipteryx* has a formula of 2–3–2, again showing a trend towards phalangeal reduction.

As Prum (2002) notes, Dahn and Fallon (2000) were able to grow digits with extreme phalangeal formulae that do not occur among known archosaurs. That is still another indication of the extreme plasticity of phalangeal formulae in vertebrates and the ease with which they can be transformed in evolution without the necessity of incurring the expense of deleterious effects of a homeotic frame-shift. Witness the similarity of the digits of Mesozoic marine reptiles and those of whales, two unrelated but convergent groups of vertebrates.

A broad comparison of digital reduction in an array of vertebrates supports a common pattern, with digits I or V being typically the first to be lost in a lineage. Such a pattern is typical of amphibians, lizards, turtles, and mammals and has been termed Morse's "law of digital reduction." The theropod hand, comprising digits I, II, II, is nearly unique in vertebrates, and its retention of digit I and loss of digit IV violates the consistent pattern of reduction.

Apart from dinosaurs, the reduction of digit IV after its precocious appearance is seen only in some African lizards, as noted by Burke and Feduccia (1997). Prum (2002) asks the question as to how the digits of theropod hands could have developed in the absence of the essential fourth metacarpal developmental axis? His question, however, is difficult to comprehend because that very pattern is seen over and over again at specific stages of development, where a structure or enzyme appears, has a biochemical or positional inductive or cascading effect, and then disappears at a later stage. Classic examples are the appearance of the notochord in man, which induces the development of the neural tube and then disappears by the fifth week, remaining only as the nuclei pulposi in the adult; and the pronephros which induces the formation of the mesonephros and
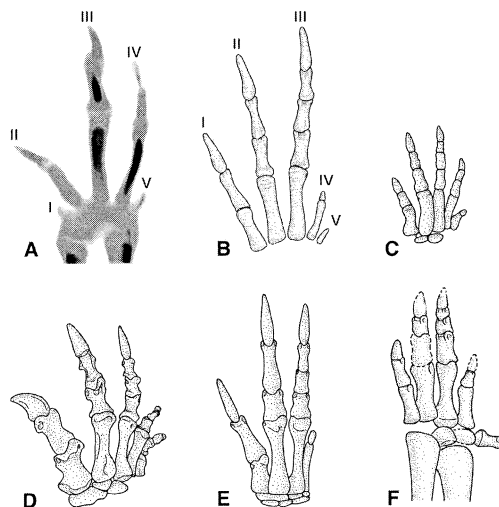

FIG. 1. The pentadactyl hand of a 14(–15) day old ostrich (A), showing the anlagen for digits I, "thumb" (left) and V (right), compared to the hands of various dinosaurs illustrating the reduction of digits IV and V (disappearance of V in E). (B) *Herrerasaurus* (putative basal theropod, late Triassic); (C) *Lesothosaurus* (basal ornithischian, late Triassic); (D) *Plateosaurus* (basal sauropodomorph, late Triassic); (E) *Syntarsus/Coelophysis* (theropods, late Triassic); (F) *Hypsilophodon* (ornithopod, early Cretaceous). Drawn to same scale, modified from a variety of drawings (primarily modified from drawings in Weishampel et al. 1990; ostrich embryo from Feduccia and Nowicki 2002).

then disappears by end of the fourth week. In amniotes, the primary axis no doubt serves as the organizer of the hand, but can later recede and disappear without any deleterious effects. "It is parsimonious to assume that the theropod limb developed with a typical primary axis through distal carpal IV followed by typical development of the digital arch and digits III, II, I, followed by a subsequent regression of the precursors of the fourth digit." (Burke and Feduccia 1997:668).

The reduction of IV and V is a salient feature of "dinosaurs" and provides further evidence for their monophyly. Interestingly, the trend in dinosaurs is for the combined reduction of the medial and lateral pedal digits, but of only the lateral manal digits. I propose that the reduction or loss of manal digits IV and V (Fig. 1) be restudied as a salient synapomorphy of the Dinosauria, especially given the extreme difficulty in defining this important clade.

In summary, if there were a homeotic frame shift in the avian manus, it would be a unique occurrence in all amniotes, in manus or pes, and the proposed homeotic frame shift would have to occur not in the lineage leading to the theropods or the earliest bird,

but within the theropod lineage leading to birds, at about the *Allosaurus* level. Galis et al. (2002) note, ''The occurrence of full homeotic shifts elsewhere would make this hypothesis more likely. To make this hypothesis really believable, one has to come up with a good adaptive scenario.''

Most importantly, the recent demonstration of all five embryonic condensations for avian digits I, II, III, IV, and V proves that the primitive avian hand was pentadactyl. Three independent studies, each using different techniques, have all reached that same conclusion (Feduccia and Nowicki 2002, Kundrát et al. 2002, Larsson and Wagner 2002; see Fig. 1). ''The presence of a first digit in the early embryo argues for a primitive avian pentadactyl hand, with adult digits II, III, IV . . . unlike the highly derived I, II, III hand of theropods'' (Feduccia and Nowicki 2002: 393). ''The direct avian ancestor is predicted to have been five-fingered with dominant digits . . . II, III, IV'' (Kundrát et al. 2002:294); and ''a prechondrogenic digital anlage has been maintained in the bird lineage for at last 220 million years since the last known pentadactylous ancestor of the lineage'' (Larsson and Wagner 2002:146).

The major problem here in the two interpretations of the hand of birds and dinosaurs involves philosophical differences in methodology. Developmental biologists use conservation of embryonic patterning to establish homology, whereas most paleontologists, including Prum, use the methodology of phylogenetic systematics to define homology *a posteriori* from cladistic analyses. Until more evidence to the contrary becomes available, it is most parsimonious to consider the avian hand II, II, IV, in contrast to the highly derived grasping, raking theropod hand with digits I, II, III.

Interestingly, Larsson and Wagner (2002:150) conclude that birds have a pentadactyl ground state and that, ''The most recent known ancestor of birds with a pentadactyl hand lived in the late Triassic Period (220 my ago).'' However, they go on to say that this age is congruent with both a dinosaurian and nondinosaurian origin of birds. Yet, the known theropod dinosaurs of that age, namely *Herrerasaurus* and *Coelophysis*, for example, are already committed to a highly derived pattern of postaxial digital reduction, the former clearly preserving vestigial digits (metacarpals) IV and V (Fig. 1). For a pentadactyl ground plan one would have to consider the basal archosaurs such as the Triassic *Lagosuchus*, considered by many to be ancestral to dinosaurs (Feduccia 1999), and whether or not it is considered a dinosaur is anyone's opinion. Whatever the case, the late Triassic is an entire geologic period before the appearance of any known dromaeosaurs.

What About the Teeth?—Perhaps the most impressive difference between theropods and birds concerns the structure of teeth and the nature of their implantation (Figs. 2–4; Martin and Stewart 1999). It is astounding that more attention has not been given to the dramatic differences between bird and theropod teeth (Table 1), especially when one considers that the basis of mammal paleontology involves largely tooth morphology.

To be brief, bird teeth (as seen in *Archaeopteryx*, *Hesperornis*, *Parahesperornis*, *Ichthyornis*, *Cathayornis*, and all toothed Mesozoic birds) are remarkably similar and are unlike those of theropods. Mesozoic bird teeth share numerous remarkable similarities with crocodilians, but not found in theropod dinosaurs. The typical bird and crocodilian tooth is characterized as having a flattened, unserrated crown that becomes constricted as it approaches the crown–root juncture. The tooth narrows at that point and then there is an expanded root crown with a cement-covered root at least as broad as the crown, usually broader. Details of the differences in morphology, implantation, and replacement can be found in Martin et al. (1980), and Martin and Stewart (1999). It is noteworthy that the Upper Jurassic bird–dinosaur ''missing link'' of 1991 was *Lisboasaurus*, later shown to be a crocodilomorph (Feduccia 1999).

Although some of the latest Cretaceous troodontids and some dromaeosaurs are said to have some posterior teeth devoid of serrations, they are certainly atypical of theropods, and the velociraptorine *Bambiraptor* has fully serrated, laterally flattened teeth.

There is essentially no shared, derived relationship of any aspect of tooth morphology between birds and theropods, including tooth form, implantation, or replacement. The abundant Chinese enantiornithine and ornithurine fossil material recently discovered has illustrated that the tooth form of Mesozoic birds is similar in all known groups and is therefore ancestral for Aves.

Much has been written about the small, late Cretaceous theropods known as alverezsaurids. Considered to be birds (Perle et al. 1993), they are perhaps the most highly derived ornithomimid dinosaurs that converged on birds in a number of features. Conforming to the general trend within the ornithomimids, those theropods were in the process of losing their teeth and the fact that they are devoid of serrations and somewhat more birdlike is not surprising; but they have nothing to do with birds (Zhou 1995). In discussing the cladistic analysis that led to avian status of the alverezsaurid *Mononykus* Ostrom (1994:172) commented that,

> Reasoning of such dubious quality, demonstrates a fundamental flaw in the cladistic methodology. Preoccupation with compilation of lengthy list of . . . characters at the expense of a well-reasoned functional analysis of the characters that are shared will result in an erroneous phylogeny every time. *Mononykus* was not a bird. . . . But it clearly was a fleet-footed fossorial theropod.

Another way of stating the problem is that cladistic methodology in paleontology has forced into algorithmic form what is arguably the most subjective and qualitative field of biology. With respect to the putative dromaeosaur–bird nexus, it is worth noting that the most recent study of dromaeosaurid and bird skulls (Elzanowski 1999), reported that, ''No specific avian similarities could be found in the jaws and palate of dromaeosaurids.'' It is in the highly derived Cretaceous oviraptorsaurids that one encounters birdlike skulls, and there are suggestions that they may represent a group of secondarily flightless Mesozoic birds, related to *Caudipteryx* (Elzanowski 1999, Maryansk et al. 2002). As Elzanowski points out (1999:331), ''The major cladistic analyses based primarily on postcranial characters . . . singled out the dromaeosaurids as the closest relatives and, thus, echoed Ostrom's . . . comparisons of *Archaeopteryx* to *Deinonychus*. This is inconsistent with cranial evidence, at least from the palate and jaws, which does not support a dromaeosaurid relationship of birds.''

Limited space does not permit me to discuss the problems involved in endothermy and dinosaur nesting and other behaviors linked to birds. I refer the reader to chapter 3 in Feduccia (1999). However, the same principle applies: almost all of the supposed avian-like behavior is gleaned from latest Cretaceous ornithischians (!) and the nest of a late Cretaceous *Troodon*. One should also keep in mind that there are more than 100 species of snakes and lizards that brood eggs or maintain a nest, and more than 10 species engage in communal nesting.

Feathered Dinosaurs.—There are two schools of thought with disparate models for feather origin: the classical ''scale-to-feather'' model (Maderson 1972), based primarily on embryological and now substantial molecular evidence, and Prum's (1999) new ''filament-to-feather'' model, based on the occurrence of dino-fuzz, a unique preservation of a halo of carbonized filaments in the Chinese dromaeosaurs.

Because Prum's (2002) ''filament to feather model'' for the origin of feathers will be reviewed elsewhere by a number of independent authors, I will only comment briefly here. Having studied most of the specimens said to sport protofeathers, I, and many others,
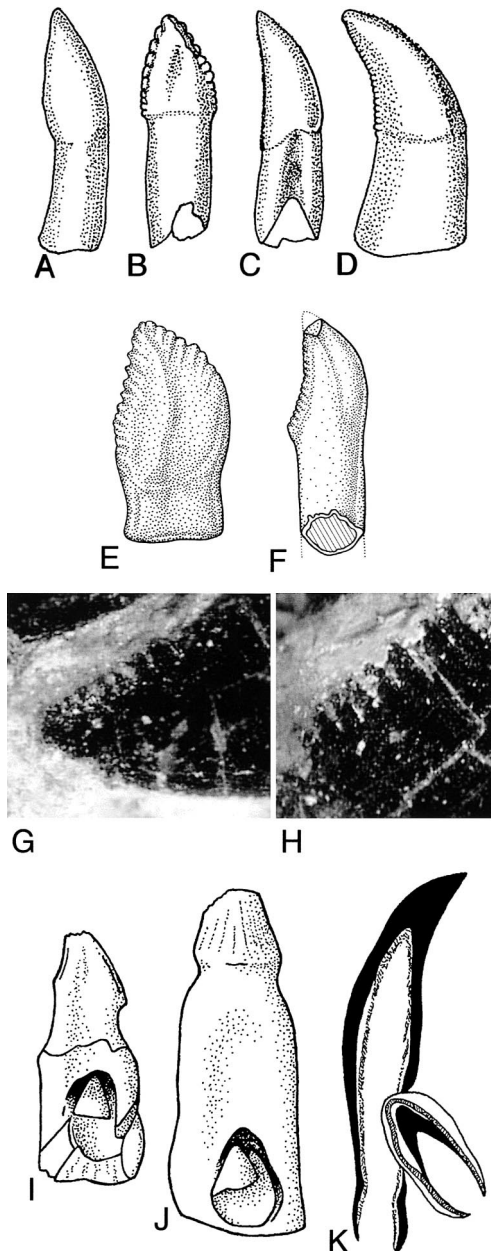
Fig. 2. (A–D) Teeth of theropod dinosaurs thought by various authors to be especially close to birds: (A) *Mononykus* (modified from Perle et al. 1993); (B) *Troodon*; (C) *Saurornitholestes*; (D) *Dromaeosaurus* (B–D modified from Currie et al. 1990). (E) Tooth of a therizinosaur (segnosaur), thought to be close to dromaeosaurs, but whose teeth more closely resemble the serrated, lanceolate teeth of prosauropods; (F) tooth of cover theropod *Microraptor* showing the typical nonavian tooth morphology of dromaeosaurs; (G–H) serrated teeth of the late

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Cretaceous *Bambiraptor*, morphologically close to *Velociraptor* and thought a close ally of birds; teeth showing constricted crown, replacement tooth tip, and expanded base: bird, (I) *Parahesperornis alexi* Martin; (J, K) crocodilian, *Alligator*; (K) lateral cross section showing the tilted replacement tooth resorbing the root of its predecessor (modified from Edmund 1962). (A–D and H–J from Martin and Stewart 1999; E from Feduccia 1999, (G–H) courtesy D. Burnham; F, modified from Xu et al. 2000).
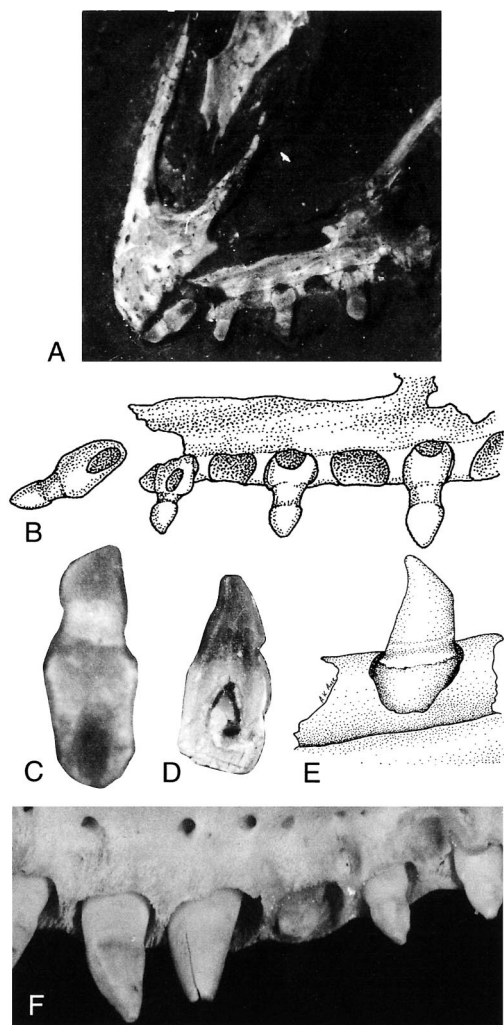
FIG. 3. Lingual views of the premaxillary and maxillary teeth of *Archaeopteryx lithographica* von Meyer, London specimen: (A) left premaxilla and right maxilla; (B) maxilla and isolated tooth; (C) isolated tooth (from right premaxilla?); (D) *Parahesperornis alexi*, left lower tooth; (E) drawing taken from photograph of a tooth of the seventh specimen of *Archaeopteryx*, showing similarity to sockets in the London maxillary; (F) right, lingual view of an alligator maxilla showing similarity of tooth and socket formation to (A) and (B). (With permission from Martin and Stewart 1999.)

do not find any credible evidence that those structures represent protofeathers. Many Chinese fossils have that strange halo of what has become known as dino-fuzz, but although that material has been ''homologized'' with avian feathers, the arguments are far less than convincing. Prum's (2002) view is shared by many paleontologists: birds are dinosaurs; therefore, any filamentous material preserved in dromaeosaurs must represent protofeathers.

Most important, ''dino-fuzz'' is now being discovered in a number of taxa, some unpublished, but particularly in a Chinese pterosaur (Wang et al. 2002) and a therizinosaur, which has teeth like those of prosauropods (Fig. 2E). Most surprisingly, skin fibers very closely resembling dino-fuzz have been discovered in a Jurassic ichthyosaur (Fig. 5) and described in detail (Lingham-Soliar 1999, 2001). Some of those branched fibers are exceptionally close in morphology to the so-called branched protofeathers (''Prum Protofeathers'') described by Xu et al. (2001).

That these so-called protofeathers have a widespread distribution in archosaurs is evidence alone that they have nothing to do with feathers. One is reminded of the famous fernlike markings on the Solnhofen fossils known as dendrites. Despite their plantlike outlines, these features are now known to be inorganic structures caused by a solution of manganese from within the beds that reprecipitated as oxides along cracks or along bones of fossils. Despite the myriad inherent problems involved with the preservation and identification of dino-fuzz, when the first specimen discovered, *Sinosauropteryx*, was examined, Currie (1997) was convinced that it possessed avian-like feathers. ''The integumentary structures were simpler than true feathers, and each seems to be composed of a central rachis and branching barbs . . . '' (Currie 1997:241).

There is substantial evidence to support the alternative hypothesis, that is, the classical scale-to-feather model, which conforms nicely with what we know about (1) feather embryology, (2) the fact that avian foot scutes can be transformed into feathers using either bone morphogenetic protein or retinoic acid, and (3) the fact that the primitive early Cretaceous birds *Confuciusornis* and *Protopteryx* have two central tail feathers that are scalelike, without branching (Zhang and Zhou 2000). However, in addition it is particularly interesting to note that in half developed ostrich embryos there is a zone of more or less delimited scales near the dorsal border of the lateral apterium. The border of each scale is a feather rudiment already sunk into a short feather-sac, near the posterior end (Holmgren 1955; A. Feduccia pers. obs.). At the margin of the scale-covered area of the pectoral callosity, particularly in *Rhea*, the scales appear to be combined with feathers, at the top end of each scale. This close developmental association of scale and feather would be remarkable if feathers evolved through a filament stage.

In a recent paper, Harris et al. (2002) attempt a complex model of feather evolution based on function and regulation of two intercellular signaling molecules, *Shh* and bone morphogenetic protein 2 (*Mnp2*). Despite a very laudable scientific effort and some truly remarkable developmental biology, their
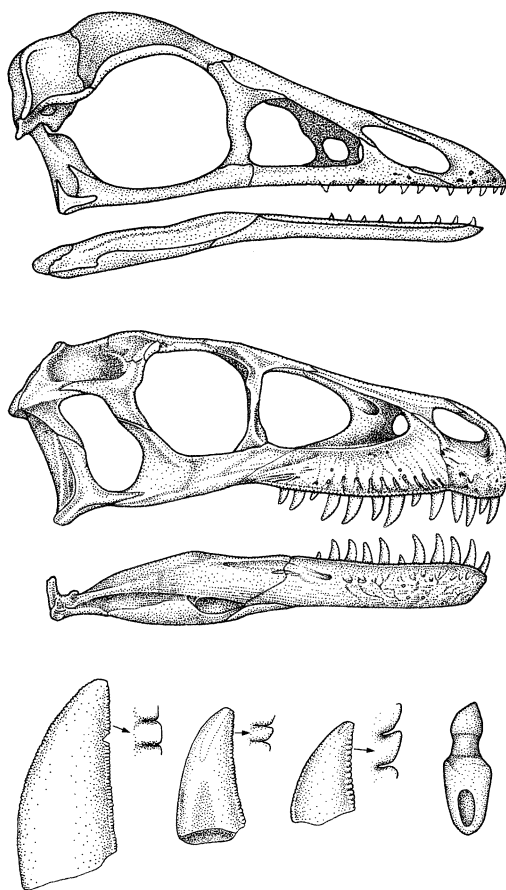
FIG. 4. Skull of *Archaeopteryx* (upper) compared to that of *Dromaeosaurus*. Virtually all anatomical features are distinct, including overall shape, laterally flattened, serrated teeth, lower jaw with a tall, slender, vertical process behind the joint. It is primarily in the hand and pubis that one sees superficially birdlike features, but even in the postcranial skeleton dromaeosaurids are highly specialized theropods with a cable-like network of delicate rods in the tail that extend anteriorly from prezygopophyses, a somewhat opisthopubic pubis, but with a non-*Archaeopteryx* pubic boot, and a large, raptorial sickle claw on the second toe, also not found in any known Mesozoic or other bird. Below, serrated teeth of theropods: left to right, plesiomorphic large theropod, *Saurornitholestes* (dromaeosaur), *Troodon*; compared to a typical tooth of *Archaeopteryx* (Pmx tooth from the London specimen). Dromaeosaur skull modified from Currie (1997); *Archaeopteryx* skull modified from Martin and Zhou (1997). Theropod teeth modified after Fiorillo and Currie (1994); *Archaeopteryx* tooth modified from Martin and Stewart (1999).

entire model is based on the ''fact'' that ''Recent paleontological discoveries have documented that feathers evolved in coelurosaurian theropod dinosaurs before the origin of birds.'' (Harris et al. 2002: 174). Those specimens preserve either dino-fuzz or feathers, and the association between the two has simply not been demonstrated. There is no credible evidence to justify the portrayal on the January 2002 *Auk* of *Microraptor* with a thick, white downy coating of putative protofeathers (A. Feduccia pers. obs.).

The morphology of *Confuciusornis* and *Longisquama* integumentary appendages suggests that modern feathers evolved through the stages involving elongated scales that became broken up into barbs and barbules. The latter discovery lends credibility to the hypothesis that the elongated integumentary appendages of the late Triassic *Longisquama* (Jones et al. 2000b) are in fact ''parafeathers.'' Those structures, contra Prum (2002), have a hollow, central shaft, which is compartmentalized, attach to the body by papillae, and were individually molted, as evidence by the many separate *Longisquama* parafeathers discovered at the fossil site. Interestingly, the scales on the posterior forearm are elongated and must have been used in steering. Minimally, this specimen proves that the most featherlike structures in a non-avian Mesozoic vertebrate are found in a late Triassic basal archosaur, a thecodont. A hypothetical arboreal, Triassic basal archosaur illustrating the scale to feather model is shown in Figure 6.

The *Longisquama* specimens were examined over a period of some 3–4 days in April 1999, by a team of eight scientists, including two highly respected Russian paleontologists and a developmental biologist specializing in reptile integument (see authors, Jones et al. 2000a). Prum, who proclaimed the study to be ''quackery'' in print, says that he ''examined *Longisquama* with the authors in April 1999,'' (Prum 2001: 1899), but his examination of that exceptional, complex Triassic reptile consisted of 5 to 10 min, at most, of a cursory perusal of the main slab, and he denied the presence of an antorbital fenestra, seen by all of the authors, and established by the careful Russian paleontologist Sharov in the 1970s. Interestingly, in addition to having a birdlike skull, *Longisquama* has a well developed furcula.

The real challenge presented by those early Cretaceous Chinese fossils is to determine exactly what is being preserved in those unique lake sediments. The so-called ''hairy devil'' pterosaur *Sordes* (Upper Jurassic lake deposits of Kazakhstan) is preserved in similar lacustrine deposits and preserves structures remarkably similar, if not identical, to dino-fuzz (Wellnhofer 1991). Yet, the finest-grained lithographic limestone, the *Archaeopteryx* bearing Solnhofen beds, do not preserve dino-fuzz on the small coelurosaur *Compsognathus*, a very close ally of the early Cretaceous Chinese *Sinosauropteryx*, which exhibits a halo of that material.

TABLE 1.   Comparison of morphology and other features of Mesozoic bird and theropod teeth (information from Currie et al. 1990, Martin and Stewart 1999, and other sources).

Archaeopteryx (and typical Mesozoic birds)	Theropod teeth
Peg-like, isodont, waisted teeth with expanded root crowns; devoid of surface ornamentation.	Blade-like, recurved ziphodont teeth, with nonexpanded roots; smooth, nonwaisted transition from tooth crown to root.
Posterior teeth with exaggerated, expanded roots.	Serrated ridges on front and back edges, consisting of closely spaced denticles, each squarish or oval in outline, separated by ''slots'' that cut meat fibers.
Subthecodont mode of insertion in deep, crater-like sockets; teeth begin in a groove and sockets form around the root.	Teeth regimented along bony shelf, attached by cancellous bone.
Vertical tooth family; replacment teeth migrate labially just after initiation and develop under crown of predecessor.	Horizontal tooth family; replacement teeth form rows on lingual side of mature tooth, with up to three generations of teeth ranked side by side.
Oval resorption pit on lingual aspect of root surrounds developing crown (resorption pit closed at base).	Oval lingual scar on lower root (not resorption pit), left by lingually migrating replacement tooth.
Tooth covered with cementum and attached by periodontal ligament that may rot and allow tooth with root to fall out and be found isolated as fossils.	Teeth almost always found as tooth crowns only, having broken off from roots. (*Troodon* with rather coarse serrations, somewhat reminiscent of prosauropods; *Dromaeosaurus* with characteristic ''twist'' of anterior serrated carina, as in carnosaurs).
Teeth designed for holding and eating whole prey.	Teeth designed for cutting and slicing flesh.

One must explain also why all theropods and other dinosaurs discovered in other deposits where integument is preserved exhibit no dino-fuzz, but true reptilian skin, devoid of any featherlike material (Feduccia 1999), and why typically Chinese dromaeosaurs preserving dino-fuzz do not normally preserve feathers, when a hardened rachis, if present, would be more easily preserved.

There are clearly two different taphonomic phenomena in the early Cretaceous lacustrine deposits of the Yixian and Jiufotang formations of China, one preserving dino-fuzz filaments, as in the first discovered, so-called ''feathered dinosaur'' *Sinosauropteryx* (a compsognathid), and one preserving actual avian feathers, as in the feathered dinosaurs that were featured on the cover of *Nature,* but which turned out to be secondarily flightless birds. The only other preservation of feathers on those Chinese fossils is in the abundant beaked bird *Confusiusornis,* other enantiornithines, and in a newly described seed-eating bird, *Jeholornis prima,* which exhibits some dromaeosaurid-like features in the tail and sec-
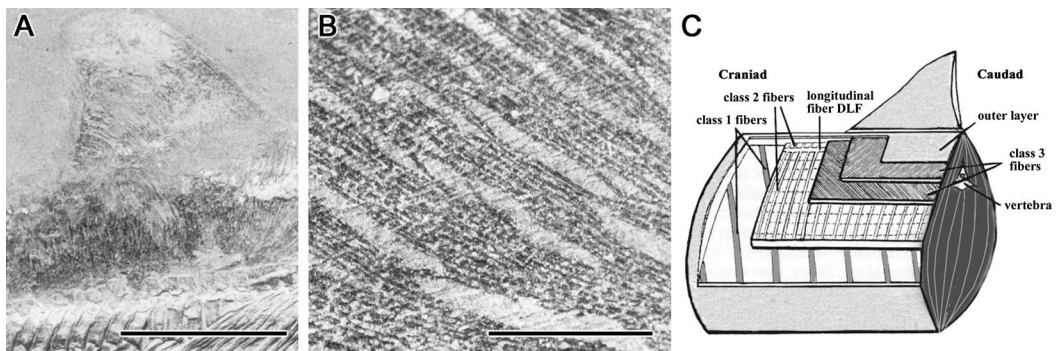

FIG. 5.   Filaments similar to proposed protofeathers have been discovered in an ichthyosaur. (A) Detail of part of body and fin of *Stenopterygius quadricissus* showing skin fibers (scale bar = 5 cm). (B) Detail of tissue showing long strands (~45 per centimeter), which closely resemble the ''branched protofeathers'' proposed by Xu et al. (2001) (scale bar = 0.5 cm). (C) Schematic representation of a radial ''dissection'' of the ichthyosaur skin, showing different classes of skin fibers preserved (''dissected'' area represents an area ~1.3 cm long × 1.0 cm wide). (Redrawn and reprinted from Lingham-Soliar; modified from Lingham-Soliar 2001; courtesy T. Lingham-Soliar by permission of Taylor and Francis AS.)

FIG. 6.   Hypothetical proavis according to Steiner (1917). This model is based on a basal archosaur (thecodont) ancestor, a trees-down model for flight origin, and the classical scale-to-feather model, supported by both embryology and new molecular data.

ond claw (Zhou and Zhang 2002). There are also asymmetric flight feathers preserved on the wing and near the hind limbs of a dromaeosaurid (Norell et al. 2002, Czerkas et al. 2002). Given the now substantial evidence that certain taxa once thought to be dinosaurs (e.g. *Caudipteryx*, *Protarchaeopteryx*, and the Oviraptosauria; Maryanska et al. 2002) are most likely secondarily flightless birds, and the new hypothesis that certain dinosaurs were secondarily flightless descendants of Mesozoic birds (Paul 2002), we must now carefully consider the possibility that there may have been a number of radiations of secondarily flightless Mesozoic birds that evolved morphologies quite similar to theropod dinosaurs.

This view is now endorsed by Czerkas et al. (2002) who describe the Chinese early Cretaceous *Cryptovolans pauli*, characterized by the presence of asymmetric, primary flight feathers, avian hand, and sternum, but with typical dromaeosaur-like teeth, a hypertrophied second sickle claw, and dromaeosaur-like stiffened tail. Such a specialized, derived tail is virtually the same in rhamphorhynchoid pterosaurs of the Jurassic.

In a series of papers, Lowe (last paper 1944) proposed that ratites and small coelurosaurian dinosaurs shared a common ancestor, and that the ancestors of ratites never acquired flight. Of course, we now know that this is wrong (Feduccia 1999), but one can only ponder how the postcranial remains of any ratite would be identified if recovered from the early Cretaceous of China. Too, given the view that "the smallest dinosaur is the bee hummingbird . . . found only in Cuba," (Norell et al. 1995), it follows that any bird, flighted or flightless, discovered in Mesozoic deposits, would be classified as a dinosaur.

It has become clear that this problem is far more complex that those on either side of the debate had anticipated, and the real challenge now may be to separate out radiations of secondarily flightless birds from true theropods. And, if birds are, as Paul (2002) argues, derived from theropods and then gave rise to secondarily flightless theropods, the problem of convergence is simply transferred to dromaeosaurs and carnosaurs. Such a convergent pattern may be even more formidable than that proposed between flightless birds and theropods. Either way, if birds were initially derived from dromaeosaurs, then the required character transformations involved going from highly derived sickle second claw to primitive avian claw, highly derived stiffened tail to primitive *Archaeopteryx*-like tail, and highly derived theropod teeth to primitive bird teeth (Table 1).

Temporal Paradox.—Despite Prum's attempt to dismiss the "temporal paradox" as irrelevant to the debate, it is a problem of great concern to most workers in the field and especially the interested public. In 1999, at a special Florida conference on the dinosaur–bird problem, the small, juvenile velociraptorine *Bambiraptor* was introduced as the then most birdlike theropod ever discovered. Yet, it dates to 70 Ma, that is, some 80 my after the appearance of the earliest known bird *Archaeopteryx*. As Dodson (2000:504) points out, "The current cladistic analysis of bird origins posits a series of outgroups that postdate the earliest bird by up to 80 million years." Going back to 1997, Novas and Puerta announced the discovery of *Unenlagia* (Feduccia 1999), a theropod later hailed as "a missing link," but dated at 90 Ma, about the same age of *Deinonychus*, that is, some 60 my after *Archaeopteryx*. Many examples exists, but the point is that the group of theropods thought to be avian ancestors is strictly a Cretaceous radiation, and of more concern, they become more and more birdlike as one approaches the latest Cretaceous. This is also true of certain relatives of the dromaeosaurs, the superficially birdlike troodontids, for which there is now a fragmentary fossil (if correctly identified; Xu et al. 2002) from the Chinese deposits dating to some 128 Ma (if the date is correct). It is worth noting that the specimen described, *Sinovenator*, is a "basal troodontid;" that is, an ancestral troodontid present in the late part of the early Cretaceous, and the same is true

of the Chinese dromaesaurs. This is further confirmation of the fact that the dromaeosaur (troodontid) radiation was a Cretaceous event.

Prum's (2002) assertion that we have ignored fragmentary fossils of dromaeosaurs from the Late Jurassic is misleading because no credible paleontologist has considered the fragments of a distal radius and femur from the Morrison Formation as anything other than unidentifiable trash. Jensen's Jurassic ''birds'' (Feduccia 1999) were more or less dismissed at the time of their discovery in 1978. It might be added that small fossils (primarily tibiotarsi) of similar age, taken from the famous African Tendaguru site (that yielded *Brachiosaurus*), were once thought to be avian, but were later described as ''avian-like tibiotarsi of pterodactyloids . . . from the Upper Jurassic.'' (Galton 1980). These are truly amazing fossils, for if these tibiotarsi were discovered in deposits of Eocene age, they would certainly be identified as belonging to some unusual bird.

According to Prum (2002) the temporal paradox is reduced to some 24 my. However, he assumes that *Archaeopteryx* is the first bird; but contrarily, *Archaeopteryx* is a well-developed avian in many anatomical features as well as in wing and feather structure. But, for discussion let us assume that there is some 24 my separating the two groups, with *Archaeopteryx* as the first bird. Such a gap would be close to half the time period of the age of mammals, and when we consider that whales evolved from land ungulates in a time frame of some 5 to 8 my, the time disparity becomes even more astounding.

As for the Chinese fossils, there has been attempt after attempt to make the fossil deposits older and older, but they still date, at the earliest, to an average of about 120–124 Ma, still some 26 to 30 my after *Archaeopteryx*. It is certainly possible that dromaeosaurs date earlier than that time, but given the advanced avian state of *Archaeopteryx*, it is also equally probable that early birds are much earlier than *Archaeopteryx*.

Of greater interest, however, is the fact that there are many dinosaurs from the Jurassic and Triassic periods, but none of the Triassic theropods (or protheropods such as *Herrerasaurus*, *Eoraptor*) have any major birdlike features. For example, the late Triassic *Coelophysis* has the typical theropod, laterally flattened serrated teeth, greatly elongated cervical ribs, five sacral vertebrae, an astragalocalcaneum with no ascending process of any development (although considered a synapomorphy of Theropoda), no pubic boot, and a carpal region with seven carpals (no semilunate bone), as in *Herrerasaurus*.

The pleas by paleontologists and now Prum (2002) for ghost lineages of unknown dinosaurs is possible, but the dinosaurs are among the best known Mesozoic vertebrates. For example, there are 173 dinosaur discoveries (some duplication) from the Late Triassic, 130, 128, and 318, from the Early, Middle, and

Late Jurassic, respectively; and 399 from the Early Cretaceous (information from DinoData, see Acknowledgments). This is not a meager vertebrate fossil record! From the famous Late Triassic Ghost Ranch in New Mexico, full or partial skeletons of some 1,000 individuals of the basal theropod *Coelophysis* have been recovered and a similar concentration of the related *Syntarsus* were discovered in Zimbabwe. Prum (2002) accuses those who advocate an earlier common ancestry of birds and dinosaurs from early archosaurs of dreaming up hypothetical ancestors, but the hypothetical ''ghost'' lineages of earlier dromaeosaurs that would qualify as avian ancestors are equally imaginary, and by whatever time span those unknown lineages are pushed back, one must equivalently push back the forebears of *Archaeopteryx*.

Finally, I feel it necessary to comment on the ''thecodonts,'' which Prum (2002) characterizes as ''a polyphyletic garbage bag assemblage of early archosaurs.'' Contra Prum (2002), it was in fact South African Robert Broom, not Heilmann, who established the idea that birds and dinosaurs shared a common ancestor among the Thecodontia. As for the thecodonts (basal archosaurs with a antorbital fenestra), if they are poorly defined, then certainly the same could be said of the Dinosauria and its various subgroups. There has been a recent revival of interest in the famous Early Triassic thecodont *Euparkeria*, and Welman (1995) has discovered a suite of avian-like anatomical features in the basicranium. Paul (2002: 179), an ardent advocate of the ''birds-are-dinosaurs,'' and more recently, ''dinosaurs-are-birds'' school, admits that, ''*Euparkeria* is a suitable ancestral type for birds . . . and . . . *Euparkeria* is a good ancestral type for all archosaurs.'' I would suggest that taxa most suitable for avian ancestry are likely to fall morphologically beyond *Euparkeria*, but prior to the appearance of the earliest and most primitive theropods. However, I do not expect some massive cladistic analysis to resolve this problem. Carroll (1988: 8) emphasized that, ''When attempting to establish relationships of any group within the fossil record, we must emphasize the earliest known members, because they have had the shortest amount of time to evolve new characters since their initial divergence. Hence, they should provide us with the best opportunity to identify the derived features that they share with their closest sister group.''

According to Sereno (1997), the most notable cranial character (synapomorphy) present throughout the Dinosauria is the loss of the postfrontal bone, but that feature is also found in the Crocodilia. Likewise, the Saurischia is equally difficult to define, especially given the large suites of theropod characters in such ''thecodonts'' as *Postosuchus* (Chaterjee 1985). The theropod-like *Postosuchus*, if included in a theropod cladistic analysis would probably crank up the phylogenetic ladder to about the ceratosaur level. Defi-

nitions of dinosaurian subgroups are equally elusive, and most workers have abandoned trying to define coelurosaur, the group for years said to include avian ancestors. Illustrating the difficulty of defining dinosaur groups, Carroll (1988:290) pointed out, ''The 'canosaur' families may each have evolved separately from different groups that have been classified as coelurosaurs.''

If, as proposed by Paul (2002) and Czerkas et al. (2002), dromaeosaurs are actually birds, either flightless or becoming flightless, then the question of bird origins is again completely reopened. But aside from the obvious problems, that proposal has major implications because both camps in the debate would have portrayed dromaeosaurs incorrectly, and as Czerkas et al. (2002:120) note, ''cladistics has presented a highly misleading interpretation of the evidence,'' and (p. 122) ''The origin of birds stems further back to a common ancestor of pre-theropod status.'' If correct, whatever the case, the presence of *Cryptovolans* as a dromaeosaur with fully developed flight feathers, an avian style hand and sternum, dromaeosaur teeth, sickle claw, and a stiffened dromaeosaur (rhamphorhyncoid) tail, should send all those involved in the debate on bird origins back to the drawing board.

Conclusion.—The origin of birds, like the origin of all the groups of Mesozoic archosaurs, is a difficult problem to resolve, with all major groups diverging from basal archosaurs in the Triassic. Like the intractable problem of pterosaur origins, the precise nature of bird origins from archosaurs, despite current dogma, still remains elusive. Much more attention should be given the small basal archosaurs of the Triassic, following the excellent study by Benton (1999) of the small archosaur *Scleromochlus*, variously thought to position phylogenetically as either a basal sister group of Pterosauria or of Dinosauromorpha. This small archosaur shows many birdlike features, as does *Megalancosaurus*, *Longisquama*, and *Coesasaurus*, and Benton (1999) established a new group name, the Avemetatarsalia (''bird feet'') for the clade consisting of *Scleromochlus* and Ornithodira.

In the *Encyclopedia of Dinosaurs* (Currie and Padian 1997), Padian (p. 178) notes that he and May (1993) proposed ''to define Ornithischia as all those dinosaurs closer to *Triceratops* than to birds, and Saurischia as all dinosaurs closer to birds than to Ornithischia. Dinosauria is defined as all descendants of the most recent common ancestor of birds and *Triceratops*;'' and (p. 494), ''Ornithischia and Saurischia are sister taxa, stem groups of Dinosauria; hence any member of Dinosauria must belong to one of these two groups. . . .'' What about the basal archosaurs *Postosuchus* (nearly a theropod), *Ornithosuchus*, or *Lagosuchus* and *Lagerpeton* (sometimes included in Dinosauria, but not belonging to either the Ornithischia or Saurischia)? And, if those forms are included, it means that the vast majority of characters used in theropod–bird cladograms are primitive. Most workers are reasonably happy with the validity of the lineage leading to theropods, with basal forms characterized by such late Triassic forms as *Eoraptor* and *Herrerasaurus*, but our knowledge of the relationships of sauropods and ornithischian dinosaurs is strictly limited. So, too, is our knowledge of basal archosaurs (thecodonts). If the thecodonts can be termed a ''garbage bag assemblage'' (Prum 2002:1), then why not the Dinosauria?

One thing is certain, if one begins to ''cherry-pick'' characters within the advanced groups of theropods to establish bird origins, then the door is open for the same procedure in other groups as well. Dodson (2000:504) rightly emphasizes that,

> Cladistics systematically excludes data from stratigraphy, embryology, ecology, and biogeography that could otherwise be employed to bring maximum evolutionary coherence to biological data. Darwin would have convinced no one if he had been so restrictive in his theory of evolution.

Phylogenetic systematics stands alone in the sciences in demanding that critics of a particular phylogenetic hypothesis not criticize the hypothesis without proposing an ''explicit alternative hypothesis'' (Prum 2002:1). Another way of stating that philosophy is that, ''a flawed hypothesis is better than no hypothesis at all.'' That approach does not conform to any standards of science. There are times when there is insufficient evidence to make the formulation of a hypothesis feasible.

According to Dingus and Rowe (1998:194), ''. . . birds are avialian, maniraptoran, tetanurine, theropod, saurischian dinosaurs.'' However, as Bock (1999:568) recently cautioned, ''it is best to consider birds as part of the great archosaurian radiation without being more specific, as has been agreed by zoologists for more than a century.'' Thomas and Garner (1998:130) question why the debate over the phylogenetic position of birds seems far from any conclusion, and note that the reason may be, ''Perhaps because where natural selection meets the strict constraints of biomechanics, convergence is inevitable, and separating common inheritance from common function may be near-impossible in a system so highly derived.''

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