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Commentary

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ARE CURRENT CRITIQUES OF THE THEROPOD ORIGIN OF BIRDS SCIENCE? REBUTTAL TO FEDUCCIA (2002)

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IN MY *Perspectives in Ornithology* essay (Prum 2002), I advocated that all ornithologists should be excited about research on the theropod origin of birds. Although I did address some criticisms of the theropod hypothesis, I spent most of the essay outlining the data in support of the theropod origin and, most exciting to me, describing the new directions in evolutionary ornithological research that have opened up as a consequence. I concluded that one of the most important frontiers in ornithological research in this century will be the establishment of a thorough scientific understanding of the evolution of avian biology in light of the theropod origin of birds. From nesting biology and physiology to behavior and locomotion, the rewards of studying ornithology as extant dinosaur biology are only just beginning to be reaped (Prum 2002).

In his critique of my essay, A. Feduccia (2002) reviewed much of his previous work but also sprang a new, surprise ending. In summary, he hypothesized that birds evolved from an unknown lineage of early basal archosaurs, and that rampant convergent evolution renders the many derived morphological characters shared by birds and theropods unreliable. However, Feduccia can no longer deny the conclusive evidence that basal dromaeosaurs had feathers (Xu et al. 1999, 2000, 2001, 2003; Czerkas et al. 2002; Norell et al. 2002). In the end, he concedes that dromaeosaurs had feathers. In a rhetorical *tour de force* that conflicts with decades of his own work and most of his commentary, Feduccia (2002) then hypothesizes that dromaeosaurs are birds, but that the birds, now including the dromaeosaurs, still originated from some unknown early archosaurian ancestor and are unrelated to theropod dinosaurs.

Rather than specifically counter the problems with his commentary, I think it would be most productive to focus my response on the intellectual framework of Feduccia's critique of the theropod origin of birds. Specifically, I will ask the question, "Is this science?" Or is it merely a form of rhetoric designed support an *a priori* belief about evolutionary process and history?

THE INTELLECTUAL STRUCTURE OF FEDUCCIA'S CRITIQUE

A critical element of science is falsifiability. To be scientific, a hypothesis must be falsifiable and yield predictions that are objectively testable. In a historical science like evolutionary biology, such tests cannot be conducted experimentally. However, we can analyze available evidence with objective repeatable methods. Another critical feature of science is the proposal of alternative hypotheses or theories that attempt to explain the scientific data at hand. Does Feduccia's critique meet these minimal criteria of science?

Feduccia (2002) offers an alternative to the theropod hypothesis of bird origins that is so vague as to be literally untestable. When Heilmann (1926) first proposed the basal archosaur hypothesis of avian origins, he described it optimistically as "wholly without short comings." Similarly, Feduccia (2002) describes his hypothesized early ancestral archosaurian lineage as having "less specialized anatomical baggage" than theropod dinosaurs. This ancestral *tabula rasa* hypothesis has survived the intervening 75 years between them only because it is permanently immune to falsification. Any potential character conflicts

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between birds and any known archosaurs can be rejected as irrelevant because the specific organisms can be claimend to not actually represent the yet unknown, hypothetical ancestor that perfectly conforms to the theory. Feduccia's advocacy of an unfalsifiable alternative hypothesis violates a fundamental tenet of science, but it also permits him to continue his permanent rhetorical battle against the theropod hypothesis of avian origin.

In response to my request for an explicit alternative hypothesis of avian origin, Feduccia (2002) concluded that "there are times when there is insufficient evidence to make the formulation of a hypothesis feasible." Here, he is not actually engaged in the search for a scientific solution to the question of avian origins. Essentially, Feduccia concedes that he would rather not do science (i.e. formulate and test alternative hypotheses with data) than to accept the theropod origin of birds. Unfortunately, Feduccia's rejection of the theropod hypothesis and advocacy of an untestable alternative does not constitute a scientific explanation of the origin of birds.

Feduccia (2002) also claims that "phylogenetic systematics stands alone among the sciences" in demanding that critics propose a testable alternative hypothesis. But, as Thomas Kuhn (1970:77) wrote, "The decision to reject one paradigm is always simultaneously the decision to accept another, and the judgment leading to that decision involves the comparison of both paradigms with nature *and* with each other." What Feduccia rejects as the irrational demands of phylogenetic zealots are actually the baseline requirements of all sciences, from astrophysics to zoology.

Because Feduccia's scenario is untestably vague, he is reduced exclusively to criticizing the theropod hypothesis. Feduccia (2002) portrayed the theropod origin of birds as a vast cladisitic conspiracy to deceive the ornithological community. Like a conspiracy theorist, he unerringly interprets evidence—even the new, ultimate evidence of feathered theropods—as favoring his preconceived conclusions. Feduccia (2002) argues that hypotheses of character homology cannot be tested by congruence with other characters, advocating a character by character approach instead. This *ad hoc* method permits him to interpret each separate character in whatever manner he prefers to support his argument, and to avoid dealing with the overwhelming volume of character evidence from all parts of the body supporting the theropod origin. He frequently argues both sides of the same issue wherever it is convenient. For example, when the first nonavian theropod furcula was described for *Velociraptor* (Norell et al. 1998), Feduccia and Martin (1998) claimed that the presence of a furcula in the basal archosauromorph *Longisquama* demonstrates that those structures have evolved multiple times in archosaurs and are "weak evidence" of phylogenetic relationship. Now, applying his "character by character" approach in this commentary, Feduccia mentions that the furcula of *Longisquama* in an effort to support the hypothesis that *Longisquama* is closely related to birds, in direct contradiction to his earlier published conclusions. Simultaneously, he ignores the discoveries since 1998 of furculae or paired clavicles in six to nine major lineages of theropod dinosaurs, including dromaeosaurs, oviraptors, tyrannosaurs, allosaurs, and coelophysids (Tykoski et al. 2002). Of course, the only scientific way to resolve alternative hypotheses of character evolution and character conflicts are by applying a repeatable, explicit, analytical method to reconstruct evolutionary history of characters and organisms. But Feduccia (2002) openly rejects available systematics methods as forcing "into algorithmic form what is arguably the most subjective and qualitative field of biology."

Feduccia's (2002) dogmatic belief in rampant evolutionary convergence in morphology literally begs the question—that is, presumes exactly the facts that need to be demonstrated. The only way to demonstrate convergence is to show that the majority of character evidence supports a hypothesis of phylogeny in which the convergent characters are shown to have evolved independently (Patterson 1982, Pinna 1991). Yet, Feduccia rejects both repeatable systematic methods and explicit, testable alternative hypotheses, making it impossible for him to demonstrate the convergence in which he believes. Feduccia (1999a,b; 2002) repeatedly cited his favorite examples of failed phylogenetic hypotheses as a justification for rejecting repeatable scientific methods, but he failed to mention that it was subsequent phylogenetic analyses that established the preferred hypotheses. Actually, the repeatable scientific methods that Feduccia rejects are the solution, not the problem. Feduccia (2002) further states that

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the theropod hypothesis implies that dromaeosaurs are "avian ancestors," and that bird are "derived from dromaeosaurs," when it is well known that the hypothesis states that the birds and dromaeosaurs (probably including troodontids) are sister groups.

Feduccia has long maintained that the 80 Ma "temporal paradox"—the temporal gap in fossil record between the earliest bird fossils and the earliest fossils of the proposed avian sister taxon (dromaeosaurs and troodontids)—was a problem for the theropod hypothesis. Recent discoveries have now uncovered basal dromaeosaurs that are 124–128 Ma old (Xu et al. 1999, 2000, 2001, 2003; Czerkas et al. 2002; Norell et al. 2002) cutting the proposed temporal paradox to 25 Ma or less, and fulfilling a specific prediction of the theropod hypothesis. Feduccia (2002) responded that the reduction of the gap is unimpressive because it is now "equally probable that early birds are much earlier than *Archaeopteryx*." Feduccia's faith in this gap is so strong that in response to new evidence reducing the supposed temporal gap by more than two thirds, he argued for a new increase in the gap because birds must now be substantially older than *Archaeopteryx*. Further, Feduccia (2002) ignored the evidence from Brochu and Norell (2000) that his preferred basal archosaur origin of birds requires hypothesizing even longer "ghost lineages" than does the theropod hypothesis.

Feduccia (2002) also tried to characterize my enthusiasm for the theropod origin as "the zeal of new school cladism." Actually, my enthusiasm is not based on ideological zeal, but on the incomparable scientific success of the theropod hypothesis (Prum 2002). Since it was first proposed cladistically by Gauthier (1986), the theropod origin of birds has been supported by numerous discoveries, including many new theropods closely related to birds (Novas and Puerta 1997; Sereno 1999; Xu et al. 1999, 2000, 2001, 2003; Czerkas et al. 2002; Norell et al. 2002), many new basal avian fossils that further blur the distinction between birds and other theropods (Forster et al. 1998; Zhou and Zhang 2002), many theropod furculae (Tykoski et al. 2002), over a dozen feathered theropods (Prum and Brush 2002), the digit frameshift hypothesis (Wagner and Gauthier 1999), and molecular developmental support for the frame-shift (Dahn and Fallon 2000)(see below), the reduction of the temporal paradox by two thirds (Xu et al. 1999, 2000, 2001, 2003; Czerkas et al. 2002; Norell et al. 2002), bird-like nesting behavior in theropods (reviewed in Prum 2002), and most recently by four winged dromaeosaurs (Xu et al. 2003). Given that the theropod origin of birds is entirely consistent with and supported by all of the new evidence discovered in the last decade, and that many testable predictions generated by the hypothesis have been independently supported, it is an overwhelmingly successful scientific theory.

Lastly, Feduccia (2002) advocated the notion that convergent evolution may make the ancestry of birds unknowable. Given the detailed support for the theropod hypothesis, that view is unscientific, and reveals a fundamental weakness of Feduccia's critique. Feduccia (2002) quoted Scottish philosopher David Hume as writing in favor of natural laws. However, Hume is actually better known for his skeptical critique of the existence of all empirical knowledge. Hume argued that inductive knowledge—conclusions based on observations and experiment—is only valid if natural processes are uniform over time, but that any evidence of such uniformitarianism is necessarily based on inductive observation, making the entire enterprise of science a circular fallacy. Like Hume, Feduccia rejects the overwhelming empirical evidence of theropod hypothesis of the origin of birds because he views the methods used to establish it as inherently circular and flawed. Although Hume's eighteenth-century criticisms of science are philosophically irrefutable, they have not prevented science from progressing substantially in the last 300 years. Likewise, the undeniable success of the theropod origin hypothesis in explaining the data and predicting new discoveries from paleontology, developmental biology, and functional morphology is the ultimate, eloquent response to Feduccia's philosophical rejection of objective systematic methods.

Dromaeosaurs are Birds?

Could anyone imagine better evidence that birds evolved from a lineage of theropod dinosaurs than the presence of modern, pennaceous feathers in the theropod dinosaur lineage that was independently hypothesized to be most closely related to birds? In the last

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FIG. 1. *Microraptor gui,* a basal dromaeosaur with a head and feathered body and asymmetrical pennaceous flight feathers extending from its wings, legs, and tail (Xu et al. 2003). The presence of elongate feathers on the hind limbs are confirmed independently by two other finds (Czerkas et al. 2002, Norell et al. 2002). Xu et al. (2003) hypothesize that avian flight evolved initially through a gliding, four winged morphology (represented by this four-winged basal dromaeosaur), and that the hind wings were lost in the ancestor of birds with the evolution of a powered forewing flight stroke (Prum 2003). (Photo courtesy of X. Xu and Z. Zhou.)

couple of years, there has been an avalanche of nonavian theropod fossil specimens from Liaoning, China with a variety of filamentous integumentary appendages including fully pennaceous modern feathers on multiple specimens of dromaeosaurs (reviewed in Prum and Brush 2002). Most recently, three papers have demonstrated perfectly pennaceous feathers on basal dromaeosaurs from the Liaoning (Czerkas et al. 2002; Norell et al. 2002; Xu et al. 2003) . Since Feduccia (2002), Xu et al. (2003) have published the description of *Microraptor gui,* a basal dromaeosaur with perfectly pennaceous, asymmetrical modern flight feathers on its tail, arms, and legs (Fig. 1). Previous specimens published by Czerkas et al. (2002: figs. 1, 11) and Norell et al. (2002) independently confirm the presence of long pennaceous leg feathers in basal dromaeosaurs. Those descriptions confirm the existence of pennaceous feathers in exactly the lineage of theropod dinosaurs hypothesized independently to be most closely related to birds. The theropod hypothesis has been stunningly supported by the discovery that the most essentially avian morphological feature—feathers—evolved in theropod dinosaurs prior to the origin of birds. The ultimate evidence of the theropod origin of birds is now a reality.

After maintaining that feathered theropods were a "myth" or "artistic inventions" (Feduccia 1999a), and stating in his commentary that he cannot find "any credible evidence" of the existence of theropod feathers, Feduccia (2002) completely capitulates and concluded, "There are also asymmetric flight feathers preserved on the wing and near the hind limbs of a dromaeosaurid (Czerkas et al. 2002, Norell et al. 2002)."

How does Feduccia integrate those new discoveries into his anti-dinosaur-origin rhetoric? Tellingly, he alters only the smallest necessary details of his scenario, he concedes no contradiction with his decades of previous writings and most of this commentary, and he concludes the same thing. He writes, "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." That is, Feduccia (2002) hypothesizes that dromaeosaurs are birds that are extraordinarily convergent with theropod dinosaurs, and that birds, including dromaeosaurs, originated from an early archosaurian ancestor and are still not closely linked to theropod dinosaurs.

Feduccia (2002) concluded that the feathered dromaeosaurs should send "all those involved

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in the debate on bird origins back to the drawing board." He might prefer to start his argument over, given that he has spent years arguing that dromaeosaurs are completely unlike and unrelated to birds. It is hard to understand how he could find "no credible evidence to justify the portrayal of the January 2002 *Auk* of *Microraptor* with a thick, white downy coating of putative protofeathers (A. Feduccia pers. obs.)" on page 1194, and then on page 1196 admit the existence of flight feathers on dromaeosaurs that are *Microraptor*'s closest relatives. Since my *Perspectives,* the description of *Microraptor gui* (Xu et al. 2003) confirms that the portrayal on the January 2002 *Auk* was actually too conservative (Fig. 1)! Feduccia's (2002) entire discussions of teeth morphology and replacement, cranial morphology, wrist bone homologies (plus three figures and a table) are completely moot and irrelevant given his acceptance of pennaceous feathers on dromaeosaurs with those serrate teeth, patterns of tooth replacement, cranial morphology, and wrist bones.

Feduccia's (2002) conclusion that feathered theropods present a new challenge to all workers in the field is disingenuous, because advocates of the theropod origin have hypothesized that dromaeosaurs were feathered for several years (Ji et al. 1998, 2001; Padian 1998, 2001; Prum 1999; Sereno 1999; Xu et al. 2000, 2001; Norell et al. 2002; Prum and Brush 2002). Feduccia never entertains the possibility that new evidence fulfilling a major prediction of the theropod origin of birds could be interpreted as definitive support for this hypothesis of evolutionary history. There are now more than a dozen nonavian theropods with feathers, and they belong to a diversity of theropod groups including oviraptorisaurs, therizinosaurs, alvarezsaurids, and basal coelurosaurs (Prum and Brush 2002). If all those feathered theropods were included in birds, as Feduccia is apparently prepared to do, it would only contribute to the indisputable phylogenetic relationship between theropods and dinosaurs (Prum and Brush 2002). Admitting that dromaeosaurs are feathered and closely related to birds makes it impossible to argue that birds are not theropod dinosaurs.

Does the discovery of asymmetrical flight feathers on the forelimbs and hind limbs of dromaeosaurs affect the debate about the evolution of avian flight. Doubless the four-winged dromaeosaurs *Microraptor gui* (Xu et al. 2003) and *Cryptovolans* (Czerkas et al. 2002) may revolutionize our understanding of the origin of avian flight (Prum 2003). Specifically, wing morphology of the four-winged theropods fulfill Feduccia's (2002: fig. 6) ideal of a gliding progenitor for avian flight, and demonstrate that there is no necessary conflict between the theropod origin of birds and a gliding origin of flight (Chatterjee 1997, Prum 2003, Xu et al. 2003). It appears that the avian flight apparatus may have evolved from a combination of terrestrial–cursorial adaptations that were exapted into the flight stroke, and subsequent selection for aerial gliding locomotion (Prum 2003). Those specimens do not adversely affect the hypothesis of theropod phylogeny and avian origins and are perfectly good dromaeosaurs, complete with, for example, the "killer claw" on the second toe, serrate teeth, and bony supporting rods in the tails. Obviously, future phylogenetic analyses including new data and taxa may change the topology of the theropod tree, but none of those findings places any doubt on the placement of birds within the theropod dinosaurs. As I concluded in my *Perspectives,* the theropod hypothesis provides an increasingly detailed and coherent perspective on the origin of birds. Now, the theropod hypothesis provides new support for Feduccia's preferred gliding hypothesis for the origin of flight, rendering moot his frequent claim that theropods are functionally inappropriate to be avian ancestors.

Digit Homology

As I discussed in my *Perspectives,* the phylogenetic hypothesis for dinosaurs leads unambiguously to the conclusion that the digits of the bird hand are digits 1–2–3. Feduccia and classical developmental biologists have long maintained that the digits of the hand of birds were digits 2–3–4 because they develop in positions distal to the metacarpals 2–3–4 (Burke and Feduccia 1997; Feduccia 1999a, 2002). Wagner and Gauthier (1999) proposed the frame-shift hypothesis as a solution to the apparent conflict. The hypothesis states that theropods, including birds, evolved to develop digits 1–2–3 distal to the metacarpals 2–3–4.

Recent molecular developmental studies have demonstrated that the simplistic positional criteria and mechanistic assumptions used by

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Feduccia to homologize digits on the basis of their positions are false (Dahn and Fallon 2000, Litingtung et al. 2002). Digit primordia are developmentally naive. Identity of those primordia is not determined by their position relative to the metacarpals, but rather by the relative concentration gradients of extracellular signaling molecules in the developing hand (Dahn and Fallon 2000). These data provide mechanistic support the homeotic shifts in digit identity proposed by Wagner and Gauthier (1999).

Feduccia (2002) can no longer claim that the "digital mismatch between birds and dinosaurs is morphologically the most serious problem" for the theropod hypothesis (Feduccia 1999a), although he continues to try to discredit the molecular support for the frame-shift hypothesis as evolutionarily outlandish and unlikely. He maintains that Dahn and Fallon's (2000) experiments yield "hopeful monsters" that are evolutionarily irrelevant, and that the proposed homeotic shifts (i.e. changes in identity among body parts) are undocumented in any amniotes. However, the evolution of vertebrae in the spinal column are premier examples of homeotic shifts in the vertebrate body. If homeotic shifts in vertebral identity had not occurred, then the homologies among vertebrae would be completely obscured by evolution in vertebrae number.

As an alternative hypothesis, Feduccia offers the possibility that the bird hand evolved through reduction in number of phalanges. He writes, "Reduction of phalanges is a simple matter, and for *Archaeopteryx*… a simple symmetrical reduction of one phalanx per digit is required." Unfortunately, this alternative hypothesis is based on a distinction without a difference. Digit identity is defined by the sum total of digit phenotype, such as phalanx number and shape (Dahn and Fallon 2000). Experimentally, in animals like the chicken in which every digit has a distinct number of phalanges, digit identity is actually equivalent to the number of phalanges**.** The homeotic "hopeful monsters" that Feduccia would like us to fear are precisely identical to "simple" reductions in the number of phalanges that Feduccia hypothesizes. Dahn and Fallon (2000) were studying precisely the molecular mechanisms by which the number of phalanges in a digit is determined. In other words, the changes in phalanx number which Feduccia finds so easy to imagine are mechanistically identical to the homeotic shifts in digit identity which he hypothesizes are so unlikely.

Feduccia demands that homeotic shifts in digit identity must require a credible adaptive scenario. He overlooked that Wagner and Gauthier (1999) explicitly hypothesized that the frame-shift occurred through simultaneous natural selection for the reduction of the number of digits and natural selection to maintain and advance the grasping function of the hand. This hypothesis explains why theropods are a singular exception to the pattern of digit loss common in other vertebrates, which occurs as a consequence of the reduction of digit function and leads to a developmentally determined, null pattern of digit reduction. Theropods including birds are a rare example of adaptive digit reduction, and that has lead to homeotic shifts in digit identity in the hand.

Feduccia specifically criticizes Wagner and Gauthier's (1999) hypothesis of a homeotic shift in the identity of the single wing digit of the kiwi (*Apteryx* spp.) as evolutionarily inexplicable given its reduced forelimb function. Yet, recent findings on the development of digit identity in mice document that a single digit one morphology is the phenotype of a loss of function mutant that lacks specific digit development and identity genes (*Shh*–/–; *Gli*–/+; Litingtung et al. 2002). A similar loss of function mutation is an entirely plausible hypothesis for the mechanism of kiwi wing digit reduction, and one such mechanism produces a single digit one. This molecular evidence supports the plausibility of Wagner and Gauthier's (1999) homeotic shift hypothesis for the kiwi wing digit, and further discredits Feduccia's assumption that homeotic shifts must be accompanied by strong natural selection.

In conclusion, there are no conflicts between developmental biology and the theropod origin of birds. Rather, Wagner and Gauthier (1999) used the theropod origin hypothesis to make bold predictions about developmental biology that have been supported (Dahn and Fallon 2000).

Feathers

Alan Brush and I have recently reviewed the developmental, paleontological, and phylogenetic evidence on the theropod origin of

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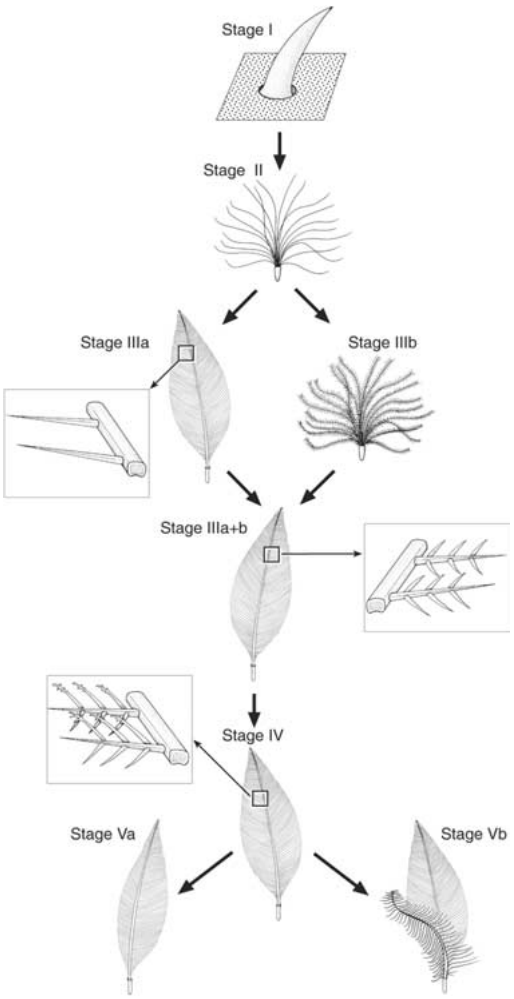


FIG. 2. The evolutionary transition series of feather morphologies predicted by the developmental theory of feather evolution (Prum 1999). The model hypothesizes the origin and diversification of feathers proceeded through a series derived evolutionary novelties in developmental mechanisms within the tubular feather germ and follicle. Stage I—The origin of an undifferentiated tubular collar and feather germ yielded the first feather, a hollow cylinder. Stage II—The origin of differentiated barb ridges resulted in a mature feather with a tuft of unbranched barbs and a basal calamus emerging from a superficial sheath. Stage IIIa—The origin of helical displacement of barb ridges and the new barb locus resulted in a pinnate feather with an indeterminate number of unbranched barbs fused to a central rachis. Stage IIIb—The origin of peripheral barbule plates within barb ridges yielded a feather with numerous branched barbs attached to a basal calamus. There is insufficient information to establish a sequence for Stage IIIa and Stage IIIb, but both those stages are required in the next stage. Stages IIIa+IIIb—The origin of a feather with both a rachis and barbs with barbules created a bipinnate, open pennaceous structure. Stage IV—The origin of differentiated proximal and distal barbules created the first closed, pennaceous vane. Distal barbules grew terminally hooked pennulae to attach to the simpler, grooved proximal barbules of the adjacent barb. Stage Va—Lateral displacement of the new barb locus by differential new barb ridge addition to each side of the follicle led to the growth of a closed pennaceous feather with an asymmetrical vane resembling modern rectrices and remiges. Stage Vb—Division and lateral displacement of the new barb loci yielded opposing, anteriorly and posteriorly oriented patterns of helical displacement producing a main feather and an afterfeather with a single calamus. The afterfeather could have evolved at any time following Stage IIIb, but likely occurred after Stage IV based on modern afterfeather morphology. See Prum (1999) for details of additional stages in the evolution of feather diversity (Stages Vc–f).

feathers (Prum and Brush 2002), so I will only address a few points here.

Feduccia defended the elongate scale-based model of the origins of feathers and criticizes my alternative developmental model (Prum 1999), but he fails to understand the implications of our recent molecular developmental research on feather evolution (Harris et al. 2002). Along the way, he makes a number of inaccurate statements. First, the developmental model I proposed is not a "filament-to-feather" model. Rather, the model hypothesizes that feathers are fundamentally tubular, and that feathers evolved through a series of derived novelties in the developmental mechanisms within the tubular feather follicle and feather germ (Prum 1999). I hypothesized that the first feathers were hollow tubes, followed by a tuft of barbs, followed by doubly branched feathers, and finally by feathers with a closed pennaceous vane (Fig. 2). Second, the developmental model is explicitly independent of all functional scenarios (Prum 1999), and is not wedded to the thermal insulation theory of feather origin, as Feduccia (2002) stated. However, the developmental model easily falsifies the hypothesis that feathers evolved for flight (Feduccia 1999b), because the first feather that could have had an aerodynamic function would have required many derived developmental mechanisms (Fig. 2, Stage IV).

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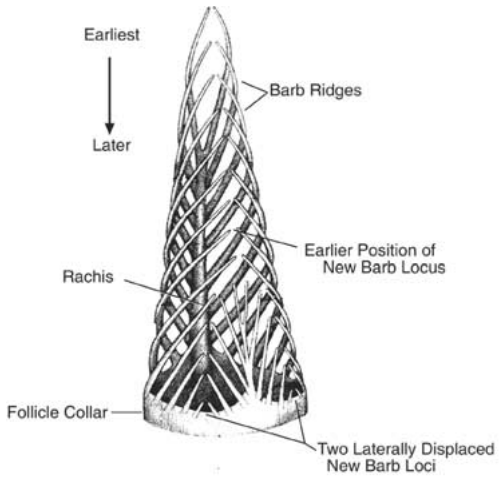


FIG. 3. A schematic illustration of the helical growth of the primary branched structure of a pennaceous feather with afterfeather from Lucas and Stettenheim (1972). Feathers are epidermal tubes that grow from the base. Pennaceous feathers obtain their planar form only after emerging from the cylindrical feather sheath when growth is complete. The obverse (upper) and reverse (lower) surfaces of a pennaceous feather vane are created by the outer and inner surfaces, respectively of the tubular feather germ. The surfaces of a planar feather are not homologous with the dorsal (upper) and ventral(lower) surfaces of a planar scale, which develop from the dorsal and ventral surfaces of the initial scale outgrowth. Thus, the planar feather could not have evolved from an elongate planar scale (Davies 1889, Prum 1999, Prum and Brush 2002).

Third, our molecular developmental experiments are not based on the theropod hypothesis (Harris et al. 2002). Rather, our data consist of observations and experiments on the cellular molecular signaling mechanisms involved in feather morphogenesis. Those data are entirely independent of, and entirely congruent with, the theropod origin of birds.

Feduccia stated that the scale-to-feather model "conforms nicely to what we know about feather embryology." That is patently incorrect. The dorsal and ventral surfaces of a scale form from the dorsal and ventral surfaces of the first primordial scale outgrowth, whereas the obverse (outer) and reverse (under) surfaces of a pennaceous feather develop from the outer and inner surfaces of the tubular feather germ, respectively (Fig. 3) (Davies 1889, Lucas and Stettenheim 1972, Prum 1999). As Davies (1889) first pointed out, because of the topology of feather development the two surfaces of a planar feather are not homologous with the two surfaces of a planar scale, and could not have evolved from them (Prum 1999, Prum and Brush 2002). Unfortunately, that fundamental fact was ignored by Heilmann (1926), who revived the elongate scale theory of feather evolution, and by the generations of ornithologists who subsequently advocated elongate scale hypotheses (Lowe 1935, Becker 1959, Parkes 1966, Maderson 1972, Regal 1975, Dyck 1985, Martin and Czerkas 2000), including two decades of publications by Feduccia (1980, 1985, 1993, 1996, 1999a, b). Elongate scale theories of feather evolution were falsified on the basis of developmental evidence more than a century ago, and no proponent of the elongate scale theory has ever countered Davies' (1889) fatal developmental observations (Prum 1999, Prum and Brush 2002). Furthermore, no elongate scale model has ever presented a satisfactorily detailed hypothesis of the evolution of feather branched structure (Prum and Brush 2002). Any theory of the origin of feathers should also explain the evolution of how feathers grow, and elongate scale theories have entirely failed that test.

Elsewhere (Prum 2001, Prum and Brush 2002), I have criticized the recent hypothesis that the elongate scales of *Longisquama* are homologous with feathers (Jones et al. 2000). Feduccia (2002) criticized my observations of *Longisquam* as cursory, but he neglected to mention that he has repeatedly published observations that are entirely in agreement with mine (Prum 2001). For example, he wrote, "In 1982 I examined the specimen of *Longisquama* in Moscow and could see no indication that the elongated scales were particularly feather-like" (Feduccia 1985:76). In 1999, he wrote, "No doubt… the scales of *Longisquama* were not transmuted into feathers, but the specimen does show the tremendous experimentation in feather-like scales in the basal archosaurs before the advent of feathers" (Feduccia 1999b: 133). Somehow, he made a complete and rapid conversion from thinking that *Longisquama* was a "bizarre and unique solution to the problem of gliding" (Feduccia 1999b: 95) to thinking that *Longisquama* is the closest known relative of birds (Jones et al. 2000).

Although Feduccia complimented our recent experimental research on feather development, he failed to grasp the consequences of our data

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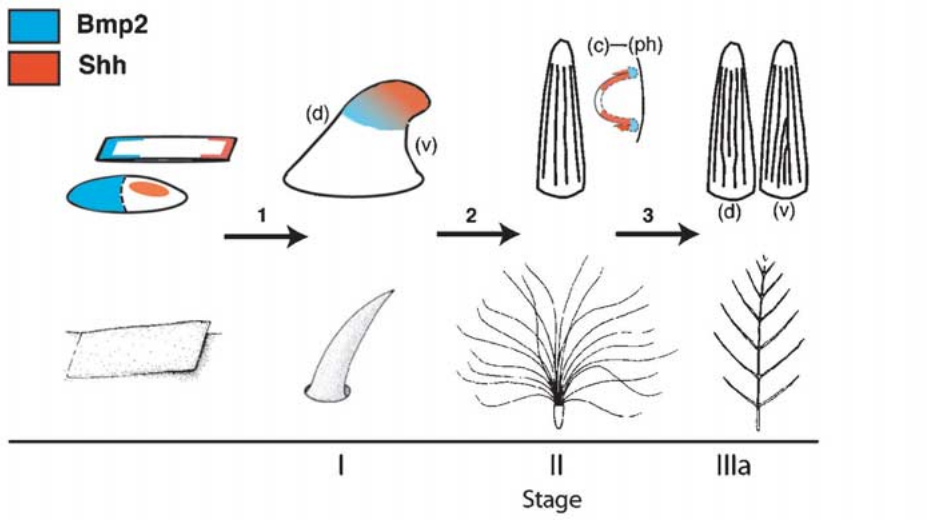


FIG 4. Congruence between patterns of expression a *Sonic Hedghog (Shh)* and *Bone Morphogenetic Protein 2 (Bmp2)* molecular module during the evolution of a feather (above), and the developmental model of feather evolution (below) (Prum 1999, Harris et al. 2002). *Shh* and *Bmp2* have distinct patterns of expression at four stage of feather growth (top, left to right): anterior–posterior polarized *Shh/Bmp2* expression in the placode stage of feathers and scales; distal coexpression during development of the tubular feather germ; longitudinal *Shh/Bmp2* expression in the folded marginal plate epithelium between barb ridges during the development of differentiated barbs (see cross-section of a barb ridge inset); and ventral bifurcation and dorsal cessation of *Shh/Bmp2* stripe expression during helical growth of a pennaceous vane. Each of those developmental evolutionary novelties evolved by cooption, or evolutionary reutilization, of the primitive *Shh/Bmp2* molecular module in a new context. The first, elongate tubular feather (Stage I) evolved from a primitive archosaurian scale by derived distal *Shh–Bmp2* coexpression (Event 1). The first, branched plumulaceous feather (Stage II) evolved by the origin of derived longitudinal *Shh–Bmp2* expression domains (Event 2) that created differentiated barbs from the tubular epithelium of the feather germ. A simple, pinnate pennceous feather (Stage IIIa) evolved by the controlled dorsal (*d*) cessation and ventral (*v*) bifurcation of the longitudinal *Shh–Bmp2* expression domains (Event 3), producing helical growth of barb ridges, indeterminate barb number, a rachis, serial fusion of barbs to the rachis, and a planar vane. Subsequent events in the development and evolution of feathers—for example, origins and differentiation of barbules—will require additional mechanistic explanations. Abbreviations: *c* = central; *d* = dorsal, *ph* = peripheral, v = ventral.

(Harris et al. 2002). We demonstrated that feathers evolved through a series of cooptions—evolutionary reutilizations—of a plesiomorphic molecular developmental molecular module (Fig. 4). The identified elements of that molecular module consists of a pair of intercellular signaling genes *Sonic Hedgehog* (*Shh*) and *Bone Morphogenetic Protein 2* (*Bmp2*). *Shh* and *Bmp2* have conserved set of developmental interactions within the integument, like mechanical components of a machine. This molecular module has been repeatedly recruited for controlled morphogenesis of novel structures during the evolution of feathers and feather complexity (Fig. 4). We have shown that in the first stage, feather placodes share an anterior–posterior polarized expression of *Shh* and *Bmp2* with the placodes of bird scales and alligator scales, but that all subsequent stages of feather development are derived and unique to feathers (Fig. 4). Then the feather bud develops by distal coexpression of *Shh* and *Bmp2*, creating the tubular feather germ (Fig. 4, Event 1). Subsequently, barb ridges develop through longitudinal stripes in *Shh* and *Bmp2* expression (Fig. 4, Event 2). Ultimately, the ventral new barb locus and the rachis develop through the coordinated ventral bifurcation and dorsal cessation of *Shh* and *Bmp2* signaling stripes (Fig. 4, Event 3).

The molecular developmental data provide a transition series in the evolution of feathers and feather branched complexity that is based en-

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tirely on the molecular developmental experiments (Fig. 4) (Harris et al. 2002). Compellingly, these independent molecular data are exactly congruent with predictions of the developmental model of the evolution of feathers which was based on the classical feather development literature (Fig. 2) (Prum 1999). Our findings demonstrate that feathers are homologous with scales at the placode stage, but that the feather bud and all subsequent feather structures are evolutionary novelties that are not homologous with a scale or parts of a scale. Many of the molecular signaling systems involved in the initial development of scales and feathers are shared between the two structures because of the homology of their placodes. These plesiomorphic similarities permit the experimental manipulation of scale development, producing the "transformation" of scale placodes into feather placodes, as cited by Feduccia (2002). In no way, however, do those experiments support the general homology of parts of feathers and scales, as required by the hypothesis that feathers evolved from elongate scales.

The developmental model of the origin of feathers (Prum 1999) has now been supported by both paleontological (Prum and Brush 2002) and molecular data (Harris et al. 2002). The developmental theory of the origin of feathers, the new *Shh–Bmp2* data of feather development (Harris et al. 2002), and the theropod hypothesis of the origin of birds provide the first coherent understanding of the origin and evolution of feathers.

Conclusion

In his commentary and previous publications, Feduccia has proposed a hypothesis of avian origins that is untestably vague, interpreted evidence inconsistently in favor of his hypothesis, rejected objective scientific methods of reconstructing evolutionary history, changed the standards of evidence when new data are produced, and assumed the existence of convergence that has yet to be demonstrated (i.e. begged the question). Now, having accepted the existence of feathered dromaeosaurs, Feduccia has contradicted decades of his own work by hypothesizing that dromaeosaurs are actually flightless birds in order to maintain the same conclusion—that birds are not theropod dinosaurs. Feduccia's rhetoric is beyond qualifying as the "most subjective and qualitative field of biology." My conclusion is that this is not science, but a rhethorical sham.

As Thomas Kuhn (1970:79) wrote in *The Structure of Scientific Revolutions*,

> To reject one paradigm without simultaneously substituting another is to reject science itself. That act reflects not on the paradigm but on the man. Inevitably, he will be seen by his colleagues as "the carpenter that blames his tools."

By offering no testable alternative to the theropod origin of birds and maintaining that the origin of birds is potentially unsolvable, Feduccia and other critics of the theropod hypothesis of avian origins reject science itself. One-sided rejections of the theropod origin reflect not on the hypothesis, but on intellectual weaknesses of the critiques.

In my *Perspectives* essay, I wrote that, "it is time to end 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." In his response, Feduccia documents that the scientific debate is indeed over because current critics of the theropod origin of birds are not doing science. The unrelenting progress and success of the theropod hypothesis in recent years is not the result of an overzealous cladistic conspiracy, but the congruence of multiple lines of evidence from many workers toward a coherent understanding of the origins of birds, feathers, and now flight (Prum 2003). In future decades, historians of science will doubtless look back on this episode in ornithological history as a classic example of the sociology of science. Ornithologists should to let these unworthy and unscientific arguments fade into scientific history, and dedicate themselves to the fascinating new scientific frontier of establishing a thorough historical understanding the origins of avian biology.

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