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Source: The Auk, 130(1) : 1-12

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2013.130.1.1

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The Auk

An International Journal of Ornithology

Vol. 130 No. 1 January 2013



The Auk 130(1):1–12, 2013

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Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

BIRD ORIGINS ANEW

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***The smallest dinosaur is the bee hummingbird…found only in Cuba* (Norell et al. 1995)**

The past three decades have witnessed a crescendo to one of the most intense and polemical debates in vertebrate evolution, the question of avian origins. Now the theory that "birds are living dinosaurs," specifically "birds are maniraptoran theropods" (the "BMT hypothesis"), predominates, and advocates of alternatives have largely been silenced, despite their growing numbers. Richard Prum has argued that ornithology be subsumed as a subfield of dinosaur paleontology and that textbooks be rewritten to conform to the BMT hypothesis (Prum 2002, 2003; James and Pourtless 2009). Perhaps *The Auk* could be renamed *The Raptor*, an appellation co-opted from ornithology, now the moniker for the dromaeosaurs like *Velociraptor*, star of Jurassic Park.

Thomas Henry Huxley is attributed with popularizing the earliest view that birds evolved from dinosaurs in the 1860s, but with little distinction between the flesh-eating theropods and herbivorous ornithischians. Although Huxley's views on bird origins were more complex than most modern authors appreciate (Switek 2010), "Darwin's Bulldog" viewed modern Aves as "dinosaur" descendants via the flightless ratites (Ostrich and allies) that never passed through a flight stage, a view later disproven, and the earliest then known bird, the Urvogel *Archaeopteryx*, was considered an intercalary bird and thus not part of the actual dino–bird transition. Huxley's view was supplanted in 1926 when the Dane Gerard Heilmann wrote the influential *The Origin of Birds*, in which he linked avian flight from the trees down with an early avian origin, from small tree-dwelling archosaurs (then, pseudosuchian thecodonts). He viewed birds and dinosaurs as derived from common archosaurian ancestry, a dominant view until Yale's John Ostrom discovered the birdlike Early Cretaceous dromaeosaur *Deinonychus* in the 1960s, reestablishing a direct dinosaurian genesis of birds, from already highly derived dromaeosaurs, relatively late in time. All this was accomplished without any use of phylogenetic systematics, with which he found fault, but cladistics would later claim to codify Ostrom's theory into solid fact, as it stands today. Ostrom realized, however, that an earthbound theropod close to the ancestry of birds required a coupling to a "ground–up" flight origin, with myriad inherent problems and a high level of biophysical improbability. Interestingly, in the early 1980s, when the debate on bird origins was raging, most paleontologists favored a dinosaurian origin of birds, but paradoxically a trees–down flight scenario, at the time an incompatible pairing. An upheaval in our knowledge occurred in the 1990s, when the remarkable period of discovery in China of the Jehol Biota revealed the most vivid and complete picture of the Early Cretaceous to date, with thousands of complete specimens emerging from lacustrine deposits in northeastern Liaoning province, many relevant to early bird evolution, and casting light on their actual origin (Feduccia 2012a, b). Unfortunately, most of these remarkable finds, largely inaccessible in China, have been published as preliminary or highly superficial reports primarily in the U.K. journal *Nature*, but also in *Science* and other prestigious journals, and the authors often received monetary awards in addition to much coveted recognition. Too, most specimens were interpreted within the context of the current mantra of the field, which has become an unchallengeable orthodoxy: birds are living maniraptoran theropods.

At the Society of Vertebrate Paleontology's fall 1996 meeting at the American Museum of Natural History, a small black-and-white photograph of a newly discovered specimen purported to be a feathered dinosaur was pinned on a bulletin board, just months following discovery. With no light or scanning electron microscopy or other biological assay, a pen-and-ink of the specimen appeared on the front page of the *New York Times* as important new support

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The Auk, Vol. 130, Number 1, pages 1–12. ISSN 0004-8038, electronic ISSN 1938-4254.

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DOI: 10.1525/auk.2013.130.1.1

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for the theory that birds are derived from dinosaurs. Following the current paleontological thought, a filamentous line along the back of the small compsognathid dinosaur *Sinosauropteryx* ("Chinese reptile wing") was described by a Chinese invertebrate paleontologist as representing protofeathers, with no evidence to support the supposition. Although John Ostrom, upon viewing the new "feathered dinosaur" in China, "literally got weak in the knees," there was never any evidence that these filaments represented anything other than a skeletal meshwork of collagen fibers supporting a lizard-like frill, scalloped along the tail as in the modern Central American basilisk lizards (Feduccia et al. 2005, Lingham-Soliar et al. 2007), and a clearly marked body outline on all specimens demonstrates that the fibers are internal, not to mention the presence of scales on the parts of the body (Martin and Czerkas 2000, Lingham-Soliar 2013; Fig. 1). Supposed evidence of melanosomes in *Sinosauropteryx* filaments (Zhang et al. 2010) cannot be substantiated and has been firmly refuted (Lingham-Soliar 2011). Other specimens, ranging from small theropods to ornithischians, and even pterosaurs, have emerged with halos exhibiting similar structures, leading to the current paleontological view that feathers at all stages of evolutionary development were widespread across the Dinosauria and perhaps even all archosaurs (Feduccia 2012b:120–136). The halos with fibers are invariably interpreted as protofeathers, but these are extraordinarily complex structures and may include a great variety of structures, some macerated and degenerate, and some representing bizarre preservational phenomena.

The most recent is a late Cretaceous ornithomimosaur reported not only with body feathers, but with wing feathers that were used only for display (Zelenitsky et al. 2012). First, no convincing evidence is presented that the "fibers" on the matrix represent feathers, and the carbonaceous markings on the ulna thought to be some form of ulnar quill nodes appear almost randomly ordered and do not remotely resemble those of modern birds. Considering that advanced avian wings were present in the Jurassic, trying to understand the origin of avian wings and remiges by studying Late Cretaceous theropod dinosaurs seems to stretch credulity. Too, if their interpretation is true, it would be the only known case of such a phenomenon, therefore demanding the highest level of evidence, which is simply not available. In another case, McKellar and colleagues recently reported a variety of feather material in Late Cretaceous Canadian amber as being of dinosaur origin (McKellar et al. 2011, 2012), but careful critique of their microscopic techniques, morphological comparisons, and potentially incomplete analysis of other biological materials by Smithsonian feather expert Carla Dove and colleague Lorian Straker suggested that there was nothing from the amber specimens that did not conform nicely to modern avian feathers or their component parts and that the authors did not convincingly rule out other biological materials or microscopic artifacts (Dove and Straker 2012). Arguments on dinosaur feather origins from this material are highly inadvisable, particularly in light of there being no actual animal identified and the temporal occurrence in the Late Cretaceous, probably ~100 million years beyond actual feather origins.

It should be noted here that a popular misconception is that ulnar quill nodes are directly correlated with flight ability, and their absence in *Archaeopteryx* has been used as evidence that the Urvogel could not fly (Ostrom 1974). Some of the largest quill nodes are found in woodpeckers, and they are only faintly present in most hawks and owls, but quite prominent in cathartids.

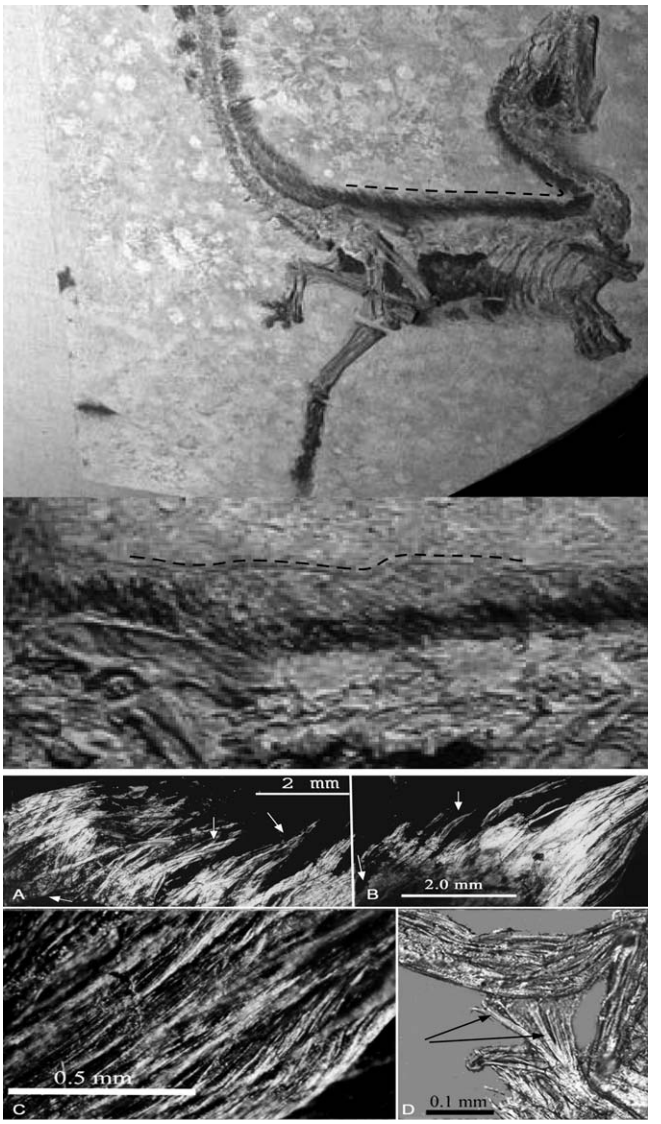


FIG. 1. (Upper) Specimen of the "Chinese reptile wing" or "downy dino" *Sinosauropteryx prima* (length 68 cm), described, with no evidence, as having a pelt of protofeathers. This small compsognathid is typical of theropods in having forelimbs 40% the length of the hindlimbs, as well as other typical theropod features. In all specimens examined, there is a clearly marked outline of the body (here shown with dotted line in the specimen and closeup of neck region below), showing that the filamentous zone is not external, but below the skin level, most likely a zone of collagen supporting a mid-dorsal, lizardlike frill (Lingham-Soliar et al. 2007; photo courtesy of John Ruben). (Lower) Protofeathers or collagen fibers? Decomposing collagen fiber bundles in the hypodermis of a dolphin, *Tursiops aduncus* (formerly *truncatus*). (A, B) Plume-like patterns of some of the fibers along the edges of the decomposing tissue. Many groups of fibers have narrow points of attachment (bottom arrow) that broaden before tapering again (due to degradation), giving the flame-like shape (top arrows). (C) Thick fiber bundles showing disorganization of the finer fibers and bundles to produce overlapping featherlike patterns. (D) Detail of large fiber bundles showing component fibers during degradation, producing branching patterns among the filaments (adapted and modified from Feduccia et al. 2005; after Lingham-Soliar 2003b).

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Too, quill nodes are virtually absent in the Mesozoic, with the exception of a dubious report of these structures on an ulna of *Velociraptor*, and a few other highly isolated cases. Larry Martin and I examined microscopically two ulnae of the Late Cretaceous toothed ornithurine *Ichthyornis* and found no evidence of the presence of any quill nodes. These structures have not been reported from the diverse array of avian fossils, both ornithurine and enantiornithine, from the Chinese Lower Cretaceous.

What was viewed back in the 1970s as a new, viable hypothesis of bird origins has now been widely lauded as the major triumph of the field of vertebrate paleontology of the past century. Birds are now considered living dinosaurs, and what was once a working hypothesis has transmuted to an unchallengeable orthodoxy, so that those who offer contrary evidence are subjects of ridicule and no longer considered scientists. Most disturbingly, the field has taken a turn away from a standard scientific falsificationist approach to verificationist arguments that are justified for a maniraptoran avian origin, based on the "vast quantity of data held to support it" (James and Pourtless 2009:27). Hypotheses are no longer tested according to standard scientific practice, but rather evidence is marshaled to bolster or "prove" what is already thought to be "known" from cladograms. As James and Pourtless continue, "The risk is that only supporting evidence will be recognized, while contradictory evidence is ignored or explained away" (p. 27).

The distillate of the problem boils down to the inability of the *de rigueur* methodology of the field, cladistics or phylogenetic systematics, to deal with the biological complexities of evolution. Cladistics is a statistical comparison of large numbers of human-coded, often trivial, skeletal features, that are computer ordered in hierarchical fashion to produce a branching cladogram that, although naive, becomes the true family tree or phylogeny until a competing cladogram, using the same methodology, offers a differing phylogeny. Aside from the obvious problem of circularity (reciprocal illumination), given myriad complexities, such a simplistic approach to the exceedingly complex problem of phylogenetic reconstruction is unreasonable, especially in view of so many morphological phylogenies being negated by subsequent DNA comparisons (Feduccia 2012b). The inability of the methodology to deal with common phenomena of vertebrate history, notably massive convergence, mosaic evolution (acquisition of characters at different rates in different lineages), and heterochrony (differences in developmental timing commonly seen in flightless birds), renders the entire scheme nonfunctional.

Consider the following. The evolutionary history of life is complex, biological phenomena often extravagant in nature. This means that evolution is not always gradualistic and linear. Even in 1860, Thomas Huxley warned Charles Darwin not to unnecessarily burden himself with his rigid gradualistic view of evolution, expressed as "natura non facit saltum" (nature does not make jumps) and instead saw evidence of the possibility of saltation, or sudden macroevolutionary change. Hence, the phenomenon of heterochrony, or differences in the timing of development—known to have played a significant role not only in vertebrate origins but also in the evolution of birds, and quite possibly in human evolution—is impossible to deal with by the current methodology. The case of man and chimpanzee is exemplary. The two species are acknowledged close kin, sharing an approximately 98.5% identical DNA profile, yet differing dramatically in adult morphology. Almost a century ago, Louis Bolk (Bolk 1926) noted the similarities between adult human and juvenile apes: "Our essential somatic properties…have all one feature in common…they are fetal conditions that have become permanent." Thus, Bolk's fetalization theory of human origins was born. One need only examine a newborn chimp to confirm the striking similarity to adult man, much more so than to adult chimpanzee. Another example involves the "darling of comparative anatomists," the amphioxus, a fishlike cephalochordate long claimed to be a putative ancestor of vertebrates. Yet recent genomic comparison argues against that conclusion, instead replacing the classic lancelet with the sea-squirt or tunicate as the most likely candidate, having evolved into a fishlike creature via the tadpole larval form, through paedomorphosis, a type of heterochrony. However, more important here is that the array of flightless birds, including the ratites (Ostrich, *Rhea*, Emu, cassowaries, kiwis, etc.), all evolved from flighted ancestors through the same process: they are all big chicks, having abandoned their adult form, and thus closely resemble, albeit superficially, the theropod dinosaurs. A not-so-subtle message from these examples is the inadvisability of combining phylogenetic data sets: DNA comparisions are a totally separate entity from simple morphological comparisons, measurements of two entirely different parameters, and may yield totally different results.

Thomas Huxley incorrectly viewed the ratites as ancient dinosaur derivatives, not having passed through a flight stage, and modern birds as being derived from them. This was followed by a similar view expressed in the 1930s by Percy Lowe, an ornithologist at the British Museum of Natural History, but this line of argument was brought to a screeching halt by another Englishman, Sir Gavin Rylands de Beer (1899–1972), who showed conclusively in his classic 1956 work that ratites were all derived from ancestors that once flew, and that there are no flightless birds that did not come from similar beginnings (de Beer 1956). Once rendered flightless, no flightless bird has ever given rise to a volant form; it is a one-way street. De Beer popularly called this evolutionary process "Peter Pan evolution," alluding to a permanence in the juvenile stage. Aside from heterochrony, two other common phenomena are also impossible to distill through cladistics: massive convergence and mosaic evolution, the latter revealed by Gavin de Beer using *Archaeopteryx* as an example (de Beer 1954).

The achievements of de Beer, a product of Oxford's stellar zoology group, are remarkable. He not only played a role in evolution's Modern Synthesis, but his enduring work still influences how we think about the genome, and his early work *Embryos and Ancestors*, first published in 1940 (de Beer 1940), molded our thinking in the field of evolutionary developmental biology, known today as evo-devo (Horder 2006). Although de Beer's great work was highly regarded in the 1960s and 70s, with the discovery of the bird-like raptors or dromaeosaurs, the lure of a ground–up flight from theropod dinosaurs superseded the more perceptive biological considerations of de Beer. His work, lauded by biologists, has been largely ignored in recent decades by the paleontological community and has faded into obscurity. But indeed, although de Beer cast a brilliant flood of light on avian evolution, the field of avian evolution seems clearly back in line with the Thomas Huxley and Percy Lowe school of thought, long since disputed.

Interestingly, while Huxley supported the view of flightless birds as dinosaurian derivatives, his nemesis Sir Richard Owen, largely disliked because of his distasteful personality, was correct on the flightless birds, and in 1875 set the record straight, implicating a heterochronic (paedomorphic) origin of flightless birds.

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Owen's theory emerged from the early discovery of moa fossils in New Zealand, noting that they evolved by the process by which juvenile features were retained in the adult. In a simple sentence, Owen, "dispensing justice to Huxley and Darwin alike," succinctly provided a cautionary note for advocates of today's unchallengeable orthodoxy of bird origins: "[S]cience will accept the view of the Dodo as a degenerate Dove rather than as an advanced Dinothere" (see Feduccia 2012b). Gavin de Beer would later show that "the adult [of flightless birds] is a permanent "chick." "No terrestrial animal became a flying animal directly; it first became… arboreal…. This is the pattern of evolutionary advance" (de Beer 1956). The same is surely true in the dinosaurian fossil record.

Vertebrate history is replete with examples of convergent evolution, the acquisition of similar features in unrelated groups of organisms, birds in particular exhibiting convergence on a massive scale. A well-known case involves foot-propelled divers, the loons and grebes, which by most cladistic analyses come out as closely allied, a clade (some now support a grebe–flamingo clade; Mayr 2004). Yet almost all other analyses show that they could not be of a single lineage and that their similitude is superficial. The hindlimb musculature and bony features differ substantially in embryology and adult structure, yet in profile are superficially identical for cladistic coding. German anatomist Max Stolpe showed in the 1930s that loons and grebes, along with the extinct Cretaceous diver *Hesperornis*, differ substantially in hindlimb anatomy, too much so to be a single lineage. All diving birds have a projection of the tibia to accommodate the diving muscles. In loons this cnemial crest is formed by a tibial projection, in grebes by fusion of the patella and tibia, and in *Hesperornis* by the patella alone. Movement of the toes in swimming differs equally dramatically. Prior to the recovery stroke, loons, with their fully webbed feet, flex the toes without rotation, whereas grebes, with lobate or scalloped webbing on individual toes, rotate the toes through a 90° arc, allowing the longer inward toes to trail while the shorter outer lobes fold against the underside of the toe. *Hesperornis* has teeth, unlike loons or grebes, but has the same rotational modifications as in the grebe foot, and therefore grebe-like toe rotation, grebe-like toe anatomy, and deductively lobate foot webbing. Thus, all three groups must be disparate diving lineages, having acquired their similarity through convergence, thus confounding cladistic analyses. A recent study utilizing 2,954 coded characters could not get past the massive convergence and, like most predecessors, placed loons and grebes together (Livezey and Zusi 2006; criticism by Mayr 2008). As Mayr (2008) noted, the analysis produced "a low ratio of phylogenetic 'signal' to 'noise' in the data."

Today, the field of origins is stuck in a rut of circularity because all conclusions are based on the *fact* that "birds are living dinosaurs." Birds are dinosaurs, thus *Archaeopteryx* is an earthbound dinosaur; flight originated from the ground up; ground-dwelling birds that resemble dinosaurs, but with true avian feathers, are feathered dinosaurs; any filamentous structures in the dinosaurian fossil record are protofeathers; and the four-winged gliders with true avian wings must be four-winged feathered dinosaurs. Because of this deeply ingrained thought process, five major paleontological precepts have emerged as focal to the current unchallengeable orthodoxy of the field and can be identified, restated with notations:

(1) *Archaeopteryx* is a feathered dromaeosaurid dinosaur, and since the early 1970s every attempt has been made to render the Urvogel earthbound, or nearly so. Yet, even Huxley stated in 1868: "In certain particulars, the oldest known bird does exhibit a closer approximation to the reptilian structure than any modern bird…. The leg and foot, the pelvis, the shoulder-girdle, and the feathers…are completely those of existing ordinary birds." Unknown to Huxley were the additional facts: *Archaeopteryx* has manual claws adapted for trunk climbing and pedal claws for climbing and perching; it has asymmetric flight feathers, with an aerofoil cross section found only in fully volant birds; it has an aerodynamically designed elliptical wing (albeit more primitive than in modern birds; Longrich et al. 2012), and wing loading in profile similar to that of a modern woodland bird, adapted for twisting flight in dense foliage; it has a brain and middle ear like that of modern birds, and in profile it is a dead ringer for a magpie (*Pica*) or a coucal (*Centropus*). *Archaeopteryx* was first temporarily grounded in the 1970s, when it was considered an endothermic earthbound dinosaur that could not fly, with feathers for insulation, and has subsequently from time to time been thrown from its perch, but always seems to regain its avian status (Lee and Worthy 2012). John Ostrom was well aware of the problem posed by having an earthbound feathered creature with avian flight wings, that of exaptation, and he developed his failed "fly-swatting" model to explain selection for early avian wings. Yet the theory appears to have had a revival: most Chinese four-winged gliders are reconstructed as cursorial fly-swatters (Fig. 2), evolving flight from the ground up, all their aerodynamic flight adaptations selected in a nonflight context.

(2) Flight must have originated from the ground up, from earthbound dinosaurs. Yet the facile method of the "trees–down" flight origin, using small size and high places—that is, cheap energy provided by gravity—is the route taken by all land vertebrates that have ventured into the volant realm, including parachuting frogs with large webbed feet to break the fall; lizards and rib-gliding snakes with varying modifications of rib projections; pterosaurs with bat-like wing membranes; and literally dozens of extinct and modern gliding mammals and fully volant bats. (Darwin first proposed a trees–down flight origin, for bats.) These groups have one thing in common: development of flight with two requisites, small size (otherwise integumentary extensions, e.g., feathers or skin extensions, would not break the fall) and high places (to take advantage of cheap energy provided by gravity; Bock 1986, Feduccia 1999). Ground–up flight from earthbound dinosaurs with laterally compressed bodies, large pelvic musculature with heavy balancing tails, and forelimbs already shortened to half or less the length of the hindlimbs is the worst possible anatomical body plan for flight origins, and renders such flight biophysically improbable if not impossible. Yet ground–up models are still popular today among paleontologists, because birds are living dinosaurs (Padian and Chiappe 1998, Chiappe 2007). As a pertinent aside, although a revival of the ground–up flight model for pterosaurs has been completely falsified (Feduccia 2012b:245–247), the idea still persists today, and is now even applied to bats (Kaplan 2011), despite a mountain of evidence to the contrary (Norberg 1990).

(3) Terrestrial Cretaceous oviraptorosaurs with fully developed avian pennaceous feathers and an advanced avian wing are flightless, feathered dinosaurs. Thus, although *Caudipteryx*

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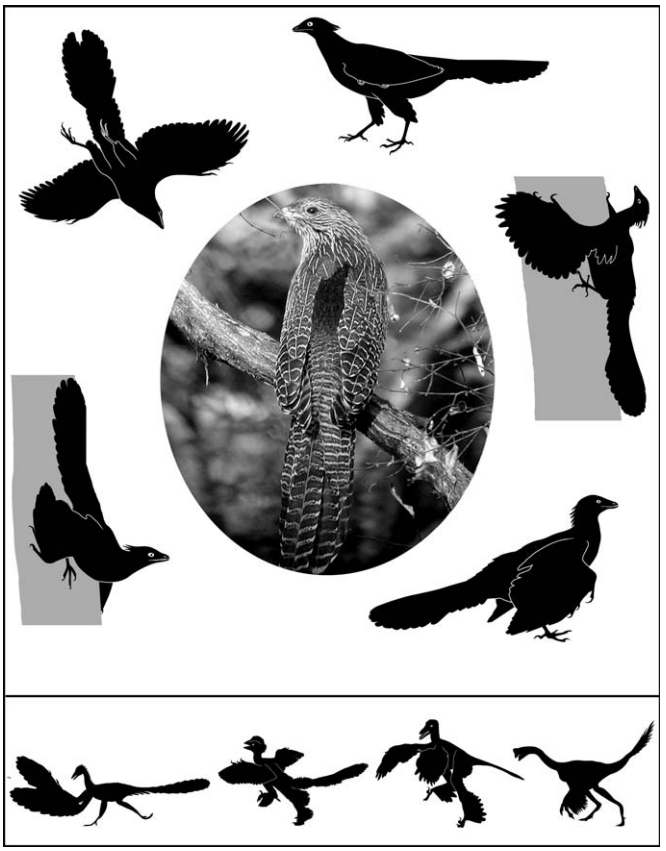


FIG. 2. Photograph of the Australian pheasant coucal (*Centropus phasianinus*), the living avian most closely approximating *Archaeopteryx* in superficial morphology and proportions, surrounded by silhouettes of Manfred Reichel's drawings of the Urvogel in different life poses. (Modified after M. Reichel, 1896–1984, *Dessins*, Basel: Geological Institute of Basel University, 1984; coucal photo from Wikimedia Commons, by Aviceda, taken in southeastern Queensland, 2003, licensed under the Creative Commons Attribution ShareAlike 3.0 License.) Below, silhouettes of reconstructions of various Mesozoic animals, attempting to bolster the ground–up flight model, with wings initially evolving in a predatory context. Left to right: Jurassic *Archaeopteryx*, Jurassic *Anchiornis*, Cretaceous *Sinornithosaurus*, Cretaceous oviraptorosaur. In reality, *Archaeopteryx* was a volant, arboreal trunk climber, *Anchiornis* and microraptors were four-winged gliders and trunk climbers, and oviraptorosaurids were most likely flightless avians. Elongate hindlimb wings would be maladaptive in a cursorial organism. (Adapted from Feduccia 2012b.)

has innumerable advanced avian characters and character complexes, including avian teeth (constricted at the base, or "waisted"), it is a dinosaur. Among the group's avian characters are a birdlike skull with a ventrally located foramen magnum, an avian foot, and a flight wing with reduced and fused bones, an advanced avian phalangeal formula, avian primary feathers attached to the manus as in birds, avian pennaceous feathers, and in some an avian pygostyle. In reality, *Caudipteryx* and other oviraptorosaurids nicely fit the bill for secondarily flightless birds, de Beer's "big chicks." Heterochrony is ignored, so that flightless birds and oviraptorosaurids are coded as they are, and in all cases flightless birds will resemble each other regardless of ancestry; the phenomenon cannot be resolved with current phylogenetic systematics. Most disturbing is that a massive, impeccably rendered cladistic analysis performed by the highly respected Polish paleontologist Maryańska (Maryańska et al. 2002; also see Lü et al. 2002), in which oviraptorosaurids clearly slotted as avians, is largely ignored by paleontologists and not even cited in a recent book on bird origins (Chiappe 2007). Flightlessness in modern birds is a pervasive phenomenon, normally produced through paedomorphosis, resulting in a "big chick" that may superficially resemble theropod dinosaurs, and the oviraptorosaurs nicely fit that model. The evidence that oviraptorosaurs represent a group of Mesozoic birds can no longer be ignored.

Another landmark paper never cited in recent paleontological literature is *Cladistics and the Origin of Birds*, by Frances James and John Pourtless (James and Pourtless 2009), in which they present two new cladistic analyses as well as an evaluation of all current hypotheses of bird origins. Their conclusion, that presently "uncertainties about the hypotheses that birds are maniraptoran theropods are not receiving enough attention (p. 1)," was apparently sufficient incentive for the paper to be totally ignored. Lack of citation has become a common but disturbing mechanism of censorship (Feduccia 2009), and in addition to the above, you will find no citation in Chiappe's book of the sophisticated work on flight origins by Ulla Norberg supporting the arboreal origin of flight (Norberg 1990; and numerous papers by Walter Bock [1986 and elsewhere]), or the extensive rebuttals to the existence of dinosaurian protofeathers by T. Lingham-Soliar (Lingham-Soliar 1999, 2001, 2003a, b, 2008, 2010a, b, 2011, 2012, 2013; Lingham-Soliar et al. 2007; Lingham-Soliar and Glab 2010; Lingham-Soliar and Plodowski 2010; Lingham-Soliar and Wesley-Smith 2008).

(4) The filamentous band running down the neck on the small compsognathid dinosaur *Sinosauropteryx*, and on other theropods, ornithischians, and allies, are protofeathers. Yet no biological assays were applied to these structures, not even proof that they are hollow, a sine qua non for feather status. In fact, the best explanation for many of these structures is that they represent a skeletogenous matrix of collagen fibers supporting a lizard-like frill as in *Sinosauropteryx* (Lingham-Soliar 2003a, b; Feduccia et al. 2005; Lingham-Soliar et al. 2007), or other integumentary derivatives in varied archosaurs. As noted, the preservational halos surrounding these fossils may be extraordinarily complex and may contain myriad structures, including preservationally degenerate and even macerated contour feathers that may be misidentified as protofeathers. If they were protofeathers they would be maladaptive, becoming wet or mucky. Successful young downy birds mature and abandon the downy state as quickly as possible. When wet, baby Ostriches must seek shelter under the mother's wing or risk hypothermia and eventual death. Despite the array of problems surrounding the identification of putative protofeathers, these structures are now conflated with true avian feathers in microraptors and other four-winged birdlike forms, which have true avian feathers (see 5 below), causing further confusion. If an Ostrich head were retrieved from the Chinese Early Cretaceous fossil beds, it would no doubt be interpreted as having protofeathers of varied types, representing stages of feather evolution.

(5) The so-called four-winged gliding microraptors and the feathered Jurassic forms with non-theropod features are all

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considered dinosaurs. Yet the microraptors have advanced avian wings with a precise arrangement of primary and secondary pennaceous feathers, and innumerable other avian features, including an avian skull and teeth, avian feet, and precise arrangement of avian hand bones. These advanced characters argue that microraptors represent derivatives of, rather than being ancestral to, the early avian radiation, with dromaeosaurids at all stages of flight and flightlessness. They are literally bristling with uncoded avian characters, but these are swamped in cladistic analyses by the background noise of co-correlated characters associated with bipedalism and a mesotarsal foot joint. Interestingly, the microraptor *Sinornithosaurus*, typically reconstructed as an earthbound cursor, had elongate hindlimb flight feathers, which would have impeded ground locomotion, and exhibits a well-developed posterolateral bony flange and a strongly bowed outer metacarpal, making its hand better suited for support of primary feathers than that of *Archaeopteryx* (Paul 2002). As Paul notes (p. 407), "The combination of a well-developed posterolateral flange and a strongly bowed metacarpal III [outer metacarpal] made the hand of flightless *Sinornithosaurus* better suited for supporting primary feathers than was the hand of flying *Archaeopteryx*." The question, of course, is this: Was it, like its close kin *Microraptor*, also volant, a four-winged glider and trunk climber? Microraptors have been reconstructed in two distinctive models, the four-winged gliding model with sprawled hindlimb wings, by which it was originally described in *Nature* (Xu et al. 2003), and a dinosaurian bipedal model, or biplane model, by which it is reconstructed with the hindlimbs held beneath the body, incapable of sprawling, in other words, like a tiny *T. rex*. The problem, of course, is that there is absolutely no reason the hindlimbs could not have been sprawled, as is the case in flying squirrels (*Glaucomys* spp.), flying lemurs (Dermoptera), etc., and even falling cats. Too, the sprawled model performs superiorly in wind-tunnel experiments (Alexander et al. 2010), most specimens are preserved with a sprawled posture, and the wing claws are adapted for trunk climbing (Burnham et al. 2011). In addition, it would be difficult to imagine how selection could produce elongate, asymmetric hindlimb flight remiges by the most current paleontological reconstructions, in which the hindlimbs are held in flight beneath the body in obligate bipedal fashion, with elongate hindlimb wing feathers trailing behind, simply slicing through the air (Balter 2012).

Microraptors qualify admirably as an early "tetrapteryx" flight stage, predicted by naturalist William Beebe (1915) to account for flight origin in birds (Fig. 3). It is as though these four-winged avians flew out of the pages of Beebe's notebook! Although a number of paleontologists have used four-winged microraptors to incorporate an arboreal flight origin into the BMT hypothesis, Luis Chiappe, Kevin Padian, and Kenneth Dial are notably insistent on promoting the improbable cursorial model, the latter two recently extending it to bats, based on application of the long-debunked "biogenetic law" of Ernst Haeckel (Kaplan 2011, Balter 2012).

A number of intriguing four-winged feathered Jurassic forms—such as the tiny scansoriopterids *Epidendrosaurus* (= *Scansoriopteryx*) and *Epidexipteryx*, the latter without preserved wing remiges, and anchiornithids (*Anchiornis* and *Xiaotingia*)—exhibit numerous non-theropod skeletal features. They are provisionally best interpreted as early birds at a pre-theropod stage, with partially closed hip joint or acetabulum, and without a dinosaurian supra-acetabular shelf, characters associated with a fully theropodan parasagittal gait, which diagnose the clade. Although there is no reasonable morphological definition of "theropod," one sine qua non for dinosaur status in general is the presence of a completely open acetabulum, associated with the suite of changes seen in posture and gait, by which a more upright posture is attained, with a parasagittal hindlimb positioning (front to back axis). A partially closed acetabulum is seen in basal archosaurs and is characteristic of the scansoriopterids and Jurassic feathered forms such as *Anchiornis* initially described as near Aves by Xu et al. (2009). Another recently described, similar four-winged genus is the Jurassic *Xiaotingia*, described by Xu et al. (2011), in an analysis in which *Archaeopteryx* was removed from Aves and slotted with deinonycosaurs. *Nature News* immediately headlined "*Archaeopteryx* no longer first bird" (27 July 2011 | *Nature* | doi:10.1038/news.2011.443), but shortly thereafter revised analysis by Lee and Worthy (2012)

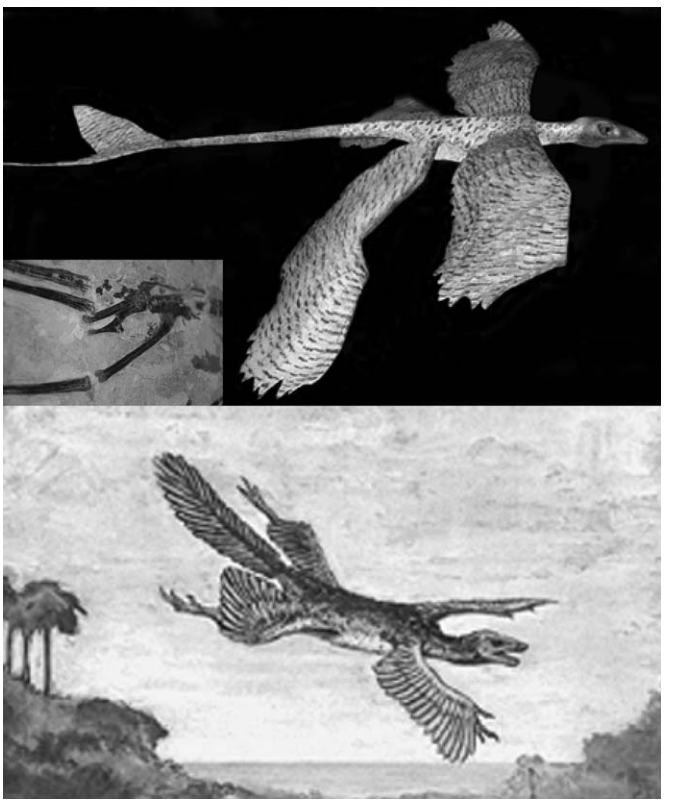


Fig. 3. (Above) Foam model reconstruction of the small dromaeosaur *Microraptor* rendered by the University of Kansas group, based on an actual skeleton, which performed superiorly to alternatives in wind-tunnel tests. Manual digits exhibit highly recurved claws adapted for trunk climbing. Inset photo showing the splayed preservational position, typical of the preservation of most specimens of *Microraptor*. (Inset photo from Shandong Tianyu Museum of Nature, Pingyi, Shandong, Director, Xiaoting Zheng.) (Below) The "tetrapteryx" stage in the evolution of flight predicted by naturalist William Beebe in 1915. (Image of *Microraptor* model painted by Elizabeth Ebert, courtesy David A. Burnham; below from W. A. Beebe 1915.)

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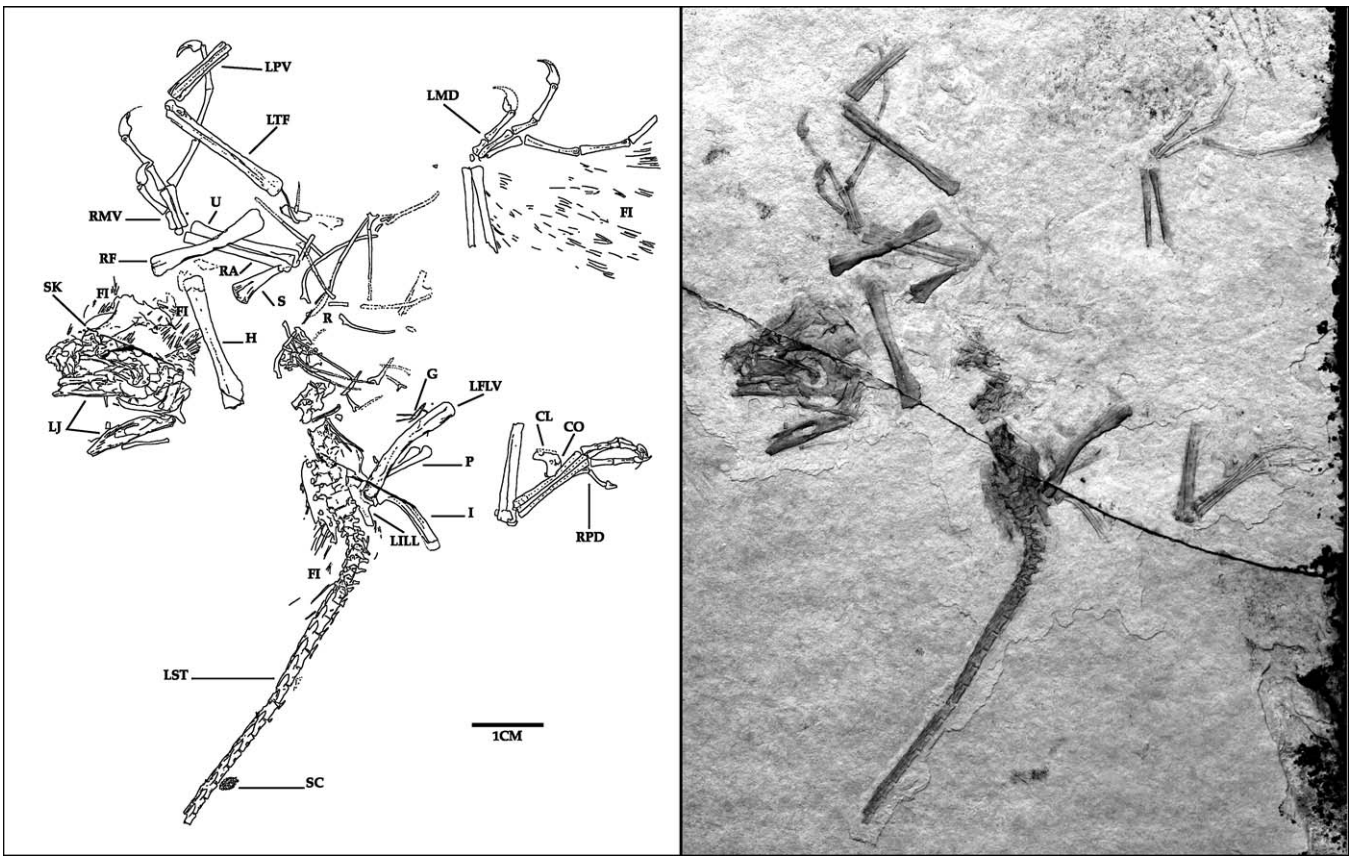


FIG. 4. The tiny, House Sparrow–sized *Epidendrosaurus* (= *Scansoriopteryx*): "[It] would not be so surprising or unexpected to find such a primitive looking animal as *Scansoriopteryx* from much earlier periods of time dating from the Middle Triassic or even further back into the Permian." (Drawing of skeleton, left; actual specimen, right.) Abbreviations: CL = clavicle, CO = coracoid, FI = filamentous impressions of wing feathers, G = gastralia, H = humerus, I = ischium, LFLV = left femur lateral view, LILL = left ilium lateral impression, LJ = lateral jaws, LMD = left manus dorsal aspect, LPV = left metatarsals ventral impression, LST = impression of left side of tail, LTF = left tibia–fibula, P = pubis, R = area with ribs, RA = radius, RF = right femur; RMV = right manus ventral impression, RPD = right pes dorsal impression, S = scapula, SC = scales, SK = skull, and U = ulna. (From Czerkas and Yuan 2002. Photo courtesy of S. A. Czerkas; copyright Stephen A. Czerkas. Reprinted with permission.)

and Senter et al. (2012) reinstated the iconic Urvogel to its rightful place. Such uncertainty illustrates that most cladograms hang by a spider's thread, and if one were to eliminate the co-correlated gait characters and emphasize the uncoded innumerable avian features of four-winged microraptors and closely allied Jurassic *Anchiornis* and *Xiaotingia*, as well as the scansoriopterids, a completely different cladogram would emerge showing avian affinity. As Clark noted years ago, "similarity lies in the eyes of the beholder, and…the particular hypothesis being advocated strongly colors perceptions of morphological resemblance" (Clark 1992:533).

The real question that remains is just why the four-winged gliders are considered theropods. Aside from the phylogenetic context, the life reconstructions of these four-winged gliders as terrestrial cursors (Fig. 2) is clearly erroneous. They all have elongate hindlimb flight feathers that would have been a hindrance in terrestrial locomotion, and they were incapable of more than occasional terrestrial journeys: clear evidence indicates that these early birds were arboreal climbers and gliders (Alexander et al. 2010, Burnham et al. 2011). Yet the theme of the theropod origin of birds is that all things avian come from the ground up; there is hardly any other explanation for this continued egregious error. Climbing four-winged gliders, most likely remnants of an earlier period in avian flight evolution, from microraptors to *Anchiornis* and *Xiaotingia*, are reconstructed as earthbound theropods learning to fly from the ground up, with extended arms as though to reinvigorate Ostrom's long-failed "fly-swatter model" for the origin of avian wings as exaptations for flight. They were tree-climbing gliders, with numerous bird-like characters but devoid of any salient theropod features. The four-winged scansoriopterids are of particular interest. Although described as coelurosaurs, this assignment is surely incorrect, and they have little to ally them with theropods; they best qualify as pre-theropods or arboreal basal archosaurs. The scansoriopterids, so extensively studied by Stephen Czerkas and Chongxi Yuan, exhibit no characters that would ally them with the Theropoda, but they have numerous features that place them as pre-theropods or proto-maniraptorans, allied perhaps more appropriately with basal archosaurs—or, to use the old term, pseudosuchians (Czerkas and Yuan 2002, Feduccia 2012b). "It is remarkable that *Scansoriopteryx* should have characteristics which not only disqualify it as a theropod, but also as even a dinosaur" (Fig. 4). "If only *Scansoriopteryx* had been discovered back

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in the days of Heilmann, he would have had the evidence to substantiate the speculation that birds evolved from arboreal ancestors which were not dinosaurs" (Czerkas and Czerkas 2008:32, 33). Stephen Czerkas has recently discovered impressions of elongate shafts set off at an angle and running across the metacarpals and metatarsals, providing exciting evidence that these tiny arboreal creatures were also four-winged gliders (S. Czerkas pers. comm.). A close Jurassic kin, *Epidexipteryx* exhibits long, ribbon-like tail feathers but is preserved devoid of wing feathers and was thus interpreted as evidence that feathers must have evolved not in an aerodynamic context, but for display. But in paleontology, absence of evidence is not necessarily evidence of absence, and *Epidexipteryx* minimally indicates that a broad variety of scansoriopterids existed in the Jurassic. Too, fossil birds can be preserved with feathers but devoid of wing feathers, as indicated by a specimen of the Lower Cretaceous *Longipteryx* (Fig. 5). Other specimens of longipterygids preserved well-developed typical avian wings. Extreme caution must be exercised in interpreting these fossil birds, and future discoveries may show that *Epidexipteryx* possessed wings. As discoveries of this age continue, we may learn a great deal more about the early evolution of birds.

Most distressing, according to the popular paleontological view (Fig. 6), with the position of maniraptorans and avian taxa on most cladograms, all the extraordinarily sophisticated flight architecture of modern birds—including aerodynamic wings and feathers; reduced, fused, and lightened skeletons; and perching feet—must have evolved in a nonflight context, in earthbound dinosaurs, as exaptations (formerly preadaptation). "If the most birdlike maniraptoran clades belong within Aves, problematic exaptational explanations, including those for the origin of flight feathers, are unnecessary" (James and Pourtless 2009:31). The current orthodoxy of flight origins, involving massive exaptation, stretches biological credulity and is practically non-Darwinian.

Attempts to silence any opposition to the current unchallengeable orthodoxy are seen in the lack of citation of contrary views (Feduccia 2009), and polemical and ad hominem reviews that are substituted for evidence have effectively silenced many nonsubscribers. Summary dismissal of other valid views is nothing new. The 19th-century German philosopher Arthur Schopenhauer astutely summarized the three stages through which all truth passes: first, it is ridiculed; second, it is violently opposed; and third, it is accepted as being self-evident. I believe this new view of bird origins is now somewhere between stages 2 and 3, with only occasional throwbacks to stage 2.

The arrogance and boldness that characterize the certitude of the cladistic catechism allow no intrusion from other fields and seem oblivious to many important biological phenomena. Being based almost solely on statistical comparisons of simplistically coded skeletal characters, the infallibility with which results are treated is totally unjustified and unscientific. Characters are often cherry picked, the problem of massive co-correlation of characters associated with a particular mode of life is ignored, and the huge number of insignificant characters, vis-a-vis a recent ornithological study (Livezey and Zusi 2006), create background noise (Mayr 2008), rendering trivial the important key characters and complex interacting character complexes, which are often derived from intricate embryological connectivity and complexity, the essence of traditional homology (Feduccia 1999). I have elsewhere termed the current methodology "cladophenetics" because it closely resembles the phenetic approach of the 1960s and 70s, which largely yielded clusters based on affinity of ecomorphotypes, certainly not clades (Feduccia 2002). As Philip Gingerich has aptly noted, "The problem is that we expect too much of morphology in asking it to tell us the genealogy of organisms as well as what they look like"(Gingerich 1988:628). Cladistics, or any other tool, should not become a hegemonic methodology. "Darwin made convincing the case for evolution because he demonstrated the coherence of independent data sets (morphology, embryology, physiology, biogeography, paleontology) rather than relying only on a single kind of data. Why should we accept as convincing a method of systematic analysis that for ideological reasons trivializes all data sets other than morphology? We can do better!" (Dodson 2000:504).

I, and many others who advocate the view expressed here, are typically accused in ad hominem fashion of not understanding cladistic methodology and, therefore, of not being scientists. But we emphatically do understand the essence of the methodology, and that is the problem—as vividly illustrated by the example below (Table 1), which shows the fragility and very tenuous nature of cladistic analyses. Alan Turner and colleagues (Turner et al. 2007) analyzed scrappy material from the small dromaeosaur *Mahakala* from the Late Cretaceous (Campanian) of Mongolia, concluding that it represents the basal divergence within Dromaeosauria and that its small size implies extreme miniaturization ancestral for Paraves (Avialae, Troodontidae, and Dromaeosauridae), phylogenetically earlier that flight evolution. Given the extremely flimsy evidence from the character matrix (Table 1) and the late geologic occurrence of the fossil, any conclusions from these data and this fossil must be considered highly speculative. Table 1 shows a sample of the data matrix, wherein a question mark represents a missing data point for a taxon, or "not applicable." *Graciliraptor* is based on a single specimen composed of a partial maxilla, nearly complete limbs, and 10 partial tail vertebrae; *Mahakala* is also based on scant material, including some skull bones, vertebrae, limb bones, and parts of the pelvis and shoulder girdle.

Anyone examining this data matrix would find it risible to call this science and would be astounded that such a paper could be published in *Science*. We must not, however, throw out the baby with the bath water just because some of the matrices do not contain enough information to yield probable results. Phylogenetic systematics is far larger than simplistic morphological cladistic analyses. Paleontological skeletal cladistics should be considered only as a starting point, for generating hypotheses that can be useful and tested against other lines of evidence, and not as the final answer, as is often the current practice. Ronald Jenner (2004) emphasized the great care needed in analyzing comparative morphology to minimize subjectivity and bias, and that phylogenetic hypotheses should be treated as an exploratory method. Today's phylogenetic systematics includes very useful approaches to molecular systematic and biogeographical analyses that provide useful starting points and reveal potentially overlooked problem areas. Other fields that employ cladistics as an exploratory methodology include historical linguistics and cultural anthropology.

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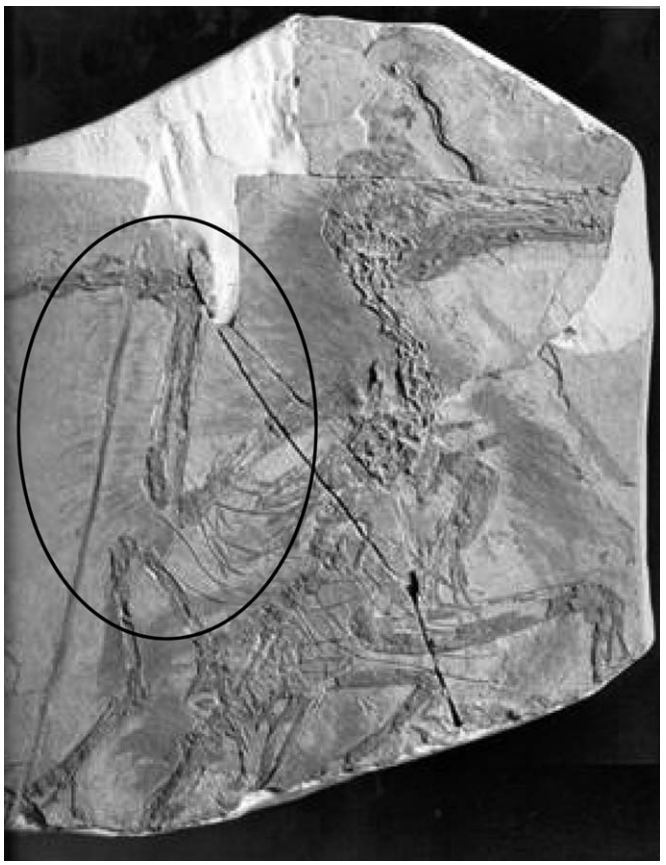


FIG. 5. Photo of the Lower Cretaceous enantiornithine *Longipteryx*, sporting a bill designed for probing feeding, a somewhat kingfisher-like ecological equivalent. Note that while wing remiges are absent, they were definitively present in life, as illustrated by skeletal flight architecture, but also the discovery of other Longipterygidae preserving complete wing feathers. The specimen shows that some feathers can be preserved without simultaneous preservation of the remiges. In the case of the Jurassic scansoriopterid *Epidexipteryx*, body feathers and elongate ribbon-like tail feathers were preserved, but no wing feathers were; it was thus portrayed in *Nature* as flightless, its feathers having originated for display. (Photo courtesy of Zhonghe Zhou.)

Another overlooked but dangerous aspect of this entire debacle involves the ever-lurking Creationists, who see the layered flaws and junk science in the current unchallengeable orthodoxy on bird origins and have leapt into the fray, like circling sharks in a feeding frenzy, terming this phenomenon "The Disneyfication of Paleontology!" (see www.csm.org.uk/news.php?viewmessage=34). As one well-known creationist noted following a presentation of an egregiously flawed study claiming the discovery of dinosaur DNA in *Triceratops* purported to be identical to turkey DNA, "This isn't science. This isn't even myth. This is comic relief!" (Wells 2000:133). It is chilling to contemplate that the Creationists may be the ones to sweep our own house clean. It is time for scientists from varied fields to begin the task of a more careful consideration of these highly speculative proposals. Otherwise this arena will continue to flounder in a world of neverending speculation, a veritable Disney *Fantasia*. Whatever happened to astronomer Carl Sagan's well-worn

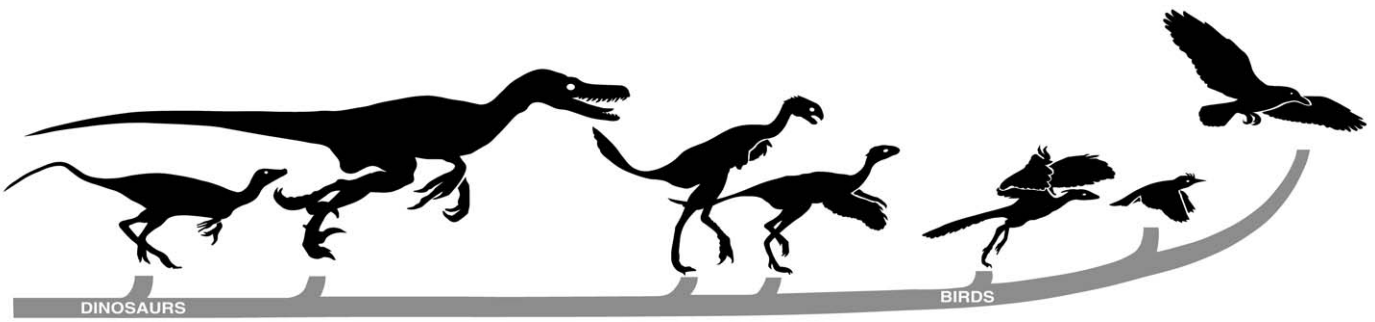


FIG. 6. Topsy-turvy progression of fossil silhouettes associated with avian ancestry, displaying the current orthodoxy of bird origins, as interpreted by an article from *National Geographic*, but outrageously flawed. Harvard's Alfred Romer would say: In discussing fossils, some notion of the geological time scale is necessary! From left, first is the so-called feathered Lower Cretaceous compsognathid *Sinosauropteryx*, with supposed protofeathers, most likely collagen fibers supporting a mid-dorsal lizard-like frill; like early dinosaurids such as the Late Triassic *Herrerasaurus*, *Coelophysis*, and *Syntarsus*, it displays the worst possible anatomical plan for avian flight origins. *Sinosauropteryx* is universally reconstructed with a coating of downy protofeathers that would, of course, be maladaptive. Second is the famed Late Cretaceous *Velociraptor*, a dromaeosaur with a birdlike wrist and putative ulnar quill nodes. The Early Cretaceous four-winged basal dromaeosaurid microraptors (not shown) have numerous avian features, including a bird hand and avian flight feathers, and are more specialialized than *Archaeopteryx*, indicating that they are not ancestral to birds, but descendents of the early avian radiation. Are deinonychosaurs, like *Velociraptor*, secondarily flightless representatives of this group? Following *Velociraptor* are two Lower Cretaceous oviraptorosaurids, *Caudipteryx* and *Protarchaeopteryx*, with fully developed avian feathers and innumerable birdlike features, many of which tell of flight ancestry. Rather than being bird ancestors, these forms are surely descendents from once volant avians, Mesozoic ratite equivalents, but were displayed on the cover of *Nature* as ancestral avians, having acquired suites of flight features as exaptations. Finally, we arrive at the Late Jurassic *Archaeopteryx*, the classic Urvogel or early bird, which still retains that distinction; it is followed by an Early Cretaceous Spanish enantiorithine, *Eoalulavis*, which exhibited the earliest known alula, and is followed by a modern crow (*Corvus*). (From Feduccia, 2012b, adapted and modified from *National Geographic*, "Dinosaurs take wing," July 1998:74–99, by J. Ackerman.)

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Table 1. A sample of the data matrix.

Species	
Graciliraptor lujiatunensis	??????????????

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Received 11 October 2012, accepted 4 December 2012

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